# Modelling the impact of an alien invasion:

# *Harmonia axyridis* in Britain

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# Contents

## Summary

**Modelling the impact of an alien invasion: *Harmonia axyridis* in Britain.**

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*Harmonia axyridis* is a ladybird native to Asia, but introduced widely as a biocontrol agent. It is invasive and detrimental to native species in North America, which meant its arrival in Britain was met with concern. Establishment was seen as an opportunity to track the spread of an invasive alien species (IAS) whilst also monitoring impacts on native species.

The aims of this thesis were to examine the responses of native British ladybirds to the arrival of *H. axyridis*, to establish the effect of the IAS on native ladybirds when compared to other drivers, and to investigate the possible facilitation of the *H. axyridis* invasion by natural enemy release.

Modelling ladybird distributions with life-history and resource-use traits found that species predatory on a wide range of prey families had larger range sizes than those which ate fewer prey types. This suggests that the wide diet breadth of the IAS is likely to have played a critical role in the species' rapid spread. Dietary niche overlap between *H. axyridis* and native ladybirds showed positive correlation with declines of native ladybirds. This indicates that the IAS is playing an important role, but the significance of urbanisation suggests habitat destruction is also significant.

Abundance of *H. axyridis* was influenced by habitat type and aphid abundance, but not by the native ladybird community, suggesting the spread of the IAS will not be slowed by biotic resistance. *Harmonia axyridis* is attacked by native parasitoids, but at a much lower rate than is the native *Coccinella septempunctata*, in line with natural-enemy release theory. There was no evidence of attack rate increasing with time since arrival in an area.

Overall, *H. axyridis* is an extremely successful IAS, with detrimental effects on native ladybirds which are likely to continue.

## Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated below.

Chapters 2 & 3: The raw sightings used to produce the distribution data were contributed by thousands of volunteer recorders and collated by the UK Ladybird Survey team.

Chapter 4, Gabriele Rondoni, Emmeline Favreau, Emma Rhule, Georgie Knibbs, Carly Hoskin, and Sarah Turner assisted with collecting pupae; Bill Phillips collected all the pupae from Loughborough. Bill Kunin and Matthew Hanson set up and monitored the Leeds bucket experiment, under direction.

Chapter 5: Gabriele Rondoni assisted with ladybird monitoring during the 2010 field season.

This dissertation is 31,043 words long exclusive of bibliography, appendices, diagrams and tables

## Dedication and Acknowledgements

To my family, near and far. Especially my parents, John and Sue, for encouraging me down this path and tolerating its early manifestations, and my grandma Olive, who died before this thesis came to fruition.

Thanks must go to my supervisory team of Helen, Beth, Owen, Richard and Chris, for keeping me on track and tolerating my deviations from concentrating on PhD work. Particular thanks to Helen for involving me in many of those diversions in the first place!

To my friends, from E41 (particularly Eleanor, Sarah, Moya, Sofia, Claudia, Jeff, Chris, Enric, Ace & Paul), CEH (especially Gary, Nick, Chris, Helen, Jim, Bjorn, Mark, Owen, Markus, & Rory), Biolist (Sally, Derek, Yssy, Chris, Helen, Dave, Andy *et al*) and beyond (Carly, Becky, Mike, and the wider community of ladybird people), who have put up with my odd working hours, complaints about workload followed rapidly by agreements to do 'just one more event', and a habit of crowbarring ladybird references into every conversation. Nb: these are unlikely to stop in the near future…

To tea, and to a lesser extent coffee, without which writing-up might never have ended. And thanks to Ros, Nadine, Moya & Becky for employing me during writing-up after my stipend finished.

"*One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise*."
— Aldo Leopold, *Round River.*

"*If you trust in yourself… and believe in your dreams… and follow your star… you'll still get beaten by people who spent their time working hard and learning things and weren't so lazy*"
— Terry Pratchett, *Wee Free Men.*

# Chapter 1. General introduction

## 1. 1.1. Defining alien species and invasive alien species

The United Nations Convention on Biological Diversity (CBD: http://www.cbd.int) defines an alien species as ‘a species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce’ (COP 6, decision VI/23). The term has many synonyms in the literature, including non-native, introduced, exotic, foreign, and non-indigenous, but is not synonymous with invasive alien species (IAS), which are defined by the CBD as ‘an alien species whose introduction and/or spread threatens biological diversity’ (COP 6, decision VI/23).

## 1. 1.2. Impacts and costs of Invasive Alien Species

IAS have long been recognised as a significant component of environmental change worldwide, often resulting in a significant loss in the biological diversity and function of invaded ecosystems (Wittenberg & Cock, 2001; Hulme *et al.*, 2009). They have been identified as one of the ‘Evil Quartet’ of major drivers of biodiversity loss worldwide (Diamond, 1984), and more recently highlighted in the Millennium (2005) and UK National (2011) Ecosystem Assessments, and included in the IUCN’s Direct Threats Taxonomy (Salafsky *et al*., 2008). It has been estimated that the direct costs of IAS amount to around US $1.4 trillion, approximately 5% of global GDP (Pimentel *et al*., 2001), with annual costs of £1.7 billion within Britain alone (Williams *et al.*, 2010).

Some biological invasions have become major public issues in the invaded countries as a result of the damage caused. For example, the cane toad *Rhinella (Bufo) maritima* (L) was first introduced into northern Australia in 1935 (Easteal, 1981) to control the cane beetle *Dermolepida albohirtum* (Waterhouse) (Doody *et al.*, 2009). It failed to control the beetle, instead having significant negative effects on native fauna including mammals, lizards, snakes and the freshwater crocodile *Crocodylus johnsoni* (Krefft) (Braithwaite & Griffiths, 1994; Doody *et al.*, 2009; Shine, 2010)

### 1. 1.3. Trends in arrival, establishment and spread of IAS

Alien species have been introduced into new areas since ancient times, particularly in Europe, and in some cases the impact of the introduction was so long ago that the biodiversity effects can no longer be seen (Genovesi & Shine, 2004). Occasionally, the introduced species has become an important link in the modern-day ecosystem, e.g. the rabbit *Oryctolagus cuniculatus* L. (Lagomorpha: Leporidae), which is the primary non-domestic grazing animal of grassland in Britain (Asher *et al.*, 2001). Although some introductions are ancient in origin, the rate of introductions has increased rapidly over the last two hundred years (Hulme *et al*., 2009), paralleling the rise global trade, particularly in the last half-century (Beggs *et al.*, 2011; Roy *et al.*, 2011c).

Within Europe, the identity of IAS, and their rate of arrival, has been catalogued by the Delivering Alien Invasive Species Inventories for Europe project (DAISIE), which currently lists 10,961 alien species introduced within Europe alone. The majority of these (6,630 species) are plants, followed by terrestrial invertebrates (2,426 species), and aquatic marine organisms (1,000) (Hulme *et al.*, 2009; DAISIE, 2013b). The rate of introduction of alien arthropods have increased from around 0.05 species per year (15 species introduced 1500-1799), to more than 19 species per year in the 21st century (174 species introduced 2000-2008) (Roy *et al.*, 2011c). Similarly, introductions of plant species have increased massively post-1800 (Pysek *et al*., 2009).

Recent analyses highlight that the invasion of new regions by alien species is closely tied to human activity (Pysek *et al.*, 2010; Essl *et al.*, 2011a). Pysek *et al*. (2010) found that economic and demographic variables were significant predictors of patterns of introduction in Europe, as they integrate the effects of factors that determine invasion success such as human disturbance and propagule pressure (a composite measure of introduction effort, comprising estimates of the number of separate introduction events, and the number of individuals introduced per event).

Essl *et al*. (2011a) stressed the relevance of the well-known time lags between introduction, establishment and spread in invasions by currently-established alien species. These analyses revealed that, for several taxonomic groups, current numbers of established IAS are more closely related to socioeconomic indicators from the year 1900, than to equivalent indicators from 2000. This `invasion debt', however, was not detected for terrestrial insects, which are better accounted for using current indicators, which may reflect the short generation times and high dispersal capacities of most arthropod species. In particular, the flight capabilities of most insects allow them the possibility of rapidly exploring a range of habitats and circumvent barriers between the original site of introduction and patches of suitable habitat in the surrounding area (Essl *et al.*, 2011a).

### 1. 1.4. Pathways of introduction and spread – how do IAS arrive?

At its simplest, alien species can arrive either by deliberate introduction, accidental human-mediated transfer, or natural spread from an introduced population, termed 'leading-edge dispersal'. However, Hulme *et al*. (2008) recognise six distinct introduction pathways, 1 – deliberate release, 2 – unintentional escape, 3 – unintentional contaminant of another commodity, 4 – unintentional stowaway on transport, 5 – natural dispersal aided by human-made corridors (such as the Suez canal), 6 – unaided natural dispersal.

The relative importance of these various pathways varies between taxa, and a single species may be introduced using multiple pathways (Pyšek *et al.*, 2011). Of the known pathways for terrestrial vertebrates arriving in Europe, the most important single pathway was deliberate release (>300 invasion events), ahead of escape (around 190 invasions), with unintentional transport (58 recorded invasions, contaminant and stowaway pathways not distinguished) and natural dispersal (56 invasions) making up much of the remainder. For terrestrial invertebrates, by contrast, the unintentional transport pathway (both stowaway and contaminant), with approximately 6750 invasion events, dwarfs all other invasion routes (the next highest is the 750 deliberate releases) (DAISIE, 2013a).

Species can also arrive by 'piggybacking' on the movement of other species. This is particularly likely where some or all of the life-histories of the two species are tightly linked, such as leaf-miners or gall-causers which spend the majority of their life cycles not just on but inside a host plant. For example, both the gall midge *Obolodiplosis robiniae* (Haldeman) (Diptera: Cecidomyiidae) and its parasitoid *Platygaster robiniae* Buhl & Duso (Hymenoptera: Playgastridae) were accidentally introduced to Europe on imported specimens of the black locust tree *Robinia pseudoacacia* L. (Fabales: Fabacaea)

(Buhl & Duso, 2008; Pernek & Matosevic, 2009; Kim *et al.*, 2010). Similarly, the worldwide movement of honey bees, *Apis mellifera* L. (Hymenoptera: Apidae), facilitates the movement of bee parasites such as the mite, *Varroa destructor* Anderson & Trueman (Parasitiformes: Varroidea) (Roy *et al.*, 2011c).

Other linked introductions may be more the product of chance. The Asian tiger mosquito, *Aedes (= Stegomyia) albopictus* (Skuse) (Diptera: Culicidae) has been introduced worldwide, and has been reported to spread as an adult stowaway in vehicles (Rabitsch, 2010), as a larva in shipments of lucky bamboo, *Dracaena sanderiana* (Mast) (Asparagales: Asparagacaea) (Linthicum *et al.*, 2003) and as a drought-resistant egg on shipments of car tyres (Adhami & Murati, 1987).

### 1. 1.5. From alien to invasive

Only a small subset of the alien species introduced to a new area will actually become established (defined as ‘the process of an alien species in a new habitat successfully producing viable offspring with the likelihood of continued survival’: COP 6, Decision VI/23), and a yet smaller subset of these will go on to become invasive (Lodge, 1993). This subsetting of establishment and invasion is often referred to as the ‘tens rule’, after one of the first papers to examine the relative proportions of introductions, establishment and invasion found that, for plants in Britain, approximately one species establishes from every ten introduced and, of every ten established species, one will become invasive (Williamson & Fitter, 1996). Later research in other areas and taxonomic groups have found little empirical evidence for these particular proportions (Jeschke & Strayer, 2005; Vander Zanden, 2005).

Blackburn *et al* (2011) set out a unified framework for biological invasions, combining the barrier-based framework of botanists (Richardson *et al.*, 2000) with the stage-based framework commonly used by zoologists (Williamson, 1996; Williamson & Fitter, 1996). This framework sets out the process of invasion as four distinct stages (transport, introduction, establishment, and spread), each containing barriers (geographical barriers containing a species in its native range, barriers to survival in captivity/cultivation, barriers to survival and reproduction in the introduced range, barriers to dispersal in the introduced range, and environmental barriers in the introduced range). Failure to circumvent a barrier results in failure to become invasive, although the exact outcome varies depending on which barrier proved impossible to circumvent, from species which persist as sustainable populations established in the introduced range, back to species which never leave their native range (Blackburn *et al.*, 2011).

### 1. 1.6. From alien to invasive – the traits of invasive species

Establishing the traits which allow species to become invasive (and drive circumvention of the barriers at each stage of the invasion process) has been a major goal of invasion biology for many years. Although no single trait has emerged as the overall driver across taxa, regions and stages, some generalisms have emerged (Jeschke & Strayer, 2008; Blackburn & Jeschke, 2009; Jeschke *et al.*, 2012). Species with large native distributions tend to be more likely to be introduced (Jeschke & Strayer, 2005, 2006), while establishment is largely dependent on the organism's tolerance of temperatures in the introduced range (particularly for overwintering survival in temperate regions) (DeBach, 1964; Walther *et al.*, 2009). For this reason, climate matching has often been used to consider the likelihood of establishment for deliberate introductions (van Lenteren *et al.*, 2006).

Some generalisations of predictors of invasiveness can be made, particularly within groups. For plants, where the majority of this work has been done, the ability to reproduce vegetatively is a good predictor of the ability to establish (Kolar & Lodge, 2001; Kuster *et al.*, 2008; Lososova *et al.*, 2008), and elevated reproductive and growth rates correlate with spread of invasive plants in most studies (Kolar & Lodge, 2001; van Kleunen *et al.*, 2010). Additionally, studies have found that several other traits correlate well with invasiveness, including the leaf-area allocation, physiology, shoot allocation, size, and fitness (van Kleunen *et al*., 2010), the presence of perfect flowers, seed size, and the length of time fruit remains on the plant (Reichard & Hamilton, 1997), amongst several others.

In animals, and particularly in insects, good dispersal ability is often important in both establishment and invasion (van Lenteren *et al.*, 2006; Robinet & Liebhold, 2009; Essl *et al.*, 2011a), as it allows rapid spread beyond the original point of introduction. Species which are able to utilise a wide range of habitat types (habitat generalists) and those which are able to feed (and survive and reproduce successfully) on a wide range of food species/types (dietary generalists) are more likely to become invasive (van Lenteren *et al.*, 2006; Jeschke & Strayer, 2008). Particularly for invertebrates, fecundity (large brood sizes and multivoltinism) appears to be important in the invasion process, particularly in circumventing the barrier between establishment and invasion (Grabowski *et al.*, 2007; van Lenteren *et al.*, 2008).

In general, the one thing that all invasive species have in common is that, when presented with an opportunity to establish and spread, they were capable of taking it. This suggests that the key features may be more to do with ecological flexibility than any innate trait of invasiveness, and this has lead to the theory than the habitats and communities invaded may be as important to an invasion's success as the species invading (Drake *et al.*, 1989; Thebaud *et al.*, 1996; Lonsdale, 1999).

### 1. 1.7. Invasibility of native communities – the diversity-invasibility hypothesis

There is evidence to suggest that the invasibility of the ecosystem may be as important as traits of the IAS in determining the success of invasions (Drake *et al.*, 1989; Thebaud *et al.*, 1996; Lonsdale, 1999; Davis *et al.*, 2000). The idea that invasibility of a community is negatively related to its diversity can be traced back to Elton's work on invasion ecology (Elton, 1958), and was generalised to a theory of resource availability by Davis *et al* (2000). It states that the displacement of native species by IAS is facilitated by degradation of the ecosystem, which moves the competitive advantage away from previously well-adapted native species, to newly-arrived IAS (Howarth, 1991; Suarez *et al.*, 1998; Davis *et al.*, 2000; Seabloom *et al.*, 2003; Evans, 2004; Powell *et al.*, 2011). This may result from increased stress for native species or the erection of larger barriers to recruitment for natives (Gurevitch & Padilla, 2004; MacDougall & Turkington, 2005; King & Tschinkel, 2008), making it easier for IAS to colonise depauperate or highly-dynamic systems, rather than replacing native species occupying niches in more settled communities.

For any species, the environment is a mosaic of habitat patches of varying quality, ranging from highly suitable to uninhabitable. IAS must establish in, and spread from, initial source habitats to populate the mosaic of habitats encountered in new landscapes, and the most invaded habitats appear to be those which have been extensively anthropogenically modified (Lopez-Vaamonde *et al.*, 2010; Evans *et al.*, 2011).

## 1. 1.8. Anthropogenic habitat change

The dominant landscape influence in the late twentieth and early twenty-first century is the huge modification of natural landscapes by humans (Evans *et al.*, 2011). Major modifications (largely for urbanisation and agriculture) include the excess supply of nutrients (direct and indirect fertilisation) and ecosystem simplifications (functional, structural, biotic, and phylogenetic homogenisations), which increase the number of vacant niches and reduce the resilience of the ecosystem, greatly increasing the likelihood of establishment and spread of alien species (Lockwood & McKinney, 2001; Shea & Chesson, 2002; Canfield *et al.*, 2010). The original hypothesis of Elton (1958) was that anthropogenic activities such as cultivation simplify ecosystems, reducing the diversity and abundance of resident native species, lowering the biotic resistance to invasion via competition and predation (Elton, 1958; MacArthur, 1972). Therefore the theory of biotic resistance states that invasibility should decrease as community biodiversity increases: IAS should be largely confined to low-diversity systems while high-diversity systems have low invasibility and are relatively immune to invasion.

Recently, however, emphasis has shifted to stress the importance of productivity (Davis *et al.*, 2000; Levine, 2000) and niche opportunity (Shea & Chesson, 2002) in the invasibility of an area or habitat, as highly-productive habitats can also favour invasion, even in the continuing presence of a highly-diverse native community. This can lead to positive correlations in the numbers of alien and native species at some spatial scales, rather than the negative correlations predicted by the hypothesis of biotic resistance (Stohlgren *et al.*, 1999; Fridley *et al.*, 2007). For example, in the Mediterranean coastal scrub habitat of southern California, both alien and native spiders occur in their greatest numbers in the most productive habitat remnants (Burger *et al.*, 2001; Bolger *et al.*, 2008). Local productivity (partially expressed as high numbers of spider prey) of individual remnants depends on landscape context, with likely enhancement from surrounding disturbed (urban) areas within this landscape (e.g., from increased water availability due to run-off from asphalt surfaces; Bolger *et al.*, 2008).

Anthropogenic habitat modifications also in part increase the invasibility of native ecosystems by deleteriously affecting the persistence of native species, both directly, and indirectly as the result of negative interactions with IAS. However, for both fish and birds in Europe and North America, different characteristics corresponded with invasion success for alien species, and extinction risk for native species, rather than opposite ends of the spectrum of each trait. Only one out of 20 characteristics, range size, was correlated both positively with invasion success, and negatively with threat status (Jeschke & Strayer, 2008; Blackburn & Jeschke, 2009).

It is possible that human-modified habitats which mimic the habitats of IAS in their native range (e.g. where the habitat itself has been introduced, such as crop species cultivated in a similar manner around the world) may be especially suitable for IAS when compared to native species confronted by a new habitat (Evans *et al.*, 2011). For example, the Indo-European ladybird *Coccinella septempunctata* L (Coleoptera: Coccinellidae) continues to reproduce more successfully in North American fields of the Indo-European crop alfalfa (*Medicago sativa* L) (Fabales: Fabacaea) than does its close relative *Coccinella transversoguttata* Faldermann (Coleoptera: Coccinellidae), a species native to North America, even as aphid populations in the alfalfa fields of northern Utah have subsided to low levels after the initial establishment of *C. septempunctata* (Kajita & Evans, 2010).

### 1. 1.9. Habitat loss and fragmentation

The major modifications of urbanisation and agriculture lead to whole-scale loss and fragmentation of natural habitats by reconfiguring entire landscapes (Forman, 1995). Habitat loss, degradation and fragmentation are considered leading causes of biodiversity loss (Millennium Ecosystem Assessment, 2005), and attention has been drawn to the likely frequent interaction between these and IAS as major drivers of global decline in biodiversity (Didham *et al.*, 2007; Bolger *et al.*, 2008).

Habitat fragmentation and degradation negatively affect native community biodiversity, particularly through the island biogeography mechanism (MacArthur & Wilson, 1967), although in general the effects are weaker, less consistent and more insidious than those of habitat loss (Fahrig, 2003; Ewers & Didham, 2006). IAS may also be more able to colonise fragmented habitats as the biotic resistance of the native community decreases. For example, the invasion of the Argentine ant in southern California was facilitated by habitat fragmentation because smaller fragments provide less refugia for native species, and increase the chances of their local extinction (Suarez *et al.*, 1998; Suarez & Case, 2003)

The ability of IAS to colonise highly-productive disturbed habitats can allow them to reach high abundance (Didham *et al.*, 2007), which promotes subsequent dispersal into habitat fragments (Evans *et al.*, 2011). The detrimental effects of this habitat spill-over can be exacerbated when the species leaving the crops become established in native habitats. For example, parasitoids of agricultural pest Lepidoptera were introduced as biological control agents to Kauai Island, Hawaii, early in the twentieth century, expanding to establish large populations attacking native moth species across the island (Henneman & Memmott, 2001; Sheppard *et al.*, 2004).

### 1. 1.10. Climate change: a particular form of anthropogenic habitat change

The abiotic context of the ecosystem can also govern the impacts of IAS. The climate of an area plays a central role in allowing alien species to establish there (Elton, 1958; Williamson, 1996). Roura-Pascual *et al*. (2011) found that climatic suitability and the extent of human modification of habitats are primarily responsible for the global distribution of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), while Kobelt and Nentwig (2008) also found greater than expected number of introductions of alien spiders to Europe from the eastern Palearctic and Indomalayan versus other geographic regions, attributed to the relatively similar climates of these regions and Europe.

Intriguingly, the microclimate of fluctuating temperature and humidity in transport (e.g., inside a standard ship container) may further influence patterns of invasion: Kobelt and Nentwig (2008) hypothesise that a superior ability to survive such conditions may account for the tendency of alien spider species to be of larger body size than counterparts in Europe, as temperature and humidity fluctuations are high stress factors for spiders, but which are buffered by body size, with smaller species disproportionately affected (Pulz, 1987), while Nedved *et al* (2011) found that most of the arachnids invasive in Europe are species able to survive long periods without food.

Climate change has the potential to remove or diminish currently-existing barriers to some alien species at every stage of the invasion process (Hellmann *et al.*, 2008; Walther *et al.*, 2009): it can change trade pathways and characteristics, e.g. by generating new consumer habits; it alters the establishment and survival probabilities by changing the climate and microclimates of an area, e.g. greenhouse species that were formerly not able to survive outdoors may have the chance to do so (for example the southern European predator *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) in the Netherlands, (Aukema & Loomans, 2005)). The distributional ranges and the niche breadth of species can change: climate change may even change the invasiveness of species, by selecting for invasive traits or allowing them to be expressed, or by tipping the competitive advantage away from one species and towards another altering the invasibility of habitats due to the breakup of biotic interactions (Walther *et al.*, 2009; Schweiger *et al.*, 2010). Hence an indirect effect of warming may occur if a change in temperature has deleterious effects on indigenous species and thereby weakens biotic resistance to invasion. For example, indigenous ants become inactive during summer afternoons whilst the non-native *L. humile*, being more tolerant of high temperatures, remains active (Human & Gordon, 1996).

As ectothermic species, invertebrates are predicted to react more severely to climate change than warm-blooded animals (Maes *et al.*, 2010). In Britain and Europe, climate change appears to be driving the northwards expansion of several taxa (Hickling *et al.*, 2006), including butterflies (Roy *et al.*, 2001; Altermatt, 2010), bush-crickets (Hochkirch & Damerau, 2009; Wissmann *et al.*, 2009), and dragonflies (Ott, 2010). Global warming is enhancing voltinism and population growth of many arthropod species in their existing ranges, which could force more individuals to disperse, so extending their native ranges (Hochkirch & Damerau, 2009; Altermatt, 2010). Additionally, the previously-suboptimal areas outside the original range have become more suitable, allowing species to establish in regions in which they previously could not survive and reproduce (Walther *et al.*, 2009). For example, dragonflies from Africa and the Mediterranean appear to have spread northwards (Walther *et al.*, 2009; Ott, 2010), while temperature and dispersal limitation have been found to drive invasion patterns in the range-expanding wasp spider *Argiope bruennichi* (Scopoli) (Aranea: Araneidae) in Europe (Kumschick *et al.*, 2011; Krehenwinkel & Tautz, 2013).

The relationship between climate and communities is far from simple, however, and there is no linear positive relationship between temperature and arthropod diversity. Many species are adapted to cooler climates and suffer when the thermal environment changes, for example alpine species (Johnson *et* *al.*, 2010). Additionally, climate change is not itself a straightforward process of thermal alteration, but involves changing almost every aspect of annual weather patterns (IPCC, 2007). Non-thermal components of climatic changes, such as an increase in annual precipitation, also have the potential to pave the way for invasion by altering the effective invasibility of a habitat. In California, *L. humile* readily invades mesic but not dry scrub and riparian habitats (Holway, 1998; Holway *et al.*, 2002), and the increasingly high summer rainfall has promoted the spread of the species into new areas in northern California, including traditionally-dry habitats such as chaparral and high elevation grasslands and woodlands (Heller *et al*., 2008).

A changing climate may act directly in widening the window of opportunity for alien populations to gain a foothold that leads to long-term persistence in a new geographic region (Walther *et al*., 2009) For example, in the River Thames in Britain, the Chinese mitten crab *Eriocheir sinensis* (Milne-Edwards) was recorded sporadically in the estuary between 1935 and 1991, but it is thought that low flow events following droughts during 1989-91 allowed the species to establish a young population upstream, where it rapidly colonized tributaries well upstream of the estuary (Attrill & Thomas, 1996; Clark *et al.*, 1998).

Although IAS are often opportunist species tolerating broad environmental conditions, specialists can also be successful if their requirements are satisfied. For example, monophagous species or host-specific parasitoids may have a difficult start after introduction, but can prosper if translocated together with their hosts, or if these are already available in the introduced range (Buhl & Duso, 2008). The same is true for predators, although prey specialisation usually is less developed in predatory species.

### 1. 1.11. Horizon scanning, risk assessment and management

Due to the threats posed by IAS, the Bern Convention on the Conservation of European Wildlife and Natural Habitats (1979) (known as ‘the Bern Convention’) required signatory governments to ‘strictly control the introduction of non-indigenous species’ and the CBD added the requirement to ‘eradicate those species which threaten ecosystems, habitats, or species’. The CBD Guiding Principles laid out a three-stage hierarchical approach as the basis for controlling IAS:

1. Prevention of IAS introductions between and within states is generally far more cost-effective and environmentally desirable than measures taken after IAS introduction and establishment.
2. If an IAS has been introduced, early detection and rapid action are crucial to prevent its establishment: the preferred response is often to eradicate the organisms as soon as possible.
3. Where eradication is not feasible or resources are not available, containment and long-term control measures should be implemented

In practical terms, this increased awareness of the potential negative effects of IAS has led to the implementation of stringent regulations (such as major pre-release risk assessments) on the release of biocontrol agents (van Lenteren *et al*., 2006). Consequently, this pathway is declining in importance for most groups compared to accidental introduction via the contaminant or stowaway pathways (Kenis *et al.*, 2007; Hulme *et al.*, 2008; Engelkes & Mills, 2011; Roy *et al.*, 2011c).

Pre-release risk assessments and horizon-scanning efforts (looking at species which may potentially arrive) attempt to quantify the risks of species in turn arriving, establishing and spreading. The movement of species – particularly deliberate releases for farming, forestry, biocontrol and others – has a net economic and social benefit, with very few species becoming problematic: for these problematic species, the most cost-effective way to reduce impacts is to prevent introduction (Keller *et al*., 2011). Accurate risk assessment tools can support policy and management efforts to reduce the overall impacts from harmful invaders while allowing importation of beneficial species. The logic of the risk assessment process is that patterns in historical data can be identified and applied to future species introduction events to determine the likelihood that each species will pass through the establishment and spread steps to become invasive.

A standard approach has been to look for traits which confer an aptitude for invasiveness, in order to identify risk species. Many studies have taken this approach for plant species (Reichard, 1997; Reichard & Hamilton, 1997; van Kleunen *et al.*, 2010), but it has also been used for some vertebrate and invertebrate species (Kolar & Lodge, 2002; Louda *et al.*, 2003; Marchetti *et al.*, 2004a, b; Vila-Gispert *et al.*, 2005; Lenz *et al.*, 2011).

This is a particularly complex area and, there is no single, consistent cause of invasiveness. It has been suggested that the different stages that IAS pass through (introduction, establishment and spread) may require separate, even conflicting traits (Marchetti *et al.*, 2004a; Burns, 2006), and that these will vary greatly depending on the type of organism and the invaded ecosystem, with different combinations of traits equipping species to invade different ecosystems (Thebaud *et al*., 1996). Some studies have even found that individual-level traits such as inquisitiveness can vary considerably between individuals, and could prove to be the difference between introduction and successful establishment, or between establishment and speed of spread (Cote *et al.*, 2010; Chapple *et al.*, 2011).

Research such as this has fed into risk assessment frameworks, particularly to assess the potential non-target effects of species deliberately introduced for biocontrol (Rosecchi *et al.*, 2001; Louda *et al.*, 2003; Bartell & Nair, 2004; Gevrey *et al.*, 2006; Essl *et al.*, 2011b; Keller *et al.*, 2011). A retrospective risk analysis of the widespread invasive ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Europe found that the species showed many of the more widely-accepted risk indicators for IAS for Europe. The species is able to establish outside, has good dispersal capabilities, both natural and anthropogenically-assisted, occupies a broad range of habitats, has high reproductive potential, broad climatic tolerance, and a wide dietary range, including a propensity to act as an intraguild predator within the aphidophagous guild (Ware *et al.*, 2005; Majerus *et al.*, 2006; Berkvens *et al.*, 2008a; Roy & Wajnberg, 2008; Brown *et al.*, 2011a). Its activities are thought to have resulted in the reduction of populations of native predators in North America, where it is also known as a nuisance species; and it may develop further as a pest of fruit in North America (van Lenteren *et al*., 2008).

### 1. 1.12. The Enemy Release Hypothesis (ERH)

The potential lack of natural enemies, particularly specialists, attacking IAS in the introduced range is the foundation of the Enemy Release Hypothesis (ERH) (also referred to as the ‘escape-from-enemy hypothesis’, ‘enemy-free space hypothesis’, or ‘enemy escape’) (Elton, 1958; Jeffries & Lawton, 1984; Wolfe, 2002). The assumptions of this theory are that natural enemies play a role in regulating populations, that the regulatory effect of natural enemies is stronger in the native range than in the introduced range for IAS, and that the decline in regulatory pressure in the invaded range allows increased population growth of the alien species (Elton, 1958; Colautti *et al.*, 2004; Roy *et al.*, 2011b). This increased population growth may arise through two mechanisms: regulatory release (where a species is released from the strong regulatory effect of a natural enemy, increasing survivorship or other demographic parameters), or compensatory release (also known as the Evolution of Increased Competitive Ability (EICA) hypothesis), where energy normally (in the native range) devoted to resisting predation can instead be diverted to population growth (Shea & Chesson, 2002; Roy *et al.*, 2011b).

Though intuitively attractive, the ERH lacks definitive supporting empirical evidence (Wolfe, 2002). For the ERH to be supported in full, a decrease in the number of successful attacks by natural enemies of an IAS in its invaded range must be the primary cause of greater population growth in the invaded range compared to the native range of the IAS (Roy *et al.*, 2011b). A decrease in abundance and species richness of natural enemies in the invaded range is a common finding in studies of IAS (Torchin *et al.*, 2001; Torchin *et al.*, 2003; Torchin & Mitchell, 2004; Cottrell & Shapiro-Ilan, 2008; Blumenthal *et al.*, 2009), but few studies have quantitatively compared the native and invaded ranges, or considered contributing factors such as time since colonisation, so the evidence for the ERH remains largely circumstantial (Torchin & Mitchell, 2004; Liu & Stiling, 2006).

The invasion process certainly seems able to act as a filter to remove some or all of the natural enemies – particularly parasites and pathogens – which co-occur with IAS in their native range (Torchin & Mitchell, 2004). This is likely to happen in several different ways: the IAS may arrive as a life-stage which is not attacked by a parasitoid species, or the invaded range may not contain another host species needed by parasites with complex life cycles (Torchin *et al.*, 2003; Torchin & Mitchell, 2004). Alternatively, the infected individuals of the invasive species may not survive the introduction process, or the parasite may not be able to survive in the invaded environment (Torchin *et al.*, 2002; Yang *et al.*, 2010). Finally, the low numbers of introduced individuals characteristic of introductions and founder populations may purge IAS of parasites, as only a subset of the native population is introduced, and density-dependent transmission breaks down at small population sizes (Torchin *et al.*, 2003; Torchin & Mitchell, 2004). While predators, and other natural enemies, are likely to occur in the invaded range, they are not co-evolved with the IAS to the same extent as predators in the native range, and may take some time to adapt to a novel food resource (Berkvens *et al.*, 2008b; Koyama & Majerus, 2008; DAISIE, 2009).

Additional environmental changes that affect alien species also can result in a disconnect or decoupling of predator-prey and parasitoid-host interactions (Schweiger *et al*., 2010). For example, larvae of the pine beauty moth *Panolis flammea* Denis & Schiffermüller (Lepidoptera: Noctuidae) in the UK exhibit lower levels of parasitism on an introduced food plant than on a native host due to a difference in the period of larval suitability on the two host species, resulting in an asynchrony between the parasitoid and larvae on the introduced plant (Hicks *et al*., 2007).

### 1.1.13. Range of impacts – from co-existence to invasional meltdown

Once established and beginning to spread, alien species can have a range of impacts. The majority of species show co-existence with the native environment, with negligible deleterious effects. For example, a population of the southern European scorpion *Euscorpius flavicaudis* (de Geer) (Scorpiones: Chactidae) has lived in a dockside wall in Sheerness, Kent, UK since the 1870s with no reported detrimental effects (Benton, 1992)

At the other end of this spectrum is the process of invasional meltdown, when the direct and indirect effects of IAS combine to produce a synergism in impacts (Simberloff & Von Holle, 1999). The best-known case of this is the impact of the supercolonial yellow crazy ant *Anoplolepis gracilipes* Smith (Hymenoptera: Formicidae) on Christmas Island. The ant was present at low densities on the island for several decades with no obvious impact on the island's biodiversity, but the formation of supercolonies greatly increased the tending of populations of scale insects, guarding them against natural enemies and feeding on the honeydew produced. The resulting high population densities of scale insects caused a major increase in mildews and sooty moulds growing on the excreted honeydew, promoting canopy dieback and tree death (O'Dowd *et al.*, 2003; Abbott, 2005). The ants also underwent population increases as a result of the abundant honeydew, and by 2001, twelve years after supercolonies were first noted in the Christmas Island ant population, c. 25 km$^2$ (25% of the island’s rainforest) was covered by supercolonies of *A. gracilipes* (O'Dowd *et al.*, 2003). The keystone species on Christmas Island is the red land crab *Gecarcoidea natalis* Pocock (Decapoda: Geocarcinidae), which virtually monopolises litter processing on the island (Green *et al*., 1999). The crab has declined massively in areas invaded by the ant supercolonies (crab burrow density decreased 42-fold in ant-invaded compared to ant-free areas), slowing litter breakdown, releasing seedling recruitment, enhancing seedling species diversity and decreasing litter and canopy diversity (O'Dowd *et al*., 2003). The combined effect is to rapidly transform the rainforest ecosystem through both top-down and bottom-up effects (O'Dowd *et al.*, 2003).

Between these two extremes, there is a spectrum of human and ecosystem impacts. Ecosystem impacts of the hundred worst IAS are detailed by Vilà *et al*. (2009), and include spreading disease to, hybridising with, or simply outcompeting native species, modifying habitats to the detriment of natives, and straightforward predation.

The impacts on humans are similarly variable. One major effects is on food security: for example, the Asian hornet *Vespa velutina* Lepeletier (Hymenoptera: Vespidae), raids and destroys honeybee nests (López *et al.*, 2011), and the western corn rootworm *Diabrotica virgifera* LeConte (Coleoptera: Chrysomelidae), is a crop pest which is predicted to have an economic impact of around €500 million per year in its invaded range in Europe (DAISIE, 2009). IAS can also affect human health: an example is ragweed, *Ambrosia artemisiifolia* L. (Asterales: Asteraceae), a North American plant species occurring as an alien in Britain, whose copious quantities of airborne pollen cause hayfever. More seriously the mosquito *Aedes albopictus* is capable of vectoring a variety of human-pathogenic viruses and parasites, and has been widely introduced, particularly in Europe (Gratz, 2004; Roy *et al.*, 2009).

Many species can have both ecosystem and human impacts. One such IAS is the Harlequin ladybird, *H. axyridis*, which is the focal species of my thesis. It can act as a nuisance pest to humans by entering houses in large numbers to overwinter (Roy *et al*., 2009), and is a major threat to many other wild species (Roy *et al.*, 2012).

### 1.2.1. The most invasive ladybird on Earth – *Harmonia axyridis*

*Harmonia axyridis* is a ladybird native to north-eastern Asia, including Japan, Korea, China, Mongolia, and Siberia, where it is most frequently found in disturbed habitats such as orchards, parks, gardens and agricultural fields (Brown *et al.*, 2011a; Osawa, 2011). It is a large species, 4.9-8.2 mm long and 4.0-6.6 mm wide (Kuznetsov, 1997) which, although primarily an aphid predator, is capable of surviving on a wide range of food types in a wide range of habitats, making it a generalist both in terms of habitat and diet (Roy *et al.*, 2011d). It is a highly-polymorphic species in terms of colouration, particularly of the elytra and pronotum (Tan & Li, 1934), and in Britain it has three main adult colour forms: two melanic, with the elytral base colour black and either one (form conspicua, Fig. 1.1) or two (f. spectabilis, F. 1.1) red spots on each elytron, and one non-melanic (f. succinea, Fig 1.2). This colour form is highly variable, with the elytral base colour varying from pale yellow to red, and with between 0 and 21 black spots (typically nineteen, with 8 on each elytron and a shared scutellary spot) (Tan & Li, 1934; Michie *et al.*, 2010). The larvae are large, reaching approximately 11 mm in length, and black in colour, with six large branching spines on each segment. Final-instar larvae bear an orange stripe down each side of the abdomen (segments 1-5), and three pairs of orange spines (one each on abdominal segments one, four and five) (Fig. 1.3). Younger larvae lack the orange spines: second and third-instar larvae show only the stripes, while first-instar larvae are completely black (Fig. 1.3). The pupa is similarly large, orange and black, and usually bears the characteristically-spiny shed larval skin at the point of attachment to the substrate (Fig. 1.3).

**Figure 1.1.** *Harmonia axyridis* melanic adults, form conspicua (l) and form spectabilis (r).

**Figure 1.2.** *Harmonia axyridis* adults of form succinea, illustrating the typical colouration (c), and variation (loss of spots, l, and spot fusions, r).

**Figure 1.3.** Juvenile stages of *H. axyridis*: 3rd-instar larva (l), final-instar larva (c), and pupa (r)

### 1.2.2. Trends in arrival, establishment and spread of *H. axyridis* across Europe

The species has a long history of introduction as a biocontrol agent of pest insects such as aphids, beginning in North America in 1916 (Gordon, 1985), including several releases into Europe (Trouve *et al.*, 1997; Adriaens *et al.*, 2003; Coutanceau, 2006). Despite many further releases across the USA, it was not recorded as established in the wild until it was found in Louisiana during 1988 (Chapin & Brou, 1991). However, from this starting point the species has spread rapidly: by 1994, 24 states in the USA had records of the beetle, and it had been found in Canada (Coderre *et al.*, 1995; Koch *et al.*, 2006).

Around the turn of the century, the species began to be found wild in other continents, particularly following release as a biocontrol agent. It has now been found in the wild in Europe (recorded from 30 countries following France, 1991, and Greece, 1998), South America (seven countries following Argentina, 2001), and Africa (five countries, starting with South Africa, 2001), and the species is now established in at least 38 countries worldwide with records from a further 14 (Brown *et al.*, 2011a) (Fig. 1.4).

Within Europe, *H. axyridis* was released into what are now Belarus and the Ukraine from 1968 and 1964 respectively (Sidlyarevich & Voronin, 1973; Katsoyannos *et al.*, 1997), although establishment was only reported from the Ukraine in 2009, and the species' current status in Belarus is unknown (Brown *et al.*, 2011a). The next phase of introductions was into Western Europe, beginning in France in 1982, and the species was made commercially available by several suppliers from 1995 (Adriaens *et al.*, 2003; Coutanceau, 2006). Wild individuals were found in Greece in 1998 (although establishment is doubtful), and the species has since spread rapidly, particularly post-2002, and is now also found in many countries where it was never officially released (Brown *et al.*, 2008b; Brown *et al.*, 2011a).

### 1.2.3. Pathways of introduction and spread of *H. axyridis*

Recent genetic studies using neutral molecular markers (18 microsatellites) have suggested that it is the eastern North American population (originating from Louisiana) which is particularly invasive, acting as a 'bridgehead', a particularly successful invasive population which serves as a source of colonists for remote new colonies (Lombaert *et al.*, 2010; Lombaert *et al.*, 2011). The western North American population is likely to have been a separate introduction from the native range, which is now mixing with the eastern North American population. The same genetic markers from the European populations reveal a mixture of biocontrol and North American origin (Lombaert *et al.*, 2010). Further afield, genetic studies on populations established in South Africa and across South America suggest a North American origin for these introductions (Lombaert *et al.*, 2010; Lombaert *et al.*, 2011) (Fig. 1.5).

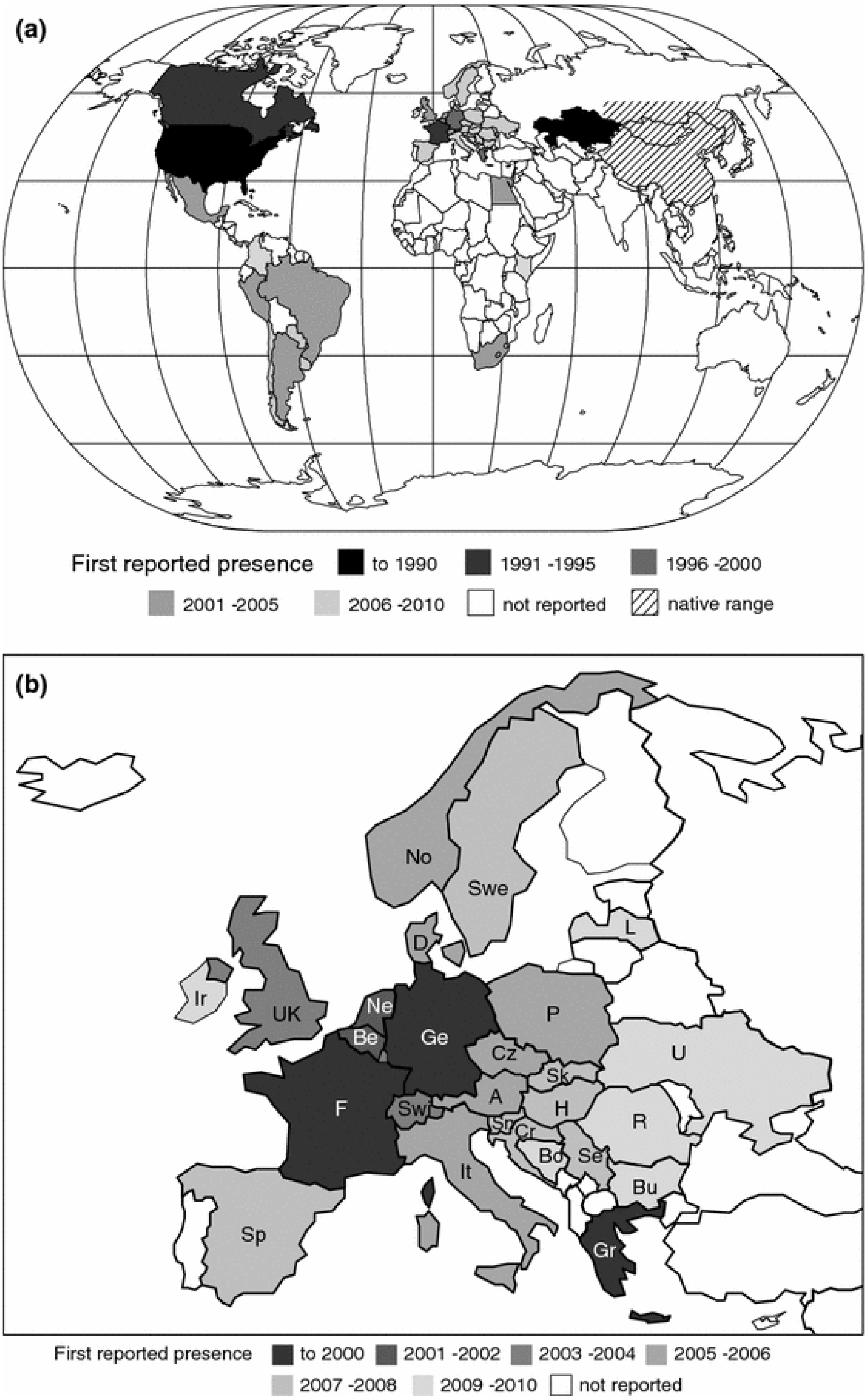

**Figure 1.4. Distribution of *H. axyridis* ≤ 2010** (confirmed wild sightings): a globally; b in Europe, originally published in Brown *et al* (2011) as figure 1. Note: entire countries are coloured, but this does not mean that *H. axyridis* necessarily occurs throughout. A Austria, Be Belgium, Bo Bosnia &Herzegovina, Bu Bulgaria, Cr Croatia, Cz Czech Republic, D Denmark, F France, Ge Germany, Gr Greece, H Hungary, Ir Ireland, It Italy, L Latvia, Ne Netherlands, No Norway, P Poland, R Romania, Se Serbia, Sk Slovakia, Sn Slovenia, Sp Spain, Swe Sweden, Swi Switzerland, U Ukraine, UK United Kingdom.

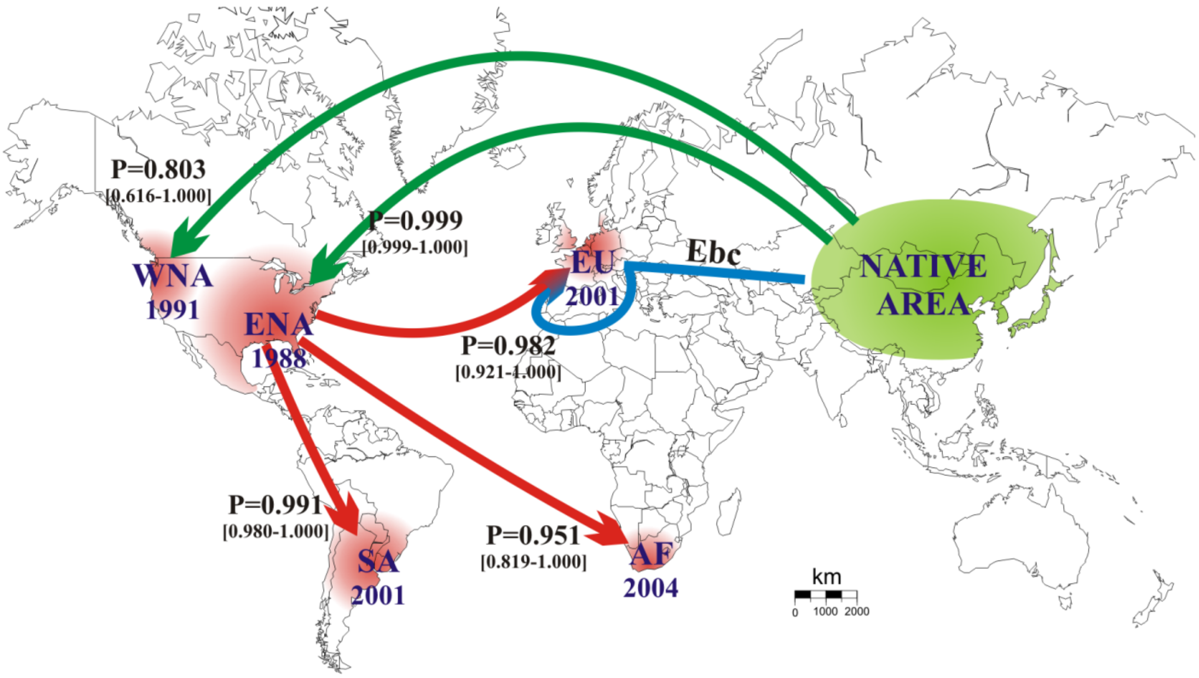

**Figure 1.5. Worldwide routes of invasion of *H. axyridis*.** The most likely scenario of invasions into eastern North America (ENA), western North America (WNA), South America (SA), Europe (EU) and Africa (AF) by *H. axyridis*, from analyses based on approximate Bayesian computation. For each invaded area the year of first detection of invasive populations is given. The arrow indicates the most likely invasion pathway and the associated posterior probability value (P), with 95% confidence intervals in brackets. The European biocontrol strain (Ebc; blue arrow) was initially collected from the native area in 1982 and was subsequently used for biocontrol efforts in both Europe and South America. Introductions to North America from the native area (green arrows) may have involved releases for biocontrol efforts (Originally published in Lombaert *et al* (2010) as figure 1).

This suggests that, in addition to deliberate releases, *H. axyridis* uses other pathways of introduction, and there is evidence to suggest that this is the case. For instance, the species has not yet established in Australia, but has twice been intercepted at the borders: several dead individuals were imported with excavating equipment in 2008, and a further 20, including live specimens, were intercepted in 2009 (Brown *et al.*, 2011a). Similarly, *H. axyridis* has been found in Britain on a shipment of packing cases from Canada (Majerus *et al.*, 2006), and more than 2000 adult beetles were discovered in a shipment of timber from the USA to Norway (Saethre *et al.*, 2010). Indeed, the first record in Norway was from a consignment of horticultural plants (*Thuja* sp.) (Staverlokk *et al.*, 2007), while the first records from Northern Ireland (Murchie *et al.*, 2008), northern England (Brown *et al.*, 2008a), and the Orkneys, northern Scotland (Ribbands *et al.*, 2009) were all on fresh produce, and the first Scottish record was from a suitcase (Majerus *et al.*, 2008).

Once a population has established, the species spreads very quickly, either by anthropogenic dispersal as above, or by local-scale natural dispersal. The species is a strong flier with a strong dispersal capability (Hodek *et al.*, 1993; Berkvens *et al.*, 2008a), and actively disperses over several kilometres to overwintering sites (Hodek & Honek, 1996; Raak-van den Berg *et al.*, 2012). In the introduced range, it has been estimated to spread at 500 km year$^{-1}$ in South Africa, 442 km year$^{-1}$ in North America, and 200 km year$^{-1}$ in Europe (Brown *et al.*, 2011a). In Britain, probably the best-studied country in the invaded range, it was estimated to disperse 105 km year$^{-1}$ northwards and 145 km year$^{-1}$ westwards between 2004 and 2008 (Brown *et al.*, 2011a) (Fig. 1.6). It is interesting to note that this north-westerly spread in Britain is against the prevailing south-westerly wind direction, so wind-borne passive transport is unlikely to have played a major role, although this is the method thought to have been employed by the species to originally arrive in the country (Brown *et al.*, 2008a; Brown *et al.*, 2011a).

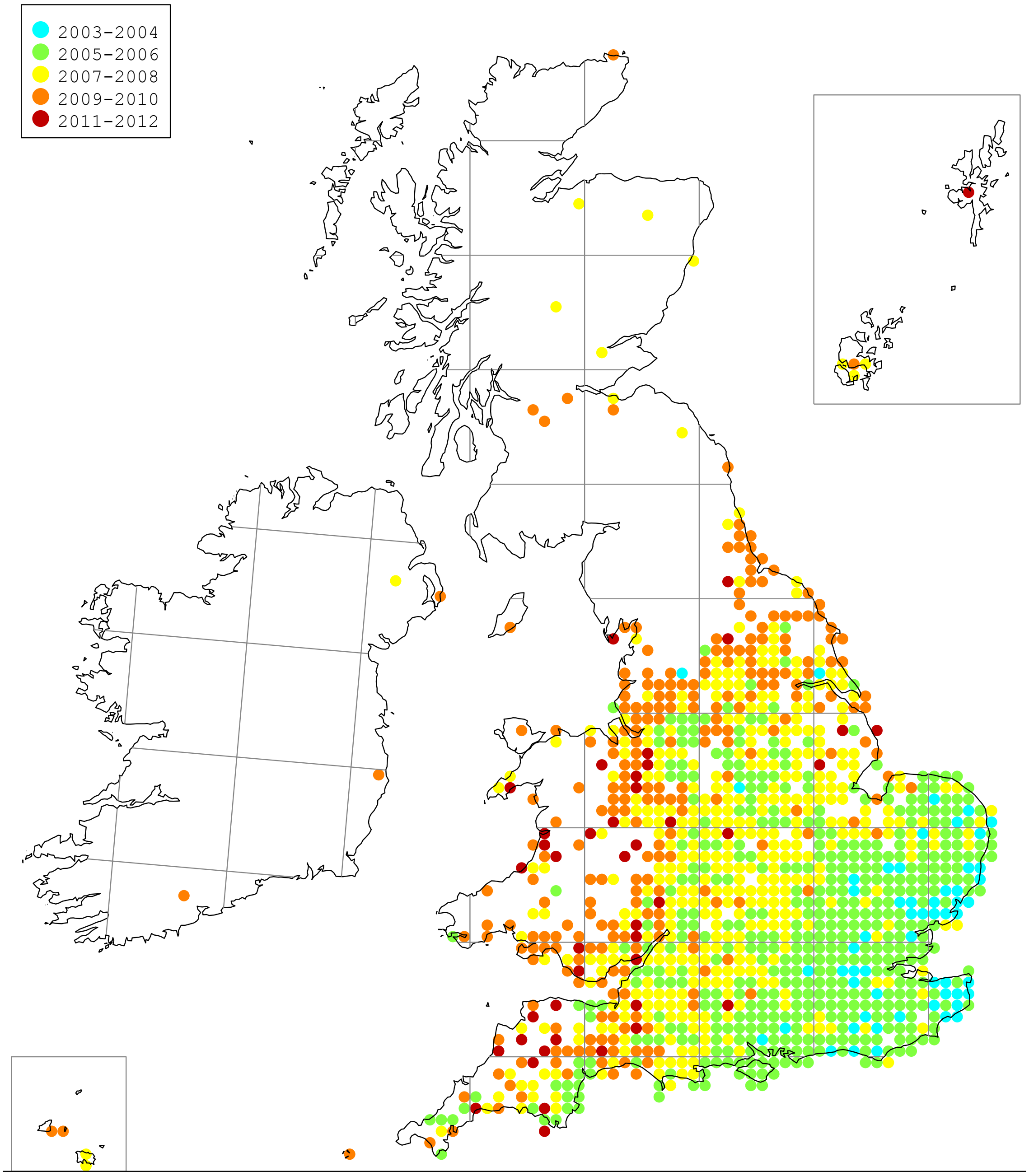

**Figure 1.6. Recorded spread of *H. axyridis* in the British Isles, 2004-2012**

### 1.2.4. Habitat range of *H. axyridis*

*Harmonia axyridis* has such a wide range of habitat suitability that it can be found, to a greater or lesser degree, in every habitat occupied by other British ladybird species, so even species which do not directly compete for prey could be at risk. For instance, the orange ladybird, *Halyzia sedecimguttata* L. (Coleoptera: Coccinellidae), is a medium-sized mildew-feeding ladybird, which reproduces mainly on sycamore, *Acer pseudoplatanus* L. (Sapindales: Sapindaceae). This tree is also a major habitat for *H. axyridis*, which feeds on colonies of the aphids *Drepanosiphum platanoidis*

(Schrank) and *Periphyllus testudinaceus* (Fernie) (Hemiptera: Aphididae). Adult aphids disperse or die during the autumn, frequently whilst larvae of *H. axyridis* are still present on the tree, leaving them looking for a food source. As another late-breeding species, the larvae of *H. sedecimguttata* are likely to be at high risk of becoming prey, and indeed have been found to be declining post-invasion (Roy *et al.*, 2012).

### 1.2.5. Invasive traits of *H. axyridis*

A major part of the extraordinary success of *H. axyridis* as an IAS appears to be the degree to which it benefits from the presence of humans. A species which, in the native range, overwinters in buildings and, outside, in caves and under exposed rocks in the Japanese uplands, is well-adapted to the artificial caves of our cities; sheds, porches and window frames. This habit is one of the main ways it impinges directly on humans, and has led to it being highlighted as a nuisance insect species in Britain, as it aggregates in homes in huge numbers during the autumn (Roy *et al.*, 2009). This allows the species to avoid the worst of the winter weather (a key mortality period for ladybirds) and so remain highly abundant at the beginning of spring (Labrie *et al.*, 2008).

These large populations can be rapidly increased as *H. axyridis* is facultatively multivoltine, and in Britain regularly produces two or even three generations per year (Katsoyannos *et al.*, 1997; Brown *et al.*, 2008a), whereas native species are usually univoltine, with some occasionally producing a partial second generation (Roy *et al.*, 2011d; Roy *et al.*, 2013). As *H. axyridis* females have been recorded laying up to 2,200 eggs each (Wang *et al.*, 2009) this allows for a rapid population expansion and very high annual abundance, with the concomitant knock-on effects of a super-abundant predator (Brown *et al.*, 2011b; Roy *et al.*, 2012).

In the native range, it is largely a species of disturbed habitats (Osawa, 2011), which makes it especially suited to establishing in similar habitats elsewhere, particularly as these highly-productive disturbed habitats are thought to be most at risk from invasion more generally (Lockwood & McKinney, 2001; Shea & Chesson, 2002). As the species is a habitat generalist, most areas are vulnerable to colonisation to some extent, particularly when high abundance in core areas causes spillover into less-preferred habitats (Comont *et al.*, 2012).

Another trait of *H. axyridis* commonly found in IAS is dietary generalism. The species feeds on a very wide range of prey, even including non-insect species (Berkvens *et al.*, 2008c; Koch & Galvan, 2008; van Lenteren *et al.*, 2008; Lundgren, 2009), which means that it can survive in more areas, so increasing the chances of establishment, and presenting a greater risk to the invaded ecosystem (van Lenteren *et al.*, 2008). *Harmonia axyridis* is a large species, with a correspondingly large appetite, which means that it provides better aphid control than many natives (Brown & Miller, 1998; Brown, 2011), but also that potential effects on native species may be greater (Brown *et al.*, 2011b; Roy *et al.*, 2012; Thomas *et al.*, 2013).

### 1.2.6. Impacts of Harmonia axyridis

The lack of predation pressure on the species, and its ability to feed on a wide range of prey species combined with its high fecundity and short generation time, means that *H. axyridis* can become abundant very quickly, and this can lead to impacts, both on humans and on the invaded ecosystems. Before aggregating in houses to overwinter, large numbers of *H. axyridis* collect within bunches of grapes in vineyards across North America, feeding on the fruit. When the bunches, complete with ladybird stowaways, are harvested and crushed, the ladybird's defensive secretions taint the wine with an unpleasant taste and odour, rendering it unfit for sale and causing significant economic loss to the vineyards (Galvan *et al.*, 2008).

The most serious effects of *H. axyridis* as an IAS are, however, on biodiversity, with the focus particularly on other members of the aphidophagous guild. There are 46 other species of the family Coccinellidae resident in Britain, and many are obligate carnivores, competing with the invader for food. The voraciousness of *H. axyridis*, particularly at the larval stage, means that virtually any species which come into contact with them are at risk, and many native species are very palatable to the invader (Ware & Majerus, 2008; Ware *et al.*, 2009). A major international study investigating the distribution and abundance of several common and widespread ladybird species in Western Europe (*Adalia bipunctata*, *A. decempunctata*, *Psyllobora vigintiduopunctata*, *Propylea quattuordecimpunctata*, *Halyzia sedecimguttata*, *Exochomus quadripustulatus*, *C. septempunctata*, and *Calvia quattuordecimguttata*) found that seven of the eight species investigated (all except *C.*

*septempunctata* ) either began to decline, or had a previous decline exacerbated, after *H. axyridis* established (Roy *et al.*, 2012).

The lack of vertebrate predators of ladybirds means that most occurrences of ladybird predation are of one ladybird larva preying on another, and the outcome is usually in favour of the larger individual (Ware & Majerus, 2008; Ware *et al.*, 2009). The large size of the final-instar larva of *H. axyridis* gives the invader an advantage over the majority of the species with which it comes into contact, with the exception of a couple of native species which are generally larger (*Anatis ocellata* L. and *Myzia oblongoguttata* L. (Coleoptera: Coccinellidae)). These species are both habitat specialists of conifers where, interestingly, *H. axyridis* does not yet dominate.

The species thought to be most at risk from the *H. axyridis* invasion is the 2-spot ladybird, *A. bipunctata*. A generalist species around half the size of *H. axyridis*, it too is found mainly in trees, feeding on aphids, in the same habitat and dietary niches as *H. axyridis* (Adriaens *et al.*, 2008). *Adalia bipunctata* even overwinters in the same sites as the invader, so overlaps with it throughout the year. Evidence of precipitous declines in the abundance of *A. bipunctata* in the invaded range of *H. axyridis*, (Brown, 2003; Roy *et al.*, 2012), laboratory studies indicating palatability (Ware & Majerus, 2008; Ware *et al.*, 2009) and anecdotal evidence of predation in the wild of *A. bipunctata* by *H. axyridis* provoked gut content analysis studies of the invader. These have found evidence for intra-guild predation (IGP) by 7-30% of *H. axyridis* on *A. bipunctata* in the field (Hautier *et al.*, 2008; Aebi *et al.*, 2011; Hautier *et al.*, 2011; Thomas *et al.*, 2013)

### 1.2.7. Predators, parasites and pathogens - what will stop the invader?

Ladybirds have aposematic colouration warning of their chemical defences, and have correspondingly few vertebrate predators; instead, they suffer from a range of parasites, parasitoids and pathogens (Cottrell & Shapiro-Ilan, 2008; Riddick *et al.*, 2009; Steenberg & Harding, 2009; Roy *et al.*, 2011a). In line with the predictions of the ERH, *H. axyridis* has a low parasite burden in the invaded range. The invasive British population is more resistant to the fungal pathogen *Beauvaria bassiana* ((Bals.-Criv.) Vuill.) than either *H. axyridis* from Japan (within the native distribution), or two species native to Britain, *A. bipunctata* or *C. septempunctata* (Roy *et al*., 2008).

Similarly, in Britain, several species of endoparasitic Hymenoptera and Diptera attack ladybirds. Some of these have a Holarctic distribution, and are known to attack *H. axyridis* in its native range: *Dinocampus (=Perilitus) coccinellae* (Schrank) (Hymenoptera: Braconidae) (Kuznetsov, 1997; Ware *et al.*, 2010); *Homalotylus flaminius* Dalman (Hymenoptera: Encyrtidae) (Kuznetsov, 1997); *Oomyzus scaposus* (=*Tetrastichus coccinellae*) Thomson (Hymenoptera: Eulophidae) (Kuznetsov, 1997) and *Medina separata* (Meigen) (Diptera: Tachinidae) (Kuznetsov, 1997) (often erroneously referred to as *M. luctuosa* (Hodek *et al.*, 2012)), while others (*Phalacrotophora fasciata* (Fallén) and *Phalacrotophora berolinensis* Schmitz (Diptera: Phoridae) (Disney & Beuk, 1997, Disney et al., 1994)) are European in distribution but are closely related to *Phalacrotophora philaxyridis* Disney (Diptera: Phoridae) which attacks *H. axyridis* in Japan (Disney, 1997). There is evidence that some natural enemies of ladybirds, notably *D. coccinellae*, *O. scaposus*, *P. berolinensis* and *P. fasciata*, can develop in the IAS, but these are only gradually beginning to utilise the abundant resource that *H. axyridis* provides, and it is parasitised at a far lower rate than equivalent native species (Firlej *et al.*, 2005; Berkvens *et al.*, 2008b; Koyama & Majerus, 2008; Hall *et al.*, 2009; Riddick *et al.*, 2009; Ware *et al.*, 2010).

### 1.2.8. Summary

IAS are clearly a major and multifaceted threat to native ecosystems, and *H. axyridis* is recognised as one of the worst (Vilà *et al.*, 2009). The species has been closely monitored since first establishing in the wild in North America in 1988 (Brown *et al.*, 2011a), but investigation of the large-scale impacts on native species has been hindered by a lack of long-term pre-invasion monitoring in much of the introduced range. In 2004, *H. axyridis* became established in south-east England, and the species' spread across Britain has since been monitored by the UK Ladybird Survey (UKLS; http://www.harlequinsurvey.org and http://www.ladybird-survey.org) (Brown *et al.*, 2008a). Britain has probably the best-studied flora and fauna in the world (Harding, 1992), and the ladybird recording scheme contains over 140,000 ladybird records from 1832 to the present day, both casual sightings and the results of systematic surveys (e.g. from county atlases). This provides an unparalleled opportunity to study an IAS in the process of invading, and to investigate its impacts on native species in the light of both historic patterns and other drivers of change.

## 1.3.1. Aims of the thesis

The primary objectives of this thesis are to quantify the responses of native UK ladybirds (with differing levels of habitat specialisation, climatic requirements and dietary preferences) to the invasion of *H. axyridis*, to establish the effect of *H. axyridis* when compared to other environmental drivers acting on native species, and to investigate the possible facilitation of *H. axyridis* invasion by natural enemy release.

Specifically:

1. What life-history and resource-use traits are important in driving the range characteristics of ladybirds in Britain?

2. What is the relative role of environmental factors, and life-history and resource-use traits, in driving the distributional trends of native ladybirds? Are native ladybirds with a high degree of ecological overlap with *H. axyridis* more likely to decline in invaded areas than are species which do not overlap?

3. Is the IAS *H. axyridis* parasitised at a lower rate at sites where it has been present for a shorter period, and is its parasitism rate lower than that of the functionally-similar native ladybird *C. septempunctata*, concomitant with the predictions of the ERH?

4. What effect does the diversity of the native ladybird community have on its resilience to invasion by *H. axyridis*, considered relative to environmental factors such as aphid abundance? At a local scale, what effect does *H. axyridis* have on the abundance of native ladybird species?

## 1.4.1. References:

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# Chapter 2. Using biological traits to explain ladybird distribution patterns

## 2.1. Abstract

**2.1.1. Aim** Species differ in terms of their respective life-history and resource-use traits (e.g. fecundity, diet niche breadth), and these differences are likely to affect the species' distribution patterns.  Determining the extent of this influence may lead to an improved understanding of the impacts of environmental change on biodiversity.  We investigated the extent to which traits can explain distribution patterns in the ladybird fauna (Coleoptera: Coccinellidae) of Great Britain.

**2.1.2. Location** The British mainland and inshore islands (Anglesey, the Isle of Wight and the Inner Hebrides).

**2.1.3. Methods** Distributions of 26 ladybirds resident in Britain were characterized in terms of their range size (from 2661 10-km grid-squares across Britain) and proportional range fill (at 10- and 50-km scales).  These were assessed relative to five traits (body length, elytral colour pattern polymorphism, voltinism, habitat specificity and diet breadth). The role of phylogenetic autocorrelation was examined by comparing the results of phylogenetic and generalized least-squares regressions.

**2.1.4. Results** Diet breadth was the only trait correlated with range size: species with broad diets had larger range sizes than dietary specialists.  Range fill was sensitive to the average recording intensity of a species across inhabited squares; models including both recording intensity and range size provided more explanatory power than models incorporating ecological traits alone.

**2.1.5. Main conclusions** Habitat specificity is often invoked to explain the distribution patterns of species, but here we found diet breadth to be the only ecological correlate of both range fill and range size.  This highlights the importance of understanding predator–prey interactions when attempting to explain the distribution patterns of predatory species.

Our results suggest that the diet breadth of predatory species is a better correlate of range size and fill than other measures such as habitat specificity.

## 2.2. Keywords

Coccinellidae, diet breadth, distribution, Great Britain, insects, niche breadth, range fill, range size, traits.

## 2.3. Introduction

The striking differences in the spatial distribution of taxonomically related species are intriguing, and understanding the processes governing these spatial distribution patterns is one of the central themes of ecology (e.g. Andrewartha & Birch, 1954; MacArthur, 1972). In recent years species distributions have been shifting in response to climate change (Hickling *et al.*, 2006; Poyry *et al.*, 2009) and so biogeographical studies have assumed an added significance. By exploring the relationships between species' distribution patterns and their life-history and resource-use characteristics, we may gain a better understanding of the biological mechanisms underpinning range size and fill (Ockinger *et al.*, 2010), which can inform conservation management.

Species' distribution patterns can be characterized either in terms of extent of occurrence (EOO, defined as the area encompassed by the outermost geographic limits of a species' occurrence) or area of occupancy (AOO, the area within those limits where the species actually occurs) (Gaston & Fuller, 2009). The AOO is usually measured in terms of the number of grid cells occupied (typically 1-, 10- and 100-km square grid cells), and can also be characterized by the proportion of the potential range that is actually occupied ('range fill' or 'aggregation') (Gregory & Gaston, 2000; Wilson *et al.*, 2004).

Life-history and resource-use characteristics (hereafter referred to as 'traits') are distinct, heritable characteristics of the species' phenotype. Traits of vertebrate and plant taxa have been widely studied and used in systematic biogeographical investigations to explain patterns of distribution (Pocock *et al.*, 2006; Van der Veken *et al.*, 2007; Bradshaw *et al.*, 2008; Blackburn *et al.*, 2009; Wang *et al.*, 2009; Astegiano *et al.*, 2010; Navarro *et al.*, 2010). Less consideration, however, has been given to assessing the relationship between multiple traits and the distribution patterns of invertebrates (e.g. Bräendle *et al.*, 2002).

Body size is often invoked as a species trait correlated with the distribution patterns of species (e.g. Juliano, 1983; Tingley *et al.*, 2010; Verberk *et al.*, 2010). However, body size is strongly correlated with other traits such as dispersal ability (Rundle *et al.*, 2007a) and trophic level (Romanuk *et al.*, 2011). Species that are generalists in terms of both dietary and habitat requirements occupy larger ranges and exhibit a greater proportion of range fill in many taxa, such as tropical sphingid moths (Beck & Kitching, 2007), and British bumblebees (Goulson *et al.*, 2005). The ability to survive in a wide range of habitats is strongly associated with commonness among native species (Cadotte & Lovett-Doust, 2002), and with an alien species' likelihood of becoming invasive (Blackburn *et al.*, 2009). The underlying factors determining the distribution of habitats (geology, land-use history, rainfall, etc.) are spatially structured, leading to patterns in the distribution of plant species (Pocock *et al.*, 2006), and thus also the distribution of species which feed on the different plant species. Therefore species which can utilize more of the available resources (food or habitat types) have a larger niche breadth (Gaston & Blackburn, 2000) and are likely to be able to survive and reproduce across a wider geographical range.

Variation in other life-history traits, e.g. polymorphism and voltinism (the number of generations per year), may also allow species to achieve larger range sizes and a greater degree of range fill. For example, species with high voltinism have, by definition, a shorter generation time than similar species with lower voltinism. This means they often achieve a higher reproductive rate, and so have more opportunities for dispersal per year, potentially resulting in greater colonization of marginal habitats, and therefore both larger range sizes and a greater degree of range fill (Altermatt, 2010). Polymorphic species, with the extended phenotypic range of several distinct forms, could potentially fill a wider niche, so colonizing larger areas. In the grasshoppers *Chorthippus parallelus* (Zetterstedt) and *Tetrix undulata* (Sowerby), for example, different colour morphs have been found to preferentially inhabit differing habitat types, and to vary in fecundity (Ahnesjo & Forsman, 2003, 2006; Unsicker *et al.*, 2008).

In this paper we investigate distribution patterns in relation to ecological traits (body size, habitat and dietary specialization, voltinism and phenotypic polymorphisms) for 26 species of ladybird (Coleoptera: Coccinellidae) resident in Great Britain. Ladybirds provide key ecological services as predators of crop pest insects (Day *et al.*, 2006; Costamagna & Landis, 2007; Obrycki *et al.*, 2009) and provide a novel contrast to previous studies of range characteristics which have focused on herbivores (Goulson *et al.*, 2005; Beck & Kitching, 2007; Unsicker *et al.*, 2008). Britain has an unparalleled history of biological recording schemes, with excellent spatial, temporal and taxonomic coverage, which presents the opportunity to carry out a detailed study on distribution patterns across a large geographical region.

By combining detailed trait data and biological records within the same model framework, we examine the relative importance of resource use (diet breadth, habitat specialisation) and life-history traits (body size, voltinism, and elytral colour pattern polymorphism) in explaining the distribution patterns (range size and fill) of ladybirds in Britain. European subfamilies and guilds of ladybirds are well represented in Britain and there is evidence to suggest that, as for other insect groups, responses to environmental change have been shown to be broadly equivalent between Britain and continental Europe (Parmesan *et al.*, 1999; Hill *et al.*, 2003).

## 2.4. Materials and Methods

### 2.4.1. Distribution data

The distribution data for the 26 ladybird species were taken from the UK Ladybird Survey (UKLS; www.harlequin-survey.org and www.ladybird-survey.org). The recording scheme contains over 140,000 ladybird records from 1832 to the present day, both casual sightings and the results of systematic surveys (e.g. from county atlases). Data are much less extensive for the 21 smaller inconspicuous coccinellids and these are excluded from the current analysis. All records used in this analysis have been identified to species by experts, either in the field or from a specimen or good photo submitted to the recording scheme.

The 30-year period from 1980 to 2009 (inclusive) was chosen as the study period because it encompasses the two main periods of intense recording activity. The first of these was during the

1980s and early 1990s, when widely publicized through the Cambridge Ladybird Survey (Majerus, 1994), and the second from 2004 to date when the arrival of the invasive alien ladybird *Harmonia axyridis* (Pallas) again raised the public profile of the recording scheme (Brown *et al.*, 2010; Roy *et al.*, 2011).

The range size of ladybirds was characterized as presence/absence at a 10-km grid square resolution over the 30-year period. The study area used was mainland England, Scotland and Wales, plus the inshore islands of Anglesey, the Isle of Wight and the Inner Hebrides, but excluding Northern Ireland and the offshore islands of Scilly, Man, Lundy, Shetland, Orkney, the Outer Hebrides and the Channel Islands, to avoid species' distribution patterns being influenced by the mosaic of land and sea common in archipelagos. This yielded a total of 86,259 records across the 26 ladybird species (ranging from eight records for *Hippodamia tredecimpunctata* L. to 21,761 for *Coccinella septempunctata* L.).

For each species, the proportion of squares occupied (counted from a nationwide total of 2662) was calculated. This was then logit-transformed to produce the variable 'range size'. This transformation has been shown to be a valid means of achieving normality in range size datasets which are bounded at the right and left of the distribution (Williamson & Gaston, 1999). Range fill was calculated from the 10-km grid square distribution pattern following a method developed by Condit *et al*. (2000), and used by Wilson *et al*. (2004, outlined in their supplementary material), modified here to account for the configuration of land and sea in coastal squares.

For each grid square, the number of occupied squares whose central point lies within circular radii of 10- or 50-km from the central point of the tested square was counted. This was divided by the total number of squares possible given a circle of this size (four or 80, respectively, minus any squares that were purely marine). This gives a value of between zero and one for each square-species combination (zero – no other squares occupied, one – all possible squares occupied). These square values were averaged for each species across the study area at each spatial scale to produce a range fill score, $D_x$ (where $x$ is the spatial scale).

### 2.4.2. Explanatory traits

Ecological traits with the potential to influence distribution characteristics were selected a priori on the basis of evidence from the literature. Overall, 352 sources were used (3–151 sources per species. An EndNote (Thompson Reuters, New York, USA) library of these references is available on request). Ecological traits were subdivided into life-history traits and resource-use traits as follows.

**1.** Life-history traits:

(i) Voltinism, defined as the number of generations per year for each species within Britain (ranging from one to three). There is variation within species between localities and years, so the modal value was used.

(ii) Elytral colour pattern polymorphism, characterized as a binomial presence/absence of melanic forms, following Roy *et al*. (2011). Individual-level variation within colour forms is not captured by this measure, but it avoids the problem of the different levels of study for different species.

(iii) Body size, defined as the length in mm from head to abdomen tip, calculated as the mid-point of the upper and lower body lengths quoted in Roy *et al*. (2011) (range from 3 to 7.8 mm). These are from Pope (1953) and Hawkins (2000), based on measurements from populations across Britain, except for *H. axyridis* which was taken from Kuznetzov (1997) and checked against specimens submitted to the recording scheme from across Britain. Although the full extent of within-species variation is not captured by this measure, we believe it provides a reasonable reflection of body size differences among species.

**2.** Resource-use traits:

(i) Habitat use, measured as the number of EUNIS level 2 habitat categories (ranging from 1 to11) which the species has been recorded from in Britain. The EUNIS (European Nature Information System) habitat classification is a pan-European classification of terrestrial, freshwater and marine habitats that has been developed for the European Environment Agency by the European Topic Centre on Biological Diversity (ETC/BD). The latest version can be accessed at http://eunis2.eea.eu.int/.

(ii) Diet breadth, measured as the number of prey families (ranging from 1 to 12) consumed by either adults or larvae of each species. Only natural diets were considered and laboratory diets such as drone powder, *Ephestia* eggs and agar-based diets were excluded.

We also included a measure of the recording intensity for each species. A potential problem with data from this kind of survey, with a high proportion of citizen science involvement, is that recording intensity may vary amongst species and across geographical regions. Some species are under-recorded, and the extent of this is likely also to depend on other traits such as habitat use, with, for example, strictly tree-dwelling species under-recorded. Although it is difficult to eliminate all such biases from the data, a range size-independent measure of recording intensity per species was included as a covariate in the pool of potential explanatory variables. This was the mean number of records across the 10-km squares occupied by a species.

### 2.4.3. Data analysis

The relationships between species traits and range characteristics were examined using generalized linear models (GLM; (McCullagh & Nelder, 1989) implemented in the statistical software program R, version 2.10.1 (R Development Core Team, 2009, Vienna, Austria). Three global GLMs were constructed with all five traits (and recording intensity) as explanatory variables and the range size, $D_{10}$ or $D_{50}$ in turn as the dependent variable. For the measures of range fill, $D_{10}$ and $D_{50}$, the best traits models were compared to models using range size and recording intensity as the only explanatory variables. This comparison was performed because although range size has been found to be a strong correlate of range fill in other taxa (Wilson *et al.*, 2004; Pocock *et al.*, 2006), the importance of primary biological traits that govern both range size and range fill was the focus of our study.

Collinearity between trait variables was tested for by calculating variance inflation factors (VIFs) for each trait in each model using the ‘car’ package (Fox & Weisberg, 2011). A common rule of thumb is that VIFs exceeding five indicate high levels of multiple collinearity. All the VIFs in the global GLMs were below five, hence severe collinearity was not observed and all traits were retained in the global models. A correlation analysis was also carried out on the traits, and found no significant correlation between them (Kendall’s $T < 0.7$ in all cases) (Table 2.1).

**Table 2.1** Table of Kendall's tau for correlations between the explanatory trait variables habitat use, diet breadth, body size, voltinism and elytral colour pattern polymorphism for British ladybirds. Significance of the tau values is indicated as * *P* =0.05, ** *P* = 0.01, *** *P* = 0.001 for these univariate comparisons.

| **Traits** | **Habitat use** | **Diet breadth** | **Size** | **Voltinism** |
|---|---|---|---|---|
| **Diet breadth** | 0.39 * | | | |
| **Size** | –0.09 | 0.02 | | |
| **Voltinism** | 0.29 | 0.30 | 0.26 | |
| **Polymorphism** | 0.11 | 0.46 ** | 0.16 | 0.29 |

The final GLM for each dependent variable was selected using a stepwise optimal model selection procedure based on corrected Akaike's information criterion ($AIC_c$) values, appropriate for small sample sizes (Akaike, 1974; McQuarrie & Tsai, 1998; Burnham & Anderson, 2002). To verify the robustness of the final model, a bootstrap procedure with 10,000 replicates was implemented in the 'boot.StepAIC' package within R (Austin & Tu, 2004). This approach uses random bootstrap samples drawn from the original dataset to investigate the variability of model selection under the step AIC stepwise algorithm (Austin & Tu, 2004). Within each bootstrap sample, forwards and backwards stepwise selection was used to determine the most parsimonious model, based on $AIC_c$ ($\Delta AIC_c$ of 2 required to incorporate an additional term). $AIC_c$ values were also calculated for the global and null (intercept-only model without any explanatory variables) models for each range characteristic to assess the importance of the final model. Goodness-of-fit was also calculated as deviance for each model.

To avoid the problem of phylogenetic autocorrelation, phylogeny was controlled for using a phylogenetic least squares approach (Freckleton *et al.*, 2002), and the performance of the phylogenetic and non-phylogenetic regression approaches compared using information criteria. Expected covariance between species was calculated on the basis of a phylogeny based on the taxonomy of Duff (2008), assuming equal branch lengths (computed after Grafen, (1989). The tree was created using the program TREEMAKER 1.3 (Crozier *et al.*, 2005) and the R package 'ape' (Paradis *et al.*, 2004). The R package 'CAIC' (Agapow & Isaac, 2002) was used to fit a phylogenetic generalized linear model (PGLM) (Freckleton *et al.*, 2002) equivalent to each of the three best GLMs, and selection between the PGLM and equivalent GLM for range characteristics was made on the basis of $\mathrm{AIC_c}$.

In the event that the PGLM performed better than the original GLM, Pagel's $\lambda$ (Pagel, 1999) was used to estimate the degree of phylogenetic autocorrelation in the model, where 0 indicates no phylogenetic signal in the data and 1 indicates perfect phylogenetic correlation. The pglmEstLambda function of the 'CAIC' package was used to identify the maximum likelihood value of the lambda parameter and to test whether this value was significantly different from 0 or 1 using a log-likelihood test (Agapow & Isaac, 2002; Freckleton *et al.*, 2002). Residuals from all models were checked for normality using normal probability graphs, and for heteroscedasticity by plotting residuals against fitted values.

Selection between PGLMs and GLMs was made on the basis of $\mathrm{AIC_c}$ and goodness of fit (deviance, $D^2$, adjusted for small sample sizes), which allows for comparison between models with different numbers of parameters. Univariate models were also constructed for each of the traits as a comparison for the best traits models.

## 2.5. Results

The degree of phylogenetic autocorrelation in relationships between range characteristics and ecological traits was found to be negligible in all three traits models and in the model for $D_{50}$ containing range size and recorder intensity only (Pagel's $\lambda$ not significantly different to 0), so GLMs were preferred for these. There was significant phylogenetic autocorrelation in the residuals of the model for $D_{10}$ containing range size and recorder intensity (Pagel's $\lambda = 0.627$, $P < 0.001$), so the PGLM was retained (Table 2.2).

Diet breadth was the only trait variable retained in the final model for range size, explaining 31.7% of the variation in range size between species ($F_{1,24} = 12.58$, $P = 0.0016$, slope = 0.32 ± 0.09, intercept = -3.71 ± 0.45) (Fig. 2.1a). A lack-of-fit sum of squares test was performed, which rejected the nonlinear model ($F_{6,18} = 0.2254$, $P = 0.9632$).

Range fill at a 10-km grid square resolution, $D_{10}$, was not significantly related to any ecological traits, but was significantly related to recording intensity (slope = 0.034 ± 0.006, intercept = 0.24 ± 0.04), which explained 54.6% of the variation in range fill at this scale ($F_{1,24} = 31.05$, $P < 0.001$) (Fig. 2.1b). The $D_{10}$ range size and recording intensity model, by contrast, explained 83.3% of the between-species variation ($F_{2,23} = 63.27$, $P < 0.001$) (Fig. 2.1b).

Three variables were significantly related to range fill at a 50-km grid square resolution, the traits model explaining 66.7% of the total variation between species in $D_{50}$ ($F_{3,22} = 17.65$, $P < 0.001$) (Fig. 2.1c). The significant variables were diet breadth, recorder intensity (both positively related to range fill), and body size (negatively related). The alternative model (containing just range size and recorder intensity as explanatory variables) explained 90.5% of the variation in $D_{50}$ ($F_{2,23} = 119.6$, $P < 0.001$) (Fig. 2.1c). The most important univariate variable in both the $D_{10}$ and $D_{50}$ models was range size (Table 2.3).

**Table 2.2** Comparative performance of models at predicting range characteristics of British ladybirds (range size and range fill at the 10-km and 50-km scale): global models (all traits: body size, voltinism, elytral colour pattern polymorphism, diet breadth, habitat use), null models (no explanatory traits: the null hypothesis), range size and recording intensity-only models, and the best ecological traits-only models. GLM = generalized linear model fitted by ordinary least squares regression. PGLM = GLM fitted using phylogenetic generalized least squares regression. Deviance is the model residual deviance. ΔAIC$_c$ (corrected Akaike's information criterion) was calculated from the model with the lowest AIC (marked by '–' in the ΔAIC$_c$ column). Models selected as 'best models' in the text are marked with *.

(a) Range size

| Model | Traits | Deviance (Adj. deviance) | AIC$_c$ | ΔAIC$_c$ | λ (PGLMs only) |
|---|---|---|---|---|---|
| Best trait PGLM | Diet breadth | 41.94 (43.64) | 91.82 | – | $5.099 \times 10^{-5}$ |
| Best trait GLM* | Diet breadth | 41.94 (43.64) | 93.31 | 1.49 | – |
| Null GLM | | 63.92 (63.92) | 101.70 | 9.88 | – |
| Global GLM | | 34.57 (34.57) | 105.66 | 13.84 | – |

(b) $D_{10}$ – Range fill at 10-km grid square resolution

| Model | Traits | Deviance (Adj. deviance) | AIC$_c$ | ΔAIC$_c$ | λ (PGLMs only) |
|---|---|---|---|---|---|
| Range size & recording intensity PGLM* | Range size, recording intensity | 0.19 (0.12) | –50.26 | – | 0.627 |
| Range size & recording intensity GLM | Range size, recording intensity | 0.18 (0.11) | –46.05 | 4.21 | – |
| Best trait PGLM | Recording intensity | 0.50 (0.48) | –23.27 | 26.99 | $6.662 \times 10^{-5}$ |
| Best trait GLM | Recording intensity | 0.50 (0.48) | –21.78 | 28.48 | – |
| Global GLM | | 0.36 (0.36) | –13.13 | 37.13 | – |
| Null GLM | | 1.15 (1.15) | –2.76 | 47.5 | – |

(c) $D_{50}$ – Range fill at 50-km grid square resolution

| Model | Traits | Deviance (Adj. deviance) | AICc | Δ AICc | λ (PGLMs only) |
|---|---|---|---|---|---|
| Range size & recording intensity PGLM | Range size, recording intensity | 0.11 (0.03) | –60.29 | – | $6.611 \times 10^{-5}$ |
| Range size & recording intensity GLM* | Range size, recording intensity | 0.10 (0.03) | –59.66 | 0.63 | – |
| Best trait GLM | Diet breadth, size, recording intensity | 0.36 (0.26) | –25.17 | 35.12 | – |
| Best trait PGLM | Diet breadth, size, recording intensity | 0.35 (0.26) | –24.9 | 35.39 | $6.004 \times 10^{-5}$ |
| Global GLM | | 0.33 (0.33) | –15.46 | 44.83 | – |
| Null GLM | | 1.20 (1.20) | –1.77 | 58.52 | – |

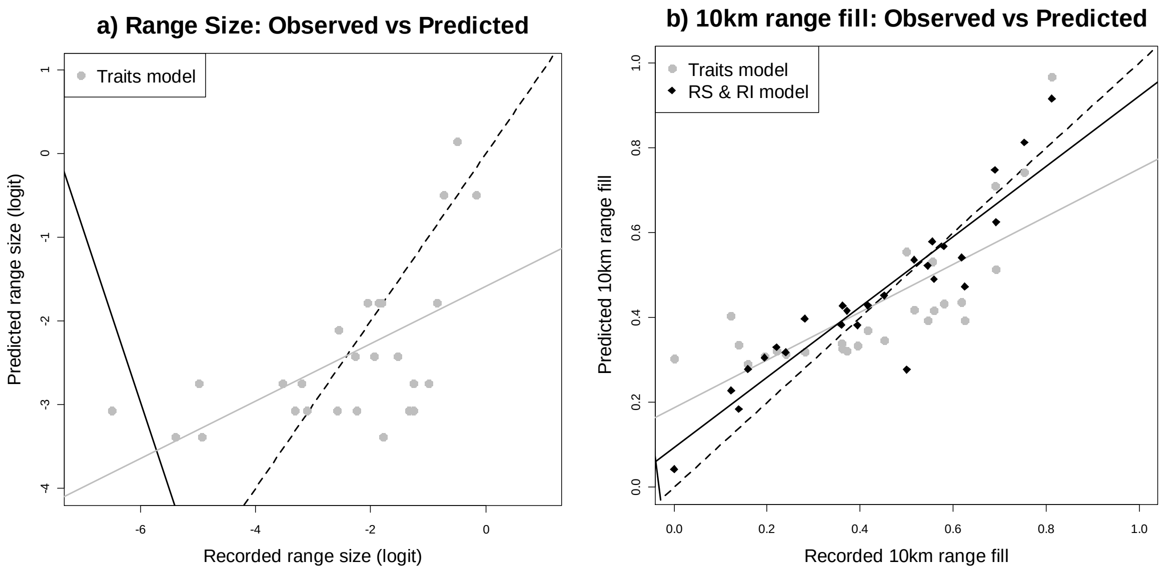
**Table 2.3** Univariate models showing the individual contribution of traits selected in the range fill models (recording intensity, diet breadth, body size) and range size, used as an explanatory trait. $\Delta \mathrm{AIC}_c$ (corrected Akaike's information criterion) was calculated as the difference between the $\mathrm{AIC}_c$ of the univariate models compared to that of the best model (at that grid square resolution), presented in Table 2.2

$D_{10}$ – Range fill at 10-km grid square resolution, component models

| Trait | Coefficients (± SE) | Intercept (± SE) | *t*-value | $R^2$ (adj. $R^2$) | *P*-value | $\mathrm{AIC}_c$ | $\Delta \mathrm{AIC}_c$ |
|---|---|---|---|---|---|---|---|
| Range size & recording intensity PGLM | RS: 0.08 (0.01)<br>RI: 0.02 (0.003) | 0.54 (0.05) | RS: 8.16<br>RI: 6.07 | 0.891 (0.881) | <0.001 | –50.26 | – |
| Range size | 0.11 (0.02) | 0.70 (0.04) | 7.20 | 0.683 (0.670) | <0.001 | –30.10 | 20.17 |
| Recording intensity | 0.03 (0.01) | 0.24 (0.04) | 5.57 | 0.564 (0.546) | <0.001 | –21.78 | 28.48 |

$D_{50}$ – Range fill at 50-km grid square resolution, component models

| Trait | Coefficients (± SE) | Intercept (± SE) | *t*-value | $R^2$ (adj. $R^2$) | *P*-value | $\mathrm{AIC}_c$ | $\Delta \mathrm{AIC}_c$ |
|---|---|---|---|---|---|---|---|
| Range size & recording intensity GLM | RS: 0.09 (0.01)<br>RI: 0.02 (0.003) | 0.42 (0.04) | RS: 9.41<br>RI: 6.25 | 0.912 (0.905) | <0.001 | –59.66 | – |
| Range size | 0.12 (0.01) | 0.61 (0.04) | 8.79 | 0.763 (0.753) | <0.001 | –36.67 | 23.66 |
| Recording intensity | 0.04 (0.01) | 0.12 (0.05) | 5.70 | 0.575 (0.557) | <0.001 | –21.45 | 38.84 |
| Diet breadth | 0.05 (0.01) | 0.10 (0.05) | 5.15 | 0.525 (0.505) | <0.001 | –18.54 | 41.75 |
| Body size | –0.01 (0.04) | 0.34 (0.18) | –0.15 | <0.001 (–0.041) | 0.88 | 0.78 | 61.07 |



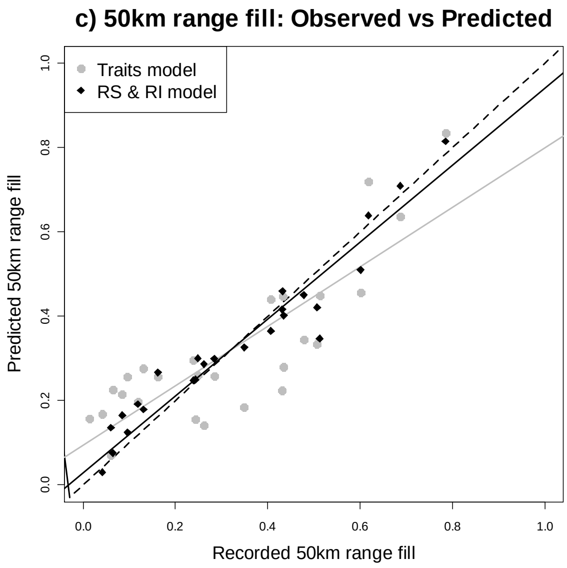


**Figure 2.1** Observed values vs. predicted values from the models of range characteristics for British ladybirds: (a) range size at a 10-km grid square resolution, (b) range fill at a 10-km grid square resolution ($D_{10}$), (c) range fill at a 50-km grid square resolution ($D_{50}$). Grey lines show the best traits models; black lines are the range size and recording intensity (RS & RI) models. Dotted lines are lines of equivalence, where observed = predicted.

## 2.6. Discussion

Diet breadth of ladybirds is positively correlated with range size. This is consistent with the literature for other groups, particularly Lepidoptera (Quinn *et al.*, 1997; Beck & Kitching, 2007; Garcia-Barros & Benito, 2010). The fact that this relationship is found across taxa, and is so strong for ladybirds, suggests that diet breadth should be considered a key niche-breadth determinant, particularly for predatory groups.

Many historical and geographical events can affect the realized distribution of species, so very precise predictions of range characteristics cannot be expected from species-specific traits alone (Beck & Kitching, 2007). Indeed, for range fill at both the 10- and 50-km grid-square level, models including range size and recorder intensity predicted observed distribution patterns far better than traits-only models. At the 10-km level, no resource-use or life-history traits were included in the minimum adequate models, although the relationship between range size and diet breadth suggests the latter may play a role in structuring the pattern of range fill and it is explicitly selected at the 50-km level. The diet breadth achieved by a species is intuitively dependent, in part, on the distribution of the prey organisms encountered in its range. In general, species that consume a greater number of species are likely to have a wider distribution than species with more limited prey ranges (although it is possible that a species which consumes a few common species could have a wider distribution than a species which feeds on several rare species, all other factors being equal). For example, *Ichneumon eumerus* (Wesmael) is a specialist parasitoid of two endangered lycaenid butterfly species, *Phengaris rebeli* (Hirschke) and *P. alcon* (Denis & Schiffermüller) (Thomas & Elmes, 1993; Tartally, 2005), but is considerably rarer than another specialist parasitoid wasp, *Listrodromus nycthemerus* (Gravenhorst), which feeds only on the widespread lycaenid butterfly *Celastrina argiolus* (L.) (Heath & Emmet, 1989; Revels, 2006).

It should be noted that no distinction was made between essential and alternative food sources within this analysis. Essential food sources are those on which the ladybird can feed solely while retaining the ability to mature and reproduce, whereas alternative food sources are those on which the ladybird can survive, but without reproducing (Hodek & Honek, 1996). The separation between essential and alternative food sources has only been categorized comprehensively for a few intensively studied species. Although individuals show decreased fecundity or increased mortality in the laboratory when fed solely on alternative prey (Hodek & Honek, 1996; Jalali *et al.*, 2009), an ability to prey on alternative species allows individuals to survive longer periods without essential prey (Hodek & Michaud, 2008). Across taxa, species with a wide diet breadth, including a wide range of alternative prey should therefore be able to persist for longer in less favourable areas than diet specialists, and exhibit a greater degree of range fill and a larger range size.

The phylogenetic signal visible in the range fill model residuals at the 10-km scale indicates that, at a local scale, closely related species share similar variance around the relationship between range fill and range size/recording intensity. This probably arises because species within the same families may be subject to a similar level of recording intensity, or may be sampled intensively within similar geographic areas. However, this phylogenetic signal was not present at the larger scales studied, reinforcing the view that different and potentially opposing factors may be important in determining species ranges at different spatial scales (Hamilton *et al.*, 2005; Cadotte *et al.*, 2009).

For range size, there is an apparent group of four species which are particularly restricted in Britain, compared to their distributions as predicted from their traits: these are *Hippodamia tredecimpunctata, Coccinella magnifica* Redtenbacher*, Henosepilachna argus* (Geoffroy), and *Coccinella quinquepunctata* L. *Hippodamia tredecimpunctata* has recently (2011) re-established itself as a breeding species on the south coast after being declared extinct in Britain in 1952, and is otherwise only recorded as an occasional immigrant (Comont & Willerton, 2012), while *H. argus* is a recent establishment in Britain (1997) and is only spreading slowly (Menzies & Spooner, 2000). Neither species is therefore likely to have a distribution in equilibrium with its environment in Britain. Neither *C. quinquepunctata* nor *C. magnifica* is currently restricted by historical factors, but each has specific habitat requirements (river shingle banks and an association with species of *Formica* ants, respectively). Both these species have restricted distributions in Britain when compared to the availability of their specific habitats, and all four species are likely to be limited in Britain by a combination of thermal and dispersal factors that are not captured by a coarse habitat categorisation system such as EUNIS. However, only *H. tredecimpunctata* is identified statistically as an outlier (Grubbs' test).

The other recent addition to the ladybird fauna of Britain, *H. axyridis*, is still found in fewer grid squares than is predicted by the models, but to a far smaller degree than the previous four species: *H. axyridis* is recorded from 1009 10-km grid squares (predicted 1428 grid squares, 70.66% colonization); *C. magnifica* 18/161, 11.18%; *C. quinquepunctata* 19/87, 21.84%; *H. argus* 12/87, 13.79%; *H. tredecimpunctata* 4/118, 3.39%. This is likely to result from the combination of extremely rapid colonization (Brown *et al.*, 2008) and a thorough recording through well-publicized citizen-science recording scheme targeted particularly at this species (http://www.harlequin-survey.org).

A species' spatial distribution pattern is the result of the interplay between its life-history traits coupled with the biotic and abiotic components of the environment (Lambdon, 2008). Our analyses cannot determine the causal mechanisms of the resulting correlations, but may allow predictions that help in the identification of conservation priorities and extinction risks as part of the wider process of identification of correlates of rarity. Whilst the direction of causality can be disputed, the large changes in AIC when traits are dropped from the best models strongly suggest that the selected traits all make independent contributions.

Our results demonstrate that, for ladybirds, species' resource-use traits better explain range size and fill than do life-history traits. Species that can utilize a greater range of prey species have larger range sizes and a greater degree of range fill (at the 50-km grid square level). A life-history trait, body size, was important at the 50-km grid square level of range fill, however, with smaller species exhibiting a greater degree of range fill than larger species, which is likely to result from the correlation between body size and other traits, particularly dispersal ability.

Dispersal ability is likely to be important for ladybirds and other predatory beetle species, as it is for freshwater invertebrates such as the Odonata (and, to a lesser extent, Plecoptera and Ephemeroptera), where it has been suggested that dispersal ability, and in particular wing size, is the trait which links size and distribution patterns (Malmqvist, 2000; Rundle *et al.*, 2007a; Rundle *et al.*, 2007b). Species with more limited dispersal abilities, such as the smaller ladybirds, tend to spread in smaller increments, creating a more clumped distribution pattern, with high levels of range fill when compared to more dispersive species.

Unfortunately, it did not prove possible to include a direct measure of dispersal ability as an explanatory variable, as this information is lacking for most ladybird species. Some ladybird species also possess wing-length polymorphisms (fully-winged, brachypterous, apterous forms), which will clearly have an effect on a species' dispersal ability, and thus also on distribution patterns, but this is rare and only one species in Britain is known to exhibit brachyptery: *Subcoccinella vigintiquattuorpunctata* (L.) (Pope, 1977). This would be an important parameter to include for taxa which exhibit this variation, e.g. the Orthoptera or Heteroptera.

A potential problem with data from this kind of survey, with a high proportion of citizen science involvement, is that recording intensity may vary among species. Widespread, common species are frequently better-studied and better-recorded than are rare species, and recorder intensity was an important contributor to range fill, with more intensively recorded species having a higher proportion of range fill than less intensively recorded species. It is interesting to note, however, that recording intensity was not a significant variable in the range size model, possibly because ladybirds are charismatic species that are all quite well recorded.

## 2.7. Conclusions

Our results suggest that a species' ability to feed on a wide range of prey taxa can be a better correlate of both range fill and range size than more usual measures, such as habitat specificity. This may be particularly true of predatory taxa, where the presence of prey species is a major factor in determining habitat suitability (Kruess & Tscharntke, 1994; Verberk *et al.*, 2010) (22 of the 26 ladybird species resident in Britain are primarily carnivorous, and only one species has not been recorded as a facultative predator). While species such as *H. argus* are likely to remain comparatively geographically restricted through reliance on a single plant species, other species may be threatened in the short to medium term not only by their narrow diet breadth but also by their niche overlap with dominant competitors such as *H. axyridis.*

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# Chapter 3. Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: Coccinellidae).

## 3.1. Abstract

Five main drivers of population declines have been identified: climate change, habitat degradation, invasive alien species, overexploitation and pollution. Each of these drivers interacts with the others, and also with the intrinsic traits of individual species, to determine species' distribution and range dynamics.

We explored the relative importance of life-history and resource-use traits, climate, habitat, and the invasive alien species (IAS) *Harmonia axyridis* in driving local extinction and colonisation dynamics across 25 ladybird species (Coleoptera: Coccinellidae). Species were classified as continually present, continually absent, extinct, or colonising in each of 4642 1-km$^2$ grid squares. The spatial distribution of local extinction and colonisation events (in the grid squares) across all species' ranges were related to ecological traits, overlap with *H. axyridis,* climate, and habitat factors within Generalised Linear Models (GLMs). GLMs were also used to relate species' traits, range characteristics, and niche overlap with *H. axyridis* to extinction and colonisation rates summarised at the species level.

Bayesian Model Averaging was used to account for model uncertainty, and produce reduced sets of models which were well-supported by data. Species with a high degree of niche overlap with *H. axyridis* suffered higher extinction rates in both analyses, while at the spatial scale extinctions were more likely and colonisations less likely in areas with a high proportion of urban land cover. In the spatial analysis, polymorphic species with large range sizes were more likely to colonise and less likely to go extinct, and sunny grid squares were more likely to be colonised. Large, multivoltine species and rainy grid squares were less likely to colonise or be colonised.

In conclusion for ladybirds, extinction and colonisation dynamics are influenced by several factors. The only factor that both increased the local extinction likelihood and reduced colonisation likelihood was urban land cover, while ecological overlap with *H. axyridis* greatly increased extinction rates.

Continued spread *of H. axyridis* is likely to adversely affect native species and urban areas may be particularly vulnerable.

**3.2. Keywords:** Climate, Coccinellidae, colonisation, extinction, habitat, niche overlap, traits

## 3.3. Introduction

Increased population-level, regional, and global extinctions of species is a major concern (Thomas *et al.*, 2004). Long-term declines have been reported for well-studied insect taxa such as Lepidoptera (Fox *et al.*, 2011; Fox, 2012), Hymenoptera (Goulson *et al.*, 2005; Connop *et al.*, 2009) and Coleoptera (Roy et al. 2012). Five main drivers of population declines have been identified: climate change, habitat degradation, invasive alien species, overexploitation and pollution (Millennium Ecosystem Assessment, 2005; UK National Ecosystem Assessment, 2011). Each of these drivers interacts with the others, and also with the intrinsic traits of individual species, to determine species' distribution and range dynamics (Brook *et al.*, 2008). As short-lived ectotherms, many of which are reliant on a single host or prey species, insects are likely to respond particularly quickly to changes in these drivers (McIntyre *et al.*, 2001; Musolin, 2007).

Controversy has arisen over whether biological invasion is a leading cause of species extinction (e.g. Gurevitch & Padilla, 2004; Ricciardi, 2004) since evidence cited in favour of this hypothesis was based on simple spatial or temporal correlations between dominance of invasive alien species and native species decline in degraded ecosystems (Didham *et al.*, 2005). Recent work, largely in marine systems, has highlighted the necessity of considering invasion impacts alongside competing causes of extinction within the same analytical framework (e.g. Light & Marchetti, 2007) and of examining extinction at the population level rather than species level (Ricciardi, 2004).

Relating population changes to ecological characteristics (traits) across taxa (Tremlova & Munzbergova, 2007; Barbaro & van Halder, 2009; Poyry *et al.*, 2009; Bell & Sotka, 2012; Salido *et al.*, 2012) has shed some light on the traits that make species more vulnerable to environmental change and permitted the design of indicator species for monitoring change (e.g. the habitat-based wild bird indicators used in the UK (Newson *et al.*, 2006). However, few studies have investigated how traits and environmental factors interact to govern species' range dynamics. These interactions have implications for predicting where, and under which conditions, species loss is likely to occur and for understanding how community composition and ecosystem function may alter under environmental change (Webb *et al.*, 2010). Long-term and large-scale presence-absence distribution datasets, such as those compiled through the Biological Records Centre (www.brc.ac.uk) within the Centre for Ecology & Hydrology, offer opportunities to understand how traits and environmental factors influence distribution changes through their impacts on the probability of local extinction and colonisation events (Doxford & Freckleton, 2011).

The breadth of trait characteristics amongst British ladybirds (Coleoptera: Coccinellidae) makes them an ideal group to investigate trait-environment relationships, particularly as range characteristics have already been shown to be dependent on ecological traits, such as diet breadth (Comont *et al.*, 2012). As well as being subject to land use and environmental changes of varying intensity across Britain, native ladybird communities are also currently being disrupted by the invasion of *Harmonia axyridis* (Pallas), a large ladybird species native to temperate Asia. This species has been widely used as a biocontrol agent against pest aphids and is now an Invasive Alien Species (IAS) in more than 30 countries worldwide (van Lenteren *et al.*, 2008; Brown *et al.*, 2011a). It became established in Britain in 2004, and has been implicated in the declines of native ladybirds (Ware & Majerus, 2008; Brown *et al.*, 2011b; Roy *et al.*, 2012). The diversity of habitat and dietary preferences amongst native ladybird species provides a spectrum of overlap with the ecological niche of the invasive alien ladybird species, *H. axyridis*. This provides an ideal system for understanding the importance of invasion versus abiotic drivers and trait-environment interactions in underpinning species declines. We investigated the influence of habitat, climate and an IAS on local extinctions and colonisations of ladybirds within Britain with the following specific objectives:

(i) to understand whether species-level rates of local extinction/colonisation and proportional range change, summarised across their ranges, are predictable from biological traits;

(ii) to understand the relative importance of biological traits, environmental factors and trait-environment interactions in determining where particular species are vulnerable to local extinction or able to colonise.

## 3.4. Methods

### 3.4.1. Distribution data

The distribution data for all ladybird species were taken from the UK Ladybird Survey (UKLS; www.harlequin-survey.org and www.ladybird-survey.org). The recording scheme contains over 140,000 ladybird records from 1832 to the present day, both casual sightings and the results of systematic surveys (e.g. from county atlases). Data are much less extensive for the 21 smaller inconspicuous coccinellids and these are excluded from the current analysis. All records used in this analysis have been verified to species either in the field or from a specimen or photograph submitted to UKLS.

Ladybird distribution was characterised as presence/absence at a 1-km$^2$ grid square resolution across mainland England, Scotland and Wales (i.e. excluding Northern Ireland and the offshore islands of Scilly, Man, Lundy, Shetland, Orkney, the Outer Hebrides and the Channel Islands). These were then aggregated into two periods: 1991-2003 (before *H. axyridis* establishment), and 2004-2010 (post-establishment), such that each database row represented a unique species-1-km$^2$-period combination.

For analysis, we included only 1-km$^2$ grid squares which were 'well-sampled' in both periods, such that if at least three species were recorded in a particular grid square-period combination, we inferred that all other species were absent (after Biesmeijer *et al.*, 2006; Roy *et al.*, 2012). These criteria restricted our dataset to a smaller subset of high-quality data (Roy *et al.*, 2012), 4642 1-km$^2$ grid squares in total (Table 3.1). *H. axyridis* was removed from the dataset as a species because, as a recent colonist, its distribution was not at equilibrium during the study period.

**Table 3.1.** Summary of ladybird distribution in Britain. Data collected by volunteers and collated through a national recording scheme, the UK Ladybird Survey: each record is one observation of a ladybird species within a 1-km$^2$ grid square in a year. Our analyses were based on a filtered data set which excluded *Harmonia axyridis*, and consisted of records from 1-km$^2$ grid squares which were 'well-sampled' i.e. contained at least three species records in both of the study periods (1991-2003 and 2004-10).

| **Category** | **Count** |
|---|---|
| Total number of records (all years, all species) | 106,952 |
| Total number of surveyed 1-km$^2$ 1991-2010 | 18,546 |
| Total number of 1-km$^2$ used for analysis | 4,642 |
| Number of 1-km$^2$ used for local extinction analysis | 2,704 |
| Number of 1-km$^2$ used for colonisation analysis | 4,642 |
| Number of 1-km$^2$ with *Harmonia axyridis* recorded present | 1,978 |

### 3.4.2. Environmental and trait data

Climate and habitat predictors were obtained for each 1-km$^2$ grid square within the subset, along with the year that *H. axyridis* was first recorded in each grid square (if at all). Habitat predictors were taken from the 1990, 2000, and 2007 editions of the Land Cover Map (LCM) of Great Britain (Barr *et al.*, 1993; Fuller *et al.*, 2002; Smith *et al.*, 2007). Although the maps were created using different methods and classification groupings, the data were extracted at the aggregate class level, where such differences were minimal. Four habitats were chosen (broadleaf woodland, coniferous woodland, natural grassland and urban areas), as these cover the major habitats for the majority of the ladybirds in Britain. Aggregate classes rejected were either of extremely limited value for ladybirds (e.g. freshwater, saltwater, and coastal), or of value only to a few rare species (e.g. the 'mountain, heath and bog' category, which is of value mainly to the scarce *Coccinella hieroglyphica* L.). A mean percentage cover value was taken for each habitat in each grid square, averaged across each of the three LCM editions (Table 3.2). We predict that a high proportion of the four specified habitats (broadleaf woodland, coniferous woodland, natural grassland and urban) within a grid square will promote colonisation and limit extinction across ladybirds (Hodek *et al.*, 2012).

Climate data were taken from the Met Office's UK Climate Projections (UKCP09) dataset (downloadable from http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). Three predictors were chosen for the analysis: rainfall, sunshine and growing degree-days (GDD) (Table 3.2). We predict that decreasing rainfall, increasing sunshine and growing degree-days will be positively associated with colonisation of a grid square, and conversely negatively associated with extinction in a grid square.

The invasion and *H. axyridis* overlap traits include measures of the dietary and habitat niche overlap between *H. axyridis* and each other ladybird species. The number of years that *H. axyridis* has been present in each grid square was calculated as a geographic measure of impact. We hypothesise that the effect of *H. axyridis* is likely to scale with duration of temporal overlap (i.e., worse impact the longer the species have co-occurred within the grid square), and with the intimacy of ecological overlap (i.e., species with a greater niche overlap will be affected to a greater extent).

The Bray-Curtis similarity index (Somerfield, 2008) was used to measure habitat use and diet overlap of each species with *H. axyridis* (cf. Adriaens et al. 2008). This is the inverse of the Bray-Curtis index of dissimilarity, and is calculated as 1/ $BCD_{i,j}$, where $BCD_{i,j}$ is the Bray-Curtis dissimilarity score between species *i* and *j*, *k* is the resource use measure (number of species eaten in family *y* or presence/absence in habitat *y*), and *n* is the total number of species. This index ranges between 0 (no similarity, i.e. no resource overlap between species) and 1 (identical resource use). See Appendices S1 and S2 in Supporting Information.

Ecological traits with the potential to influence population and distribution characteristics were selected *a priori* from the literature (Table 3.2). We predict that large, polymorphic, multivoltine species with a wide diet breadth but with limited overlap with *H. axyridis* are more likely to colonise and resist local extinction in comparison to species not exhibiting these traits.

To account for variation in recording intensity amongst species and geographic regions, range size and recording intensity (measured at both the species and grid-square levels) were included as covariates (Doxford & Freckleton, 2011) (Table 3.2).

### 3.4.3. Modelling approach

#### 3.4.3.1. Spatial models

We performed a spatially-explicit, local scale (1-km$^2$ grid squares) analysis to consider the relative importance of environmental factors (climate and habitat, recording intensity), species traits, range characteristics, and measures of niche overlap with *H. axyridis* in determining where ladybirds are vulnerable to local extinction or able to colonise (hereafter referred to as spatial models). From species' presence or absence in the two periods, we determined whether each species had colonised, persisted, gone locally extinct, or never occupied each 1-km$^2$ grid square. Extinction/persistence and colonisation/continued absence were then extracted and used as binary response variables in separate analyses of local extinction and colonisation. For these, we used generalised linear models (GLMs) with Bernouilli errors (special case of binomial where there is a single observation of an event per sample unit) fitted using R version 2.15 (R Development Core Team, 2011). Interactions included were between 'years with *H. axyridis'* and the habitat use and dietary niche overlap predictors, as overlap with *H. axyridis* would only be relevant if *H. axyridis* was present in the grid square. Model residuals were assessed for spatial and phylogenetic autocorrelation using the package ‘ape’ version 3.0-6 within R (Paradis *et al.*, 2004). Though both species and grid square effects are incorporated in these models, for convenience we hereafter refer to these as local extinction and colonisation models.

To reduce the uncertainty implicit in model predictor selection, Bayesian Model Averaging (BMA) was applied throughout, as implemented in the R package ‘BMA’, version 3.15.1 (Raftery *et al.*, 2012). Rather than try to identify a single best model, BMA averages over a set of competing well-fitting alternatives, weighted by their posterior probabilities (the likelihood of each model being the best fit to the data) (Raftery, 1995). This package uses the ‘leaps and bounds’ algorithm to identify up to 1000 good models per number of predictors, which were fitted and then further reduced to a set of well-fitting models by the Occam’s window method, whereby models 20 times less likely than the best-supported model were discarded (Madigan & Raftery, 1994). All models in the well-fitting set have Bayesian Information Criteria (BIC) values within 6 BIC units of the model with the highest posterior probability. As a measure of the overall conformity of the top models to the data, the Area Under the Curve (AUC) (Fielding and Bell 1997) statistic is calculated. AUC ranges between 0.5 and 1.0, with 0.5 indicating no discrimination ability; values below 0.7 are low, values between 0.7 and 0.9 are useful in some cases, and values > 0.9 indicate high discrimination (Swets 1988).

#### 3.4.3.2. Species models

We used binomial GLMs to examine which species-level traits were best correlated with local extinction and colonisation rates, calculated for each species at a national scale by summarising the 1-km$^2$-scale data. Local extinction rate was calculated as the total number of extinction events out of the number of grid squares reported occupied in the first period (formatted as a two column binomial dependent variable – number of extinctions, number of sustained presences) , whilst colonisation rate was the total number of colonisation events out of the number of grid squares unoccupied in the first period (formatted as a two column binomial dependent variable – number of colonisations, number of sustained absences).

**Table 3.2.** The traits and environmental predictors used to model local-scale extinction and colonisation in the British ladybirds. Climate data were extracted from the Met Office's UK Climate Projections (UKCP09) dataset, and habitat data from the 1990, 2000, and 2007 editions of the Land Cover Map of Great Britain at the aggregate class level. Resource use and life-history predictors were taken from the literature (352 sources examined, see Comont *et al* (2012) for details), and ecological overlap predictors were calculated from data in the literature. Range characteristics and invasion predictors were calculated from the distribution data of the UK Ladybird Survey (1991-2010).

| **Predictor type** | **Predictor** | **Description** |
|---|---|---|
| *Environmental* | | |
| Climate | Growing degree-days | 20-year mean (1987-2006) of annual degree-days over 5.5°C, per 1-km$^2$ grid square. |
| | Sunshine | 20-year mean (1987-2006) of annual hours of sunshine, per 1-km$^2$ grid square. |
| | Rainfall | 20-year mean (1987-2006) of annual millimetres of rainfall, per 1-km$^2$ grid square. |
| Habitat | Broadleaf woodland | % cover of broadleaf woodland per 1-km$^2$ grid square. |
| | Coniferous woodland | % cover of coniferous woodland per 1-km$^2$ grid square. |
| | Natural grassland | % cover of unimproved grassland per 1-km$^2$ grid square. |
| | Urban | % cover of urban and suburban habitats per 1-km$^2$ grid square. |
| Invasion | Years with *H. axyridis* | Number of years between the arrival of *H. axyridis* in a grid square and the end of the study period (0 if never present in a grid square). |
| *Traits* | | |
| Ecological overlap with *H. axyridis* | Dietary niche overlap | Calculated as an inverse Bray-Curtis dissimilarity index, such that 1 indicates the same diet composition and 0 indicates no shared dietary items between *H. axyridis* and native species. See Appendix S1. |
| | Habitat niche overlap | Calculated as an inverse Bray-Curtis dissimilarity index, such that 1 indicates the same habitat use and 0 indicates no shared habitats between *H. axyridis* and native species. See Appendix S2. |
| Resource use | Diet breadth | Number of prey families (ranging from 1 to 12) recorded as consumed by either adults or larvae of each species. Only natural diets were considered and laboratory diets such as drone powder, *Ephestia* eggs and agar-based diets were excluded. |
| Life-history | Polymorphism | Elytral colour pattern polymorphism, characterised as a binomial presence/absence of melanic forms, following Roy *et al*. (2011). |
| | Body size | Length (mm) from head to abdomen tip, calculated as the mid-point of the upper and lower body lengths quoted in Roy *et al*. (2011) (3 to 7.8 mm). Data from Pope (1953) and Hawkins (2000), based on measurements from populations across Britain, except for *H. axyridis* which was taken from Kuznetzov (1997) and checked against specimens submitted to the recording scheme from across Britain. |
| | Maximum voltinism | The maximum number of generations per year recorded in the field in Britain for each species. |
| Range characteristics | Recording intensity | Mean number of records per 1-km$^2$ grid square for each species (2004-2010). |
| | Range size | Number of grid squares that each species was recorded from (2004-2010). |

## 3.5. Results

Ladybirds were more likely to go extinct than colonise over the study period. The mean local extinction rate for the species models was 0.84 (SD ± 0.20) (where 1 is complete local extinction and 0 is complete local persistence) and the mean colonisation rate was 0.098 (± 0.15). Species only occurred in a fraction of the studied grid squares: each species colonised 161.4 (± 194.0) grid squares on average, but went locally extinct in a mean of 210.44 (± 242.9) squares.

The BMA set (all the models with a BIC within six units of the best model) for species-level local extinction rates contained eight models, with a cumulative posterior probability (the likelihood of each model being the best fit to the data) across the best five models of 0.891 (see Appendix S1). Within this model set four predictors had a significant impact on species extinction rates, i.e. had a greater than 90% probability that the coefficient was not equal to 0 (p!=0) (Table 3.3). This showed that species with a higher dietary niche overlap with *H. axyridis*, a lower maximum voltinism, a lower range size or a lower recording intensity were more likely to go extinct.

**Table 3.3. Model-averaged coefficients for trait effects on species-level local extinction, colonisation and net change rates (in 1-km$^2$ grid squares) for British ladybirds.** Values presented are means across each Bayesian Model Averaging (BMA) model set. For each predictor, EV is the coefficient, averaged across models, SD is the standard deviation of the coefficient, p!=0 is the probability that the coefficient is not equal to zero (i.e., the probability that that predictor should be included in the model), and % included is the percentage of models within the BMA set which include that predictor. Terms in bold are those which have a greater than 90% probability that the coefficient (EV) is not equal to 0, terms in italics are where this probability is between 80 and 90 percent.

| **Trait group** | **Predictors** | **Local extinction rate** | | | | **Colonisation rate** | | | | **Net change rate** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **p!=0** | **% included** | **EV** | **SD** | **p!=0** | **% included** | **EV** | **SD** | **p!=0** | **% included** | **EV** | **SD** |
| | (Intercept) | **100** | **100** | **1.27** | **0.06** | **100** | **100** | **-0.07** | **0.03** | **100** | **100** | **0.03** | **0.05** |
| Ecological overlap with *H. axyridis* | Dietary niche overlap | **100** | **100** | **0.30** | **0.09** | 11.2 | 20.0 | 0.00 | 0.01 | *80.0* | *72.9* | *-0.11* | *0.08* |
| | Habitat niche overlap | 12.0 | 22.2 | -0.00 | 0.03 | 28.3 | 36.0 | -0.01 | 0.03 | 19.5 | 37.1 | -0.00 | 0.04 |
| Resource use | Diet breadth | 11.6 | 22.2 | -0.00 | 0.00 | 15.9 | 28.0 | 0.00 | 0.00 | 24.1 | 40.0 | 0.00 | 0.00 |
| Life history | Body size | 14.8 | 33.3 | -0.00 | 0.01 | *87.9* | *80.0* | *0.01* | *0.01* | 33.2 | 34.3 | 0.00 | 0.01 |
| | Polymorphism | 14.9 | 33.3 | 0.00 | 0.01 | 10.0 | 16.0 | 0.00 | 0.00 | 61.6 | 58.6 | -0.03 | 0.03 |
| | Maximum voltinism | **100** | **100** | **-0.19** | **0.05** | 9.8 | 16.0 | -0.00 | 0.00 | 57.6 | 51.4 | 0.03 | 0.04 |
| Range characteristics | Range size | 9.1 | 11.1 | -0.00 | 0.00 | **100** | **100** | **0.00** | **0.00** | **94.0** | **85.7** | **0.00** | **0.00** |
| | Recording intensity | **100** | **100** | **-0.08** | **0.01** | 25.6 | 36.0 | 0.00 | 0.00 | 28.4 | 30.0 | -0.00 | 0.01 |

**Table 3.4. Results of colonisation and local extinction of British ladybirds obtained by Bayesian Model Averaging (BMA) of spatial Generalised Linear Models (GLMs).** Model diagnostics include the area under the receiver operating characteristics curve (AUC) and the posterior probabilities that the model terms are equal to zero, compared to the null model.

| **Model diagnostics** | **Local extinction** | **Colonisation** |
|---|---|---|
| No. data points | 6276 | 51734 |
| No. species | 25 | 25 |
| No. 1-km$^2$ | 2699 | 4642 |
| No. models in BMA dataset | 16 | 11 |
| Posterior probability of best model | 0.163 | 0.260 |
| Cumulative posterior probability of BMA dataset best five models | 0.612 | 0.811 |
| AUC | 0.854 | 0.900 |
| AIC best model (AIC null model) | 4201 (4542) | 19808 (22974) |
| BIC (null model) | 4282 (4562) | 19941 (23001) |
| LogLik (null model) | -2089 (-2268) | -9889 (-11484) |
| Deviance (null model) | 4177 (4536) | 19778 (22968) |

The species-level colonisation rate BMA set contains seven models, the best five of which have a cumulative posterior probability of 0.921 (see Appendix S2). Within this model set five predictors had a significant impact on species colonisation rates (Table 3.3). Species a higher habitat overlap with *H. Axyridis* and which had larger range sizes or were small bodied were more likely to colonise new grid squares, (Table 3.3).Species that were recorded less intensively and had a lower maximum voltinism were more likely to colonise new grid squares, as well as being more likely to go extinct across their distributions (see above).

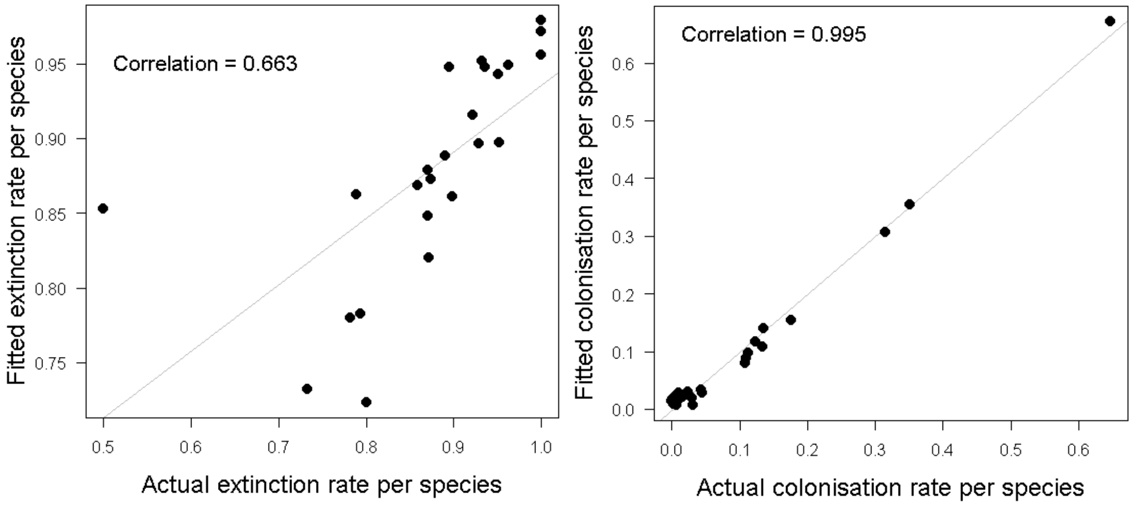
The BMA set for spatial models of local extinction contained 16 models and had a cumulative posterior probability for the best five models of 0.612. The equivalent set for spatial models of colonisation contained 11 models (best five models cumulative posterior probability 0.811) (Table 3.4). Both analyses had a good discriminatory ability (high Area Under Curve (AUC) score), and were well calibrated (Table 3.4).

The BMA model set for spatial models of local extinction contains six predictors with a >90% probability that the coefficient is not equal to zero. Local extinctions were more likely in grid squares with a higher proportion of urban area. Species were also more prone to local extinction if they were had smaller range sizes, were not facultatively multivoltine, or had a greater dietary niche overlap with

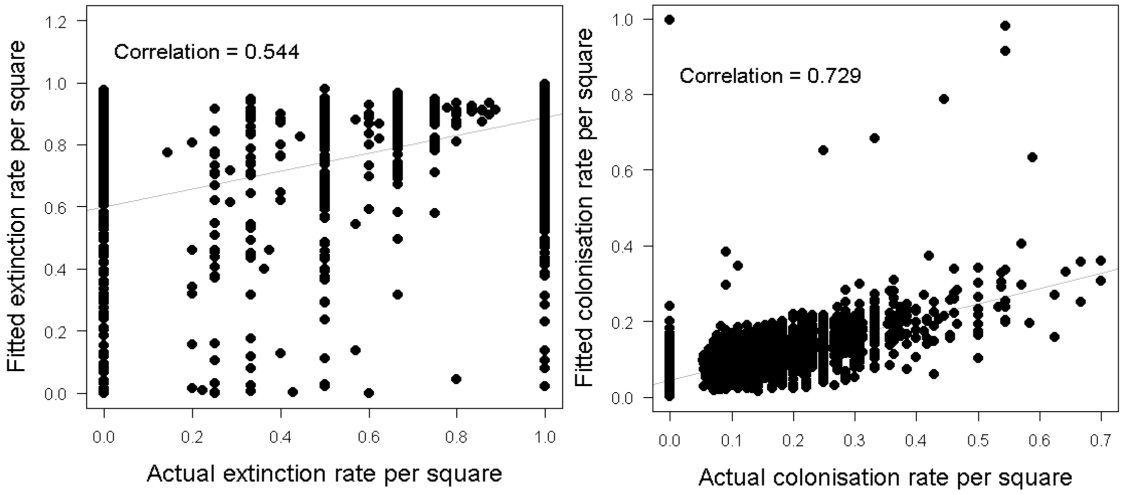
*H. axyridis* and in squares that were recorded less intensively. Local extinctions were negatively correlated with the interaction between habitat niche overlap with *H. axyridis* and the number of years that the invader was present in the grid square, suggesting that species which share habitat preferences with *H. axyridis* were less likely to be lost from a grid square when the invader has been present for a longer period (Table 3.5).

**Figure 3.1. Goodness-of-fit plots for the models of local-scale extinction and colonisation in the British ladybirds, actual values plotted against fitted values extracted from the best models (a. local extinction per species, b. colonisation per species, c. local extinction per 1-km$^2$ grid square, d colonisation per 1-km$^2$ grid square).** Expected rates for individual species and grid squares were calculated from the means of the fitted probabilities of the best model (Cox, 1970).

**a) Actual vs fitted extinction per species** **b) Actual vs fitted colonisation per species**



**c) Actual vs fitted extinction per grid sq.** **d) Actual vs fitted colonisation per grid sq.**



The BMA set for spatial models of colonisation contains ten predictors with a >90% probability that the coefficient is not equal to zero. Colonisations were more likely in grid squares which received more sunshine and less rainfall, and which contained a lower proportion of urban areas. Species were more likely to colonise new grid squares if they had a smaller body size, had larger range sizes, were not facultatively multivoltine, had a smaller diet breadth, or were polymorphic and in squares that were recorded more often,. Colonisation was also positively correlated with the interaction between habitat niche overlap and years with *H. axyridis* (0.26 ± 0.026), suggesting species which share habitat preferences with *H. axyridis* were more likely to colonise grid squares where the invader has been present for longer (Table 3.5).

**Table 3.5. Model-averaged coefficients for environmental and trait effects on the 1-km$^2$-scale probabilities of local extinction and colonisation in British ladybirds (spatial models).** Values presented are means across each Bayesian Model Averaging (BMA) model set. For each predictor, EV is the coefficient, SD is the standard deviation of the coefficient, p!=0 is the probability that the coefficient is not equal to zero, and % included is the percentage of models within the BMA set which include that predictor. Terms in bold are those which have a greater than 90% probability that the coefficient (EV) is not equal to 0, terms in italics are where this probability is between 80 and 90 percent.

| | | **1-km$^2$ extinction** | | | | **1-km$^2$ colonisation** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Trait group** | **Predictor** | **p!=0** | **% included** | **EV** | **SD** | **p!=0** | **% included** | **EV** | **SD** |
| | (Intercept) | **100.0** | **100.0** | **4.98** | **1.02** | **100.0** | **100.0** | **-2.25** | **0.34** |
| Climate | Growing degree-days | 52.5 | 37.50 | -0.00 | 0.00 | 3.8 | 9.1 | 0.00 | 0.00 |
| | Sunshine | 39.2 | 37.50 | -0.02 | 0.02 | **96.2** | **90.9** | **0.03** | **0.01** |
| | Rainfall | *86.7* | *87.50* | *0.00* | *0.00* | **100.0** | **100.0** | **-0.00** | **0.00** |
| Habitat | Broadleaf woodland | 38.6 | 50.0 | -0.00 | 0.01 | 46.0 | 54.6 | -0.00 | 0.00 |
| | Coniferous woodland | 48.2 | 50.0 | -0.01 | 0.01 | 70.5 | 72.7 | 0.01 | 0.00 |
| | Natural grassland | 0.0 | 0.0 | 0.00 | 0.00 | *86.5* | *81.8* | *-0.00* | *0.00* |
| | Urban | **97.0** | **87.50** | **0.01** | **0.00** | **100.0** | **100.0** | **-0.01** | **0.00** |
| Invasion | Years with *H. axyridis* | 0.0 | 0.0 | 0.00 | 0.00 | 1.5 | 9.1 | 0.00 | 0.01 |
| Ecological overlap with *Harmonia axyridis* | Dietary niche overlap | **100.0** | **100.0** | **2.45** | **0.51** | 9.5 | 27.3 | 0.04 | 0.14 |
| | Habitat niche overlap | 0.0 | 0.0 | 0.00 | 0.00 | 0.0 | 0.0 | 0.00 | 0.00 |
| | Dietary niche overlap * Years with *H. axyridis* | 0.0 | 0.0 | 0.00 | 0.00 | 0.0 | 0.0 | 0.00 | 0.00 |
| | Habitat niche overlap * Years with *H.axyridis* | **100.0** | **100.0** | **-0.40** | **0.05** | **100.0** | **100.0** | **0.26** | **0.03** |
| Resource use | Diet breadth | 0.0 | 0.0 | 0.00 | 0.00 | **100.0** | **100.0** | **-0.07** | **0.01** |
| Life-history | Body size | 0.0 | 0.0 | 0.00 | 0.00 | **100.0** | **100.0** | **-0.36** | **0.02** |
| | Polymorphism | 0.0 | 0.0 | 0.00 | 0.00 | **100.0** | **100.0** | **0.21** | **0.05** |
| | Maximum voltinism | **100.0** | **100.0** | **-0.68** | **0.19** | **100.0** | **100.0** | **-0.26** | **0.06** |
| Range characteristics | Range size | **100.0** | **100.0** | **-0.00** | **0.00** | **100.0** | **100.0** | **0.00** | **0.00** |
| | Recording intensity | **100.0** | **100.0** | **-0.05** | **0.00** | **100.0** | **100.0** | **0.01** | **0.00** |

The observed and predicted extinction and colonisation rates were highly correlated (Figure 3.1) showing that the models explained substantial proportions of spatial and species variability in these ratesalthough this correlation was lower for spatial models, particularly for local extinction.

## 3.6. Discussion

Most studies exploring the interactions between ecological traits of species and environmental factors do not consider population or distribution changes. A few recent studies have examined the role of ecological traits in explaining distribution patterns of animals. For example, habitat use and diet breadth are important traits in explaining distribution patterns of isopods (Purse *et al.*, 2012) and coccinellids (Comont *et al.*, 2012) respectively. However, the dual effects of both ecological traits and environmental drivers in determining distribution trends (colonisation and local extinction) of species have largely been ignored, making it difficult to understand where species with particular ecological characteristics (and performing particular ecosystem functions) will decline, and, why. Here we investigated determinants of local extinction and colonisation events at both the species and population level (as recommended by Ricciardi, 2004), and detected significant impacts of both ecological traits and environmental factors on the dynamics of ladybirds. Additionally we revealed that an invasive alien species, *Harmonia axyridis*, constitutes a key biotic environmental pressure on native ladybirds, and has species-specific impacts, depending on overlap of resource use of individual species with the invader. Here we discuss the potential biological mechanisms underpinning the significant trait and abiotic environmental affects before considering the wider implications of the impacts of *H. axyridis* on native ladybirds.

Local extinction and colonisation rates were predict more accurately at the spatial level rather than for species (Fig. 3.1), but taking a spatially-explicit, population approach (so-called spatial models above) revealed the environmental conditions that made species more vulnerable to local extinction (e.g. areas with a high degree of urban cover) and indicated a wider range of traits to be involved in buffering species against environmental change. Key impacts of intrinsic traits that were consistent between species-level and spatial models included those of range size, voltinism and habitat overlap with *H. axyridis* on colonisation rates, and those of range size, voltinism and diet overlap with *H. axyridis* on local extinction rates. The key environmental factor that both increased the likelihood of local extinction and reduced that of colonisation was urban land cover. More marginal effects included diet breadth, polymorphism, body size, recording intensity, sunshine and rainfall.

Urbanisation was shown to be an important driver of both local extinction and colonisation at the 1-km$^2$ scale. Although gardens and parks in urban areas often seem to be favourable for individual ladybird species (Roy *et al.*, 2011), our results indicate that overall increases in urban land cover are not favourable for ladybirds as a group. In terms of habitat specificity, ladybirds in Britain span the range from generalist (e.g., *Coccinella septempunctata* L. and *H. axyridis*) to highly specialist (*Myrrha octodecimguttata* L., found in the canopies of mature pines, and *Coccinella hieroglyphica*, found in heather on heath and moorland). Urban areas are probably good for the small subset of eurytopic (habitat-generalist) species but poor for specialist species, leading to decreasing colonisations and increasing local extinctions. This may be the result of destruction and fragmentation of the preferred habitats of specialist species, promoting biotic homogenisation (McKinney, 2006), but may also be exacerbated by competition from increased prevalence of eurytopic species such as *H. axyridis* in urban areas.

Ladybird species with larger range sizes were more likely to colonise new grid squares and less likely to suffer local extinctions. Large range sizes (high occupancy) are often associated with high abundances (Quinn *et al.*, 1997; Freckleton *et al.*, 2005) and more abundant species are less likely to go locally extinct and more likely to colonise by virtue of their larger population size (Breininger *et al.*, 1999; McCarthy & Thompson, 2006). As expected, colonisation events were more likely and extinction events less likely in grid cells that were recorded more intensively. However, at the species level, species recorded more intensively were less likely to colonise new grid squares across their distribution overall. Species may be intensively recorded because they are common and abundance and encountered frequently or because they are rare and their records are much sought after (Roy *et al.* 2011). In fact the direction of the relationship between recording intensity and species colonisation rates was determined largely by *Coccinella quinquepunctata* which is absent from much of Britain and colonised only a single square of between the two periods, but which has been recorded very intensively in that square (Roy *et al.* 2011). This illustrates the potential superiority of geographical versus species measures of recording intensity for understanding drivers of colonisation and extinction

- by averaging across common and rare species, geographical measures smooth out impacts of species attractiveness on recording effort.

Species which are capable of having more than one generation were less likely to go extinct, and were also less likely to colonise new grid squares. This produces a more stable distribution pattern than is present in species which are declining or colonising. Species which are facultatively multivoltine may be more buffered against changes in the environment, as they can produce more offspring in favourable conditions (Pereira *et al.*, 2012) and may also benefit from greater genetic exchange between generations (Watts & Thompson, 2011).

The negative impacts of *H. axyridis* were greater in species with high dietary niche overlap with the invader, both at a species and spatial scale: native species which had a high dietary niche overlap with *H. axyridis* were more likely to go locally extinct than species with a low niche overlap. This supports recent studies which have implicated *H. axyridis* in the declines of native ladybird species. Ware & Majerus (2008) found that *H. axyridis* was a predator of native species in captivity, and declines have been found in native species after the arrival of *H. axyridis* at a local (Brown *et al.*, 2011b) and European scale (Roy *et al.*, 2012). Diet overlap was a more consistent predictor of local extinction or colonisation than habitat niche overlap, suggesting that competition for food is the most important mechanism by which *H. axyridis* causes declines in native ladybird species. This is despite the existence of species such as *Halyzia sedecimguttata* (L) and *Exochomus quadripustulatus* (L), which share habitat with *H. axyridis* but have very limited dietary niche overlap. However, it should be noted that predation may also play an important role: within a given habitat, species exploiting the same food resource as *H. axyridis* are likely to come into contact with the invader more frequently, and so be at a greater risk of predation, which correlates positively with encounter rate (Raak-van den Berg *et al.*, 2012). Phenology may also play a role in regulating both competition and predation: larval *H. sedecimguttata* are thought to be more at risk from predation by *H. axyridis* larvae as a consequence of developing late in the year, when aphids are scarce (Roy *et al.*, 2012).

The interaction between habitat use and the number of years that *H. axyridis* has been present in a grid square was positively associated with continued presence in a grid square, and with local colonisation.  This suggests that the negative effects of *H. axyridis* were reduced in eurytopic species, even where more of this niche was potentially shared with the invader. This may indicate that these species are able to utilise habitat patches which are less-favoured by *H. axyridis* as refugia, due to their low habitat specificity.  This has been found in North America (Evans, 2004), where native ladybird species were displaced from agricultural areas after the arrival of *C. septempunctata*, and in freshwater fish species in Lake Nabugabo, Uganda, after the establishment of the Nile perch, *Lates niloticus* L (Chapman *et al.*, 1996).  Alternatively, it may indicate that eurytopic species are colonising the same grid squares as *H. axyridis*, at a higher rate than are oligotrophic species, for an as-yet unknown reason, or that areas with *H. axyridis* become more suitable for eurytopic species several years after invasion, possibly because of the lack of competition other than *H. axyridis*

Species which are polymorphic are more likely to colonise new grid squares than are monomorphic species, and grid squares which receive more hours of sunshine are more likely to be colonised than less sunny areas.  It is probable that the effect of polymorphism results from species with an extended phenotypic range of several distinct forms being able to inhabit a wider range of habitats/microclimates, so colonising more grid squares.  Differences in large-scale distribution patterns have been found to be related to changes in colour pattern in the ladybird *A. bipunctata* in the Netherlands (Brakefield, 1985; de Jong *et al.*, 1996; de Jong & Brakefield, 1998), and the grasshopper *Chorthippus parallelus* (Zetterstedt) and the groundhopper *Tetrix undulata* (Sowerby) have been found to have different colour forms preferentially inhabiting different habitat types (Ahnesjo & Forsman, 2003, 2006).  As ectotherms, ladybirds are dependent on environmental heat sources, particularly temperature.  Sunshine and temperature are usually positively correlated, and ladybirds can minimise their reliance on the external temperature by basking in sunshine to raise their body temperatures above ambient (de Jong *et al.*, 1996; Clusella Trullas *et al.*, 2007), which seems to be important in allowing dispersal to colonise new grid squares.

At a local (1-km$^2$) scale, increased rainfall decreases the probability of colonisation.  This is probably because wet weather tends to be unsuitable for insect activity, so reducing both dispersal into a grid square and the chances of establishing there. For example, rainfall has been found to be strongly negatively correlated with apparent butterfly abundance on transects (Pollard, 1988), and to be a strong driver of decreased adult survival in *Culex* mosquito species (Jones *et al.*, 2012). Ladybirds with a large body size, and those which had a wide diet breadth were also less likely to colonise new grid squares. This may be because these species were already at their range limit during the first period, as range size and range fill in ladybirds is driven by diet breadth (Comont *et al.*, 2012), and body size is often found to correlate strongly with range size in insects (Bräendle *et al.*, 2002; Chown & Gaston, 2010).

Overall, it is clear that external environmental factors, species-level life-history and resource-use traits are having effects on ladybird local extinction and colonisation dynamics, both at a species level and 1-km$^2$ spatial scale. However, even with these effects taken into account, the invasive alien ladybird *H. axyridis* is having a significant deleterious impact on native species, greatly increasing extinction rate at both the 1-km$^2$ and large scale. These results, particularly when considered with those of Roy *et al*. (2012), who found that seven of eight common native ladybird species began to decline, or began to decline faster than before, after the arrival of *H. axyridis* at a local level across Britain and Belgium, suggest that the continued spread *of H. axyridis* will lead to the ecological extinction (Estes *et al.*, 1989) of native species, particularly those with a high niche overlap with *H. axyridis*. Areas of Britain that are urban or undergoing urbanisation in which *H. axyridis* has invaded may be particularly vulnerable to loss of ladybird biodiversity.

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### 3.9.1. Appendix S1. Bray-Curtis similarity index measures of dietary overlap between each native ladybird species and *H. axyridis.*

| **Species** | *Adalia bipunctata* | *Adalia decempunctata* | *Anatis ocellata* | *Anisosticta novemdecimpunctata* | *Aphidecta obliterata* | *Calvia quatuordecimguttata* | *Chilocorus bipustulatus* | *Chilocorus renipustulatus* | *Coccinella hieroglyphica* | *Coccinella magnifica* | *Coccinella quinquepunctata* | *Coccinella septempunctata* | *Coccinella undecimpunctata* | *Exochomus quadripustulatus* | *Halyzia sedecimguttata* | *Harmonia axyridis* | *Harmonia quadripunctata* | *Henosepilachna argus* | *Hippodamia tredecimpunctata* | *Hippodamia variegata* | *Myrrha octodecimguttata* | *Myzia oblongoguttata* | *Propylea quattuordecimpunctata* | *Psyllobora virgintiduopunctata* | *Subcoccinella vigintiquattuorpunctata* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Adalia bipunctata* | **1.00** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Adalia decempunctata* | 0.42 | **1.00** | | | | | | | | | | | | | | | | | | | | | | | |
| *Anatis ocellata* | 0.26 | 0.63 | **1.00** | | | | | | | | | | | | | | | | | | | | | | |
| *Anisosticta novemdecimpunctata* | 0.05 | 0.17 | 0.22 | **1.00** | | | | | | | | | | | | | | | | | | | | | |
| *Aphidecta obliterata* | 0.09 | 0.14 | 0.35 | 0.44 | **1.00** | | | | | | | | | | | | | | | | | | | | |
| *Calvia quatuordecimguttata* | 0.29 | 0.70 | 0.77 | 0.24 | 0.18 | **1.00** | | | | | | | | | | | | | | | | | | | |
| *Chilocorus bipustulatus* | 0.15 | 0.26 | 0.25 | 0.15 | 0.13 | 0.26 | **1.00** | | | | | | | | | | | | | | | | | | |
| *Chilocorus renipustulatus* | 0.07 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 | **1.00** | | | | | | | | | | | | | | | | | |
| *Coccinella hieroglyphica* | 0.07 | 0.21 | 0.26 | 0.44 | 0.29 | 0.27 | 0.19 | 0.00 | **1.00** | | | | | | | | | | | | | | | | |
| *Coccinella magnifica* | 0.05 | 0.08 | 0.11 | 0.40 | 0.20 | 0.11 | 0.07 | 0.00 | 0.40 | **1.00** | | | | | | | | | | | | | | | |
| *Coccinella quinquepunctata* | 0.07 | 0.24 | 0.32 | 0.80 | 0.40 | 0.33 | 0.22 | 0.00 | 0.60 | 0.33 | **1.00** | | | | | | | | | | | | | | |
| *Coccinella septempunctata* | 0.79 | 0.36 | 0.21 | 0.04 | 0.04 | 0.23 | 0.16 | 0.06 | 0.07 | 0.04 | 0.06 | **1.00** | | | | | | | | | | | | | |
| *Coccinella undecimpunctata* | 0.45 | 0.84 | 0.55 | 0.13 | 0.11 | 0.60 | 0.31 | 0.06 | 0.17 | 0.06 | 0.19 | 0.42 | **1.00** | | | | | | | | | | | | |
| *Exochomus quadripustulatus* | 0.22 | 0.30 | 0.35 | 0.15 | 0.19 | 0.31 | 0.83 | 0.40 | 0.19 | 0.15 | 0.22 | 0.16 | 0.31 | **1.00** | | | | | | | | | | | |
| *Halyzia sedecimguttata* | 0.05 | 0.16 | 0.21 | 0.80 | 0.40 | 0.22 | 0.15 | 0.00 | 0.40 | 0.33 | 0.67 | 0.04 | 0.13 | 0.15 | **1.00** | | | | | | | | | | |
| *Harmonia axyridis* | 0.62 | 0.56 | 0.38 | 0.07 | 0.10 | 0.41 | 0.13 | 0.00 | 0.13 | 0.11 | 0.11 | 0.51 | 0.59 | 0.23 | 0.07 | **1.00** | | | | | | | | | |
| *Harmonia quadripunctata* | 0.07 | 0.08 | 0.11 | 0.40 | 0.20 | 0.11 | 0.07 | 0.00 | 0.20 | 0.67 | 0.33 | 0.02 | 0.06 | 0.22 | 0.33 | 0.11 | **1.00** | | | | | | | | |
| *Henosepilachna argus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | |
| *Hippodamia tredecimpunctata* | 0.20 | 0.58 | 0.72 | 0.36 | 0.25 | 0.75 | 0.30 | 0.00 | 0.38 | 0.17 | 0.50 | 0.17 | 0.49 | 0.36 | 0.33 | 0.29 | 0.17 | 0.00 | **1.00** | | | | | | |
| *Hippodamia variegata* | 0.52 | 0.78 | 0.54 | 0.12 | 0.10 | 0.55 | 0.29 | 0.11 | 0.15 | 0.06 | 0.17 | 0.47 | 0.87 | 0.32 | 0.11 | 0.66 | 0.06 | 0.00 | 0.44 | **1.00** | | | | | |
| *Myrrha octodecimguttata* | 0.11 | 0.30 | 0.48 | 0.57 | 0.50 | 0.40 | 0.28 | 0.00 | 0.50 | 0.25 | 0.75 | 0.08 | 0.24 | 0.34 | 0.50 | 0.17 | 0.25 | 0.00 | 0.57 | 0.22 | **1.00** | | | | |
| *Myzia oblongoguttata* | 0.05 | 0.15 | 0.40 | 0.67 | 0.36 | 0.21 | 0.14 | 0.00 | 0.36 | 0.29 | 0.57 | 0.04 | 0.13 | 0.14 | 0.57 | 0.07 | 0.29 | 0.00 | 0.31 | 0.17 | 0.44 | **1.00** | | | |
| *Propylea quattuordecimpunctata* | 0.49 | 0.79 | 0.51 | 0.12 | 0.11 | 0.57 | 0.18 | 0.00 | 0.16 | 0.06 | 0.18 | 0.43 | 0.81 | 0.22 | 0.18 | 0.69 | 0.06 | 0.00 | 0.45 | 0.86 | 0.22 | 0.11 | **1.00** | | |
| *Psyllobora virgintiduopunctata* | 0.09 | 0.29 | 0.36 | 0.50 | 0.31 | 0.38 | 0.27 | 0.00 | 0.46 | 0.22 | 0.67 | 0.08 | 0.24 | 0.27 | 0.67 | 0.14 | 0.22 | 0.00 | 0.53 | 0.21 | 0.73 | 0.40 | 0.32 | **1.00** | |
| *Subcoccinella vigintiquattuorpunctata* | 0.02 | 0.07 | 0.08 | 0.20 | 0.13 | 0.09 | 0.06 | 0.00 | 0.13 | 0.18 | 0.18 | 0.02 | 0.06 | 0.06 | 0.36 | 0.07 | 0.18 | 0.00 | 0.12 | 0.05 | 0.15 | 0.17 | 0.10 | 0.29 | **1.00** |
| *Tytthaspis sedecimpunctata* | 0.04 | 0.14 | 0.09 | 0.22 | 0.14 | 0.09 | 0.06 | 0.00 | 0.14 | 0.20 | 0.20 | 0.07 | 0.06 | 0.06 | 0.40 | 0.10 | 0.20 | 0.00 | 0.13 | 0.05 | 0.17 | 0.18 | 0.21 | 0.31 | 0.27 |

## 3.9.2. Appendix S2. Bray-Curtis similarity index measures of dietary overlap between each native ladybird species and *H. axyridis*

| Species | *Adalia bipunctata* | *Adalia decempunctata* | *Anatis ocellata* | *Anisosticta novemdecimpunctata* | *Aphidecta obliterata* | *Calvia quatuordecimguttata* | *Chilocorus bipustulatus* | *Chilocorus renipustulatus* | *Coccinella hieroglyphica* | *Coccinella magnifica* | *Coccinella quinquepunctata* | *Coccinella septempunctata* | *Coccinella undecimpunctata* | *Exochomus quadripustulatus* | *Halyzia sedecimguttata* | *Harmonia axyridis* | *Harmonia quadripunctata* | *Henosepilachna argus* | *Hippodamia tredecimpunctata* | *Hippodamia variegata* | *Myrrha octodecimguttata* | *Myzia oblongoguttata* | *Propylea quattuordecimpunctata* | *Psyllobora vigintiduopunctata* | *Subcoccinella vigintiquattuorpunctata* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Adalia bipunctata* | **1.00** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Adalia decempunctata* | 0.43 | **1.00** | | | | | | | | | | | | | | | | | | | | | | | |
| *Anatis ocellata* | 0.17 | 0.00 | **1.00** | | | | | | | | | | | | | | | | | | | | | | |
| *Anisosticta novemdecimpunctata* | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | | | | | | | | | | | | | | | |
| *Aphidecta obliterata* | 0.17 | 0.00 | 1.00 | 0.00 | **1.00** | | | | | | | | | | | | | | | | | | | | |
| *Calvia quatuordecimguttata* | 0.53 | 0.29 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | | | | | | | | | | | | | |
| *Chilocorus bipustulatus* | 0.40 | 0.29 | 0.40 | 0.00 | 0.40 | 0.50 | **1.00** | | | | | | | | | | | | | | | | | | |
| *Chilocorus renipustulatus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 | **1.00** | | | | | | | | | | | | | | | | | |
| *Coccinella hieroglyphica* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | | | | | | | | | | |
| *Coccinella magnifica* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | | | | | | | | | |
| *Coccinella quinquepunctata* | 0.40 | 0.29 | 0.00 | 0.33 | 0.00 | 0.75 | 0.50 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | | | | | | | | | |
| *Coccinella septempunctata* | 0.64 | 0.29 | 0.17 | 0.00 | 0.17 | 0.40 | 0.40 | 0.00 | 0.00 | 0.00 | 0.27 | **1.00** | | | | | | | | | | | | | |
| *Coccinella undecimpunctata* | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.67 | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | 0.15 | **1.00** | | | | | | | | | | | | |
| *Exochomus quadripustulatus* | 0.53 | 0.29 | 0.40 | 0.00 | 0.40 | 0.50 | 0.25 | 0.00 | 0.00 | 0.00 | 0.25 | 0.40 | 0.67 | **1.00** | | | | | | | | | | | |
| *Halyzia sedecimguttata* | 0.53 | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 | 0.25 | 0.00 | 0.00 | 0.00 | 0.50 | 0.40 | 0.33 | 0.25 | **1.00** | | | | | | | | | | |
| *Harmonia axyridis* | 0.64 | 0.29 | 0.00 | 0.00 | 0.00 | 0.27 | 0.13 | 0.00 | 0.00 | 0.00 | 0.27 | 0.55 | 0.15 | 0.27 | 0.53 | **1.00** | | | | | | | | | |
| *Harmonia quadripunctata* | 0.17 | 0.00 | 1.00 | 0.00 | 1.00 | 0.00 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.40 | 0.00 | 0.00 | **1.00** | | | | | | | | |
| *Henosepilachna argus* | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.27 | 0.00 | 0.00 | 0.50 | 0.40 | 0.00 | **1.00** | | | | | | | |
| *Hippodamia tredecimpunctata* | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.67 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** | | | | | | |
| *Hippodamia variegata* | 0.43 | 0.00 | 0.00 | 0.00 | 0.00 | 0.57 | 0.00 | 0.00 | 0.00 | 0.00 | 0.29 | 0.14 | 0.80 | 0.57 | 0.29 | 0.29 | 0.00 | 0.00 | 0.50 | **1.00** | | | | | |
| *Myrrha octodecimguttata* | 0.17 | 0.00 | 1.00 | 0.00 | 1.00 | 0.00 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.40 | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 | 0.00 | **1.00** | | | | |
| *Myzia oblongoguttata* | 0.17 | 0.00 | 1.00 | 0.00 | 1.00 | 0.00 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.40 | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 | 0.00 | 1.00 | **1.00** | | | |
| *Propylea quattuordecimpunctata* | 0.80 | 0.33 | 0.20 | 0.00 | 0.20 | 0.62 | 0.46 | 0.00 | 0.00 | 0.00 | 0.46 | 0.80 | 0.36 | 0.62 | 0.62 | 0.50 | 0.20 | 0.31 | 0.20 | 0.33 | 0.20 | 0.20 | **1.00** | | |
| *Psyllobora virgintiduopunctata* | 0.53 | 0.29 | 0.00 | 0.00 | 0.00 | 0.50 | 0.50 | 0.00 | 0.00 | 0.00 | 0.50 | 0.53 | 0.00 | 0.00 | 0.75 | 0.40 | 0.00 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | **1.00** | |
| *Subcoccinella vigintiquattuorpunctata* | 0.29 | 0.00 | 0.00 | 0.00 | 0.00 | 0.57 | 0.29 | 0.00 | 0.00 | 0.00 | 0.29 | 0.29 | 0.40 | 0.29 | 0.29 | 0.14 | 0.00 | 0.00 | 0.50 | 0.33 | 0.00 | 0.00 | 0.33 | 0.29 | **1.00** |
| *Tytthaspis sedecimpunctata* | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.50 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.67 | 0.40 | 0.00 | 0.00 | 0.18 | 0.00 | 0.80 |

# Chapter 4. Escape from parasitism by the invasive alien ladybird, Harmonia axyridis.

## 4.1. Abstract

Alien species are often reported to perform better than functionally-similar species native to the invaded range, resulting in high population densities, and a tendency to become invasive. The Enemy Release Hypothesis (ERH), explains the success of invasive alien species (IAS) as a consequence of reduced mortality from natural enemies (predators, parasites and pathogens) compared to native species. The harlequin ladybird, *Harmonia axyridis,* a species alien to Britain, provides a model system for testing the ERH.

Pupae of *H. axyridis* and the native ladybird *Coccinella septempunctata* were monitored for parasitism between 2008 and 2011, from populations across southern England in areas first invaded by *H. axyridis* between 2004 and 2009. Additionally, a semi-field experiment was established to investigate the incidence of parasitism of adult *H. axyridis* and *C. septempunctata* by *Dinocampus coccinellae*.

*Harmonia axyridis* pupae were parasitised at a much lower rate than conspecifics in the native range, and both pupae and adults were parasitised at a considerably lower rate than *C. septempunctata* populations from the same place and time (*H. axyridis*: 1.67%; *C. septempunctata*: 18.02%) or in previous studies on Asian *H. axyridis* (2-67%). We found no evidence that the presence of *H. axyridis* affected the parasitism rate of *C. septempunctata* by *D. coccinellae*.

Our results are consistent with the general prediction that the prevalence of natural enemies is lower for introduced species than for native species at early stages of invasion. This may partly explain why *H. axyridis* is such a successful IAS.

## 4.2. Keywords:

*Coccinella septempunctata,* enemy release hypothesis, *Harmonia axyridis*, invasive alien species, native species, natural enemies

## 4.3. Introduction:

Biological invasions are a major threat to native ecosystems (Millennium Ecosystem Assessment, 2005, UK National Ecosystem Assessment, 2011), and the rate of establishment of alien species is accelerating (Roy, Bacon, Beckmann *et al.*, 2012b, Roy, Roy & Roques, 2011). Not all the species introduced to an area establish: 10% is commonly acknowledged as the proportion of new arrivals that establish successfully, but this is based on an assessment of plant species in Britain (Williamson & Fitter, 1996) and there is evidence that this rate may not hold true for other taxa (Jeschke, Aparicio, Haider *et al.*, 2012, Jeschke, 2008).

Some introduced species have become spectacularly successful in the new regions they occupy, and are termed invasive alien species (IAS) in view of their rapid spread and high impact on native diversity. Many new arrivals do less well, failing to establish or surviving only as small, isolated populations (Lodge, 1993). One commonly-cited potential explanation for this discrepancy is the Enemy Release Hypothesis (ERH) (Elton, 1958, Torchin, Lafferty, Dobson *et al.*, 2003), also known as enemy-escape (Brown, Abrahamson, Packer *et al.*, 1995) or the escape-from-enemy hypothesis (Wolfe, 2002). This predicts that an alien species introduced to a new region will experience reduced mortality from specialised natural enemies (e.g., predators, parasites and pathogens) compared to native species. The co-evolved natural enemy species remain in the native range of the IAS, while natural enemies native to the introduced range of the IAS will not be co-evolved with it, and will often take time to adapt to a novel prey or host species. This gives the IAS a competitive advantage, assuming that natural enemies are important in regulating populations (Roy & Lawson Handley, 2012c), and allows a rapid increase in the abundance and distribution of the alien species (Elton, 1958, Torchin *et al.*, 2003, Colautti, Ricciardi, Grigorovich *et al.*, 2004).

Two mechanisms have been proposed to account for the increase in population growth of the alien species in comparison to the native species: regulatory or compensatory release (Colautti et al. 2004). For hosts that are strongly regulated by enemies in their native range a reduction in enemies in the introduced range may lead to direct changes in survivorship, fecundity, biomass or other parameters (regulatory release). Alternatively, for hosts that are well-defended and, consequently, lack natural enemies within their native range, a reduction in enemies may be of minimal consequence for hosts.

Indeed for well-defended hosts, fewer enemies may lead to a reallocation of resources from defence to population growth over ecological time (Roy & Lawson Handley, 2012), so-called compensatory release or as the Evolution of Increased Competitive Ability (EICA). Empirical evidence for the role of the ERH or EICA in invasion success is lacking (Roy et al. 2011), particularly for invertebrates,

The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is considered to be a highly successful IAS (Roy, Brown & Majerus, 2006, Brown, Adriaens, Bathon *et al.*, 2008a, Roy & Wajnberg, 2008). It is native to temperate Asia, but is now established across Europe, Africa, and both North and South America (Brown, Thomas, Lombaert *et al.*, 2011b). There has often been a time lag between introduction of *H. axyridis*, as a biological control agent for aphids and coccids, and establishment (Koch, 2003). This species is also known to colonise through natural spread but also anthropogenically on produce and along transport networks (Brown, Adriaens, Bathon *et al.*, 2008b). *Harmonia axyridis* established in Britain in 2004 (Majerus, Mabbott, Rowland *et al.*, 2006), and spread at more than 100 km per year (Brown, Roy, Rothery *et al.*, 2008), contributing to declines in several native species (Roy, Adriaens, Isaac *et al.*, 2012a, Ware & Majerus, 2008, Brown, Frost, Doberski *et al.*, 2011a) most likely through competition and predation (Ware & Majerus, 2008).

The invasive nature of *H. axyridis* is thought to result from several factors. The species has good dispersal capabilities, occupies a broad range of habitats, has high reproductive potential, broad climatic tolerance, and a wide dietary range, including a propensity to act as an intraguild predator within the aphidophagous guild (Majerus *et al.*, 2006, Ware, Majerus, Roy *et al.*, 2005, Roy & Wajnberg, 2008, Berkvens, Baverstock, De Clercq *et al.*, 2008, Brown *et al.*, 2011b, Soares, Borges, Borges *et al.*, 2008). As a well-defended species, with strong chemical defences and large larval spines (Sloggett, Magro, Verheggen *et al.*, 2011, Ware *et al.*, 2008) introduced to a new continent many thousands of kilometres from its native range, there is also a strong possibility that enemy release plays a role in the success of *H. axyridis*.

In Britain, several species of endoparasitic Hymenoptera and Diptera attack ladybirds. Some of these have a Holarctic distribution, and are known to attack *H. axyridis* in its native range: *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae) (Kuznetsov, 1997, Ware, Michie, Otani *et al.*, 2010);

*Homalotylus flaminius* Dalman (Hymenoptera: Encyrtidae) (Kuznetsov, 1997); *Oomyzus scaposus* (=*Tetrastichus coccinellae*) Thomson (Hymenoptera: Eulophidae) (Kuznetsov, 1997) and *Medina separata* (Meigen) (Diptera: Tachinidae) (Kuznetsov, 1997) (often erroneously referred to as *M. luctuosa* (Hodek, van Emden & Honek, 2012)), while others (*Phalacrotophora fasciata* (Fallén) and *Phalacrotophora berolinensis* Schmitz (Diptera: Phoridae) (Disney & Beuk, 1997, Disney et al., 1994)) are European in distribution but are closely related to *Phalacrotophora philaxyridis* Disney (Diptera: Phoridae) which attacks *H. axyridis* in Japan (Disney, 1997).

There is evidence that some natural enemies of ladybirds, particularly the holarctic species known to attack *H. axyridis* in Asia, are beginning to attack it in Britain too (Ware *et al.*, 2010, Hall, Ware & Michie, 2009). It is unclear what effect this will have on native ladybird species. As parasitoids are shared across ladybird species, there is the potential for apparent competition (Holt, 1977, Bonsall & Hassell, 1997), where high abundance of *H. axyridis* elevates rates of parasitism in susceptible native species. Alternatively, *H. axyridis* may act as a parasitoid sink, whereby the parasitoid may oviposit in the IAS but the eggs do not produce an adult, potentially reducing the population density of the parasitoid and thus the parasite burden on native populations. This has been suggested for the parasitoid wasp *D. coccinellae*, which in laboratory studies oviposited approximately equally into *H. axyridis* and *Coccinella septempunctata* L., the primary native host in Britain, but which successfully eclosed from a significantly greater proportion of *C. septempunctata* (Koyama & Majerus, 2008). Additionally a study comparing parasitism of *Coleomegilla maculata* De Geer with that of *H. axyridis* by *D. coccinellae* also concluded that *H. axyridis* was an unsuitable host (Hoogendoorn & Heimpel, 2002). Teratocyte cells, produced by *D. coccinellae*, are involved in immunosuppression of the host and nutrition of the parasitoid, interestingly follow an abnormal pattern of growth within *H. axyridis* which could explain the impeded development of *D. coccinellae* within this marginal host (Firlej, 2012). Therefore, it is unlikely that *D. coccinellae* will limit the population growth of *H. axyridis* within invaded ranges (Berkvens, Moensa, Berkvens *et al.*, 2010, Hoogendoorn *et al.*, 2002). Intriguingly a recent study demonstrated that *H. axyridis* individuals contain high numbers of obligate parasitic microsporidia which while not seemingly harmful to *H. axyridis* are lethal when artificially injected into the native ladybird *C. septempunctata* (Vilcinskas, Stoecker, Schmidtberg *et al.*, 2013).

In this paper, we examine the following hypotheses:

- Time since establishment will affect parasitism of the IAS *H. axyridis* resulting in low rates of parasitism at sites which have been colonised relatively recently by *H. axyridis*.

- The parasitism rate of the functionally-similar native ladybird *C. septempunctata* will be higher than for *H. axyridis*, concomitant with the predictions of the ERH.

We examined these hypotheses through a field survey of pupal parasitism (monitoring pupae of the two ladybird species for parasitism by the native parasitoids *P. fasciata, P. berolinensis* and *O. scaposus*, at a large spatial and temporal scale) and a semi-field experiment of adult parasitism (monitoring parasitism by the parasitoid wasp *D. coccinellae* in overwintering aggregations of adults of the two ladybird species within mesocosms).

## 4.4. Methods:

### 4.4.1. Field Survey - pupal parasitism:

Mature pupae of *C. septempunctata* and *H. axyridis* were collected between May and September from Loughborough, Leicestershire (during 2008-2011), Oxfordshire (2010-11), London (2010-11), Cambridge (2011) and Plymouth, Devon (2011) (Table 4.1). Pupae were collected by visually searching vegetation, primarily sycamore (*Acer pseudoplatanus* L.), lime (*Tilia* spp.) and nettle (*Urtica dioica* L.), between ground level and 2.5 metres and removing the leaf on which the pupae were attached.

Collected pupae were kept in individual containers at a constant temperature and light regime (18°C, 16:8 L:D), and checked for emergence or parasitism on a daily basis. Parasitoids which emerged were allowed to reach adulthood and then identified after death. Owing to time constraints the few pupae from which nothing emerged were not dissected. Individual Phoridae from 66 *C. septempunctata* pupae and 32 *H. axyridis* pupae (representing half of the Phoridae broods) were dissected to determine species.

### 4.4.2. Semi-field survey - adult parasitism:

Both *H. axyridis* and *C. septempunctata* were collected from field sites in Crowmarsh Gifford, South Oxfordshire, in late September 2011. Native ladybirds at this time of year in Britain are still active but begin to move to overwintering sites. *Harmonia axyridis* has been observed to be active much later than native species in Britain and larval stages have been recorded in November (and exceptionally early December). As these individuals had been exposed to the possibility of parasitism in the field, they were monitored for parasitoid eclosion for a week in the laboratory, within a controlled environment (18°C, 16:8 L:D), before being placed outside in overwintering conditions. During the time spent within the laboratory the ladybirds were fed artificial diet, to ensure hydration, every other day (see Roy, Brown, Comont *et al.*, 2013 for details) and supplied with pea aphids (*Acyrthosiphon pisum* Harris) *ad libitum*.

Mesocosms were placed outdoors underneath Lombardy poplar trees (*Populus nigra* L. var. 'Italica') from the beginning of October 2011 (the usual time to begin overwintering) until mid-January 2012 (before the end of the winter dormancy period). Each individual mesocosm consisted of a black 14-litre bucket, with three holes drilled in the base to allow rainwater to drain. Mesocosms were filled with 2.5l of compost (John Innes No. 10), pressed down firmly and covered by 6.5l of fresh uncompressed leaf litter, collected from the area surrounding the mesocosms and frozen at -20°C for five days between collection and use in the mesocosms to kill any animals present. A 300x18x18mm L-shaped section of wood was placed on the leaf litter leaning against the side of the bucket. The top of the bucket was covered with dark green netting, with a mesh size (approximately 2 mm) small enough to prevent the ladybirds escaping, but large enough to allow *D. coccinellae* to enter.

The field-collected ladybirds were placed in the mesocosms so that each contained 40 adult ladybirds, either all *H. axyridis*, all *C. septempunctata*, or 20 of each of the two species. Twenty-four mesocosms (eight of each treatment) were located in Crowmarsh Gifford, Oxfordshire (10 km square SU68 in the UK Ordnance Survey grid system where the first *H. axyridis* was recorded in 2007), and a further 15 (5 of each treatment) were located at the Leeds University Farm, Tadcaster, West Yorkshire (10 km square SE44 in the UK Ordnance Survey grid system where the first *H. axyridis* was recorded in

2009). An additional fifty individuals of each species were kept individually in the laboratory and monitored for the duration of the experiment as a control, to test for pre-trial parasitism rates.

The mesocosms were collected in from the field in mid-January and the individual ladybirds were recovered. The number of individual ladybirds which had been parasitised by *D. coccinellae* was recorded at time of collection. All remaining ladybirds were monitored for *D. coccinellae* emergence over a period of six weeks. Owing to time constraints the individuals from which nothing emerged were not dissected.

### 4.4.3. Analysis:

Analysis was restricted to pupae from which either a ladybird or a parasitoid emerged. Parasitism rate was the proportion of these pupae which were parasitised.

For both datasets, the relationship between parasitism rate, host species, and years with *H. axyridis* presence was analysed using binomial General Linear Models (McCullagh & Nelder, 1989) in R version 2.15.2 (R Development Core Team, 2011), with full subsets model selection using Akaike's Information Criterion (AIC) values (Burnham & Anderson, 2002, Akaike, 1974).The model with the lowest AIC was chosen unless a model with fewer parameters was within 2 AIC units of this model, in which case the simpler model was preferred. The discriminatory ability of the models was evaluated using the Area Under the Receiver Operating Curve (AUC) (Fawcett, 2006).

For the pupal parasitism dataset, Generalized Linear Mixed Models (GLMMs) were constructed using the R package LME4 (Bates, Maechler & Bolker, 2011) and used to evaluate the relationship between parasitism rate and host species (*C. septempunctata* or *H. axyridis*), years of *H. axyridis* presence (1-6 years, mean 4.17 ± 1.19) and the interaction between host species and years of *H. axyridis* presence. The 10 km sq of collection was included as a random effect to take account of site-level effects not explained by the years of *H. axyridis* presence.

For the adult parasitism dataset, Generalized Linear Models (GLMs) were used to evaluate the per-mesocosm relationship between parasitism rate and host species (*C. septempunctata* or *H. axyridis*), treatment type (40 *C. septempunctata*, 40 *H. axyridis*, or a mixture of 20 *C. septempunctata and* 20 *H.*

*axyridis*), and site (Oxfordshire or Yorkshire). Site was included as a fixed effect in this analysis, to test whether *H. axyridis* is parasitised at a lower rate in Yorkshire, where it had invaded more recently, than in Oxfordshire, having standardised the mesocosm environment as far as possible.

## 4.5. Results:

### 4.5.1. Field survey: pupal parasitism:

Overall, *H. axyridis* was parasitised at a much lower rate than *C. septempunctata*. Of the 4,595 live pupae collected (Table 4.1), 219 were parasitised (67/3868 *H. axyridis* (1.73%), 152/727 *C. septempunctata* (20.91%); see Table 4.2). Gregarious wasps (*O. scaposus*) emerged from one *H. axyridis* pupa and 21 of the *C. septempunctata* pupae, resulting in 423 individual wasps: 18 from the *H. axyridis* pupa and a mean 19.29 ± 7,79 (range 10-42) per *C. septempunctata* pupa.

**Table 4.1**. Number of pupae of the native ladybird *Coccinella septempunctata* and the invasive alien species *Harmonia axyridis* collected from sites given as 10km squares (10 x 10 km grid squares of the Ordinance Survey British National Grid) across England (Cambridge, Cambridgeshire; London, Middlesex; Loughborough, Leicestershire; various locations in south Oxfordshire; and Plymouth, Devon) between 2008 and 2011. Numbers in brackets indicate living pupae which produced either an adult ladybird or a parasitoid. 0 indicates no pupae found while – indicates population not monitored.

| **Site** | **10km square** | ***H. axyridis* arrival** | ***Coccinella septempunctata*** | | | | ***Harmonia axyridis*** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | **2008** | **2009** | **2010** | **2011** | **2008** | **2009** | **2010** | **2011** |
| **Cambridge** | TL36 | 2005 | - | - | - | 72 (72) | - | - | 0 | 94 (94) |
| **London** | TQ27 | 2004 | - | - | 0 | - | - | - | 227 (212) | - |
| | TQ28 | 2005 | - | - | 0 | 0 | - | - | 342 (316) | 311 (297) |
| | TQ39 | 2004 | - | - | 0 | - | - | - | 164 (141) | - |
| **Loughborough** | SK51 | 2007 | 0 | 97 (92) | 0 | 58 (58) | 35 (35) | 62 (58) | 28 (28) | 272(272) |
| | SK52 | 2007 | 0 | 31 (30) | 0 | 73 (73) | 63 (61) | 191 (191) | 230 (230) | 581 (581) |
| **Oxfordshire** | SP30 | 2007 | - | - | 19 (18) | - | - | - | 21 (21) | - |
| | SP50 | 2006 | - | - | - | 0 | - | - | - | 9 (9) |
| | SU58 | 2009 | - | - | 14 (14) | - | - | - | 279 (270) | - |
| | SU59 | 2007 | - | - | 0 | 3 (3) | - | - | 165 (147) | 331 (265) |
| | SU68 | 2007 | - | - | 38 (37) | 171 (148) | - | - | 197 (190) | 446 (388) |
| | SU69 | 2008 | - | - | 189 (182) | - | - | - | 3 (2) | - |
| **Plymouth** | SX45 | 2007 | - | - | - | 0 | - | - | - | 60 (60) |

**Table 4.2**. Summary of the observations on emergence of *H. axyridis* and *C. septempunctata* pupae. Of the 4111 *H. axyridis* and 766 *C. septempunctata* pupae collected 3868 and 727 respectively produced either an adult ladybird or parasites. The number and percentage of adult ladybirds emerging is given along with the pupae successfully parasitised is provided. The parasites were identified as *O.scaposus* and Phoridae. The number and percentage of the hosts from which these parasites emerged is documented. The data is summarised across all collection sites and dates (2008-2011: Cambridge, Cambridgeshire; London, Middlesex; Loughborough, Leicestershire; various locations in south Oxfordshire; and Plymouth, Devon). Live pupae are those from which either a ladybird or a parasitoid emerged.

| **Ladybird species** | ***Harmonia axyridis*** | | ***Coccinella septempunctata*** | |
|---|---|---|---|---|
| | **Number** | **% of live pupae** | **Number** | **% of live pupae** |
| Adult ladybirds emerged | 3801 | 98.27 | 575 | 79.09 |
| Pupae successfully parasitised | 67 | 1.73 | 152 | 20.91 |
| Pupae parasitised by *Oomyzus scaposus* | 1 | 0.03 | 21 | 2.89 |
| Pupae parasitised by flies of the family Phoridae | 66 | 1.71 | 131 | 18.02 |

Gregarious flies of the family Phoridae (“phorids”) parasitised both *H. axyridis* (66 pupae parasitised, mean 3.44 ± 2.72 parasitoids per brood (range 1-15)) and *C. septempunctata* (131 pupae parasitised, mean 5.38 ± 3.15 parasitoids per brood (range 1-15)), producing 932 individual parasitoids. *A*ll 241 individuals (66 broods) examined from *C. septempunctata* were *P. fasciata,* as were 114 individuals (28 broods) from *H. axyridis,* while a further 10 individuals (4 broods) from *H. axyridis* were *P. berolinensis*. There was no evidence of hyperparasitism or cross-species multiparasitism in either host species.

Overall pupal parasitism rate was significantly lower in the IAS *H. axyridis* than in the native *C. septempunctata* (slope from *C. septempunctata* to *H. axyridis* -2.67 ± 0.18, z = -15.23, p < 0.001, AUC = 0.86). There was no significant effect on parasitism rate of the years of *H. axyridis* presence, or of the interaction between host species and years of *H. axyridis* presence (Table 4.3).

**Table 4.3.** Comparison of the GLMMs for the field survey of pupal parasitism by *Phalacrotophora fasciata*, *Phalacrotophora. berolinensis* & *Oomyzus scaposus* on the IAS *H. axyridis* and native *C. septempunctata*. Δ AIC is calculated as the AIC of each model in turn minus that of the null model; lower AIC values indicate better-fitting models. The best model is highlighted in bold.

| **Explanatory variables within the model** | **AUC** | **AIC** | **Deviance** | **Model comparisons (to best model)** | | |
|---|---|---|---|---|---|---|
| | | | | **Δ AIC** | **Δ Deviance** | **p-value** |
| **Species** | **0.85** | **1319.7** | **1313.67** | **-** | **-** | **<0.001** |
| Species + years *H. axyridis* present | 0.86 | 1321.2 | 1313.25 | 1.5 | -0.42 | <0.001 |
| Species + years *H. axyridis* present + species*years *H. axyridis* present | 0.86 | 1323.2 | 1313.25 | 2.5 | -0.42 | <0.001 |
| Null (intercept-only) | 0.78 | 1577.7 | 1573.71 | 258 | 260.04 | 1 |
| Years *H. axyridis* present | 0.77 | 1578.0 | 1572.03 | 258.3 | 258.36 | 0.20 |

### 4.5.2. Semi-field survey: adult parasitism

Of the 1560 ladybirds originally placed in the mesocosms (780 of each species), 1475 were recovered (Table 4.4: 759 *C. septempunctata*, 716 *H. axyridis*) and the remaining 85 individuals were missing (presumably dead and decomposing, indeed elytra were found within the leaf litter). No successful parasitism was found in *H. axyridis*, but 43 (5.67%) *C. septempunctata* were successfully parasitised by *D. coccinellae*. There were no deaths from parasitism in the control samples, so the pre-experiment background parasitism rate was taken to be zero.

The best model to explain parasitism by *D. coccinellae* contained species and region (Table 4.5). Ladybirds were significantly more likely to be parasitised in Yorkshire than in Oxfordshire (Table 4.6: -2.63 ± 0.45, z=-5.859, p <0.001), and the native *C. septempunctata* was more likely to be parasitised than the IAS *H. axyridis*. Although not significant in the model (Table 4.6), inclusion of species as an explanatory variable improved overall model performance considerably (Table 4.5), and the model containing only 'species' was the best of the univariate models (Table 4.5), and was significant under the Kruskal-Wallis test ($X^2_1$= 17.11, p = <0.001). Parasitism rate did not differ significantly between the single- and mixed-species treatments for either ladybird species (Table 4.5).

**Table 4.4.** Number and percentage of *C. septempunctata* or *H. axyridis* parasitized by *D. coccinellae* from mesocosms, situated in Oxfordshire (Crowmarsh Gifford) or Yorkshire (Leeds), in which overwintering aggregations of single species (either 40 *C. septempunctata* or 40 *H. axyridis*) or both species (20 *C. septempunctata* and 20 *H. axyridis*) had been placed. n = total number of individuals recovered whereby in Oxfordshire there were a total of 320 individuals per treatment (80 mesocosms) and in Yorkshire there was a total of 160 individuals per treatment (40 mesocosms). The number of individuals recovered is lower than the total number of individuals originally placed in the mesocosms because a small proportion of individuals were not retrieved.

| | **Single species** | | | | **Both species** | | | |
|---|---|---|---|---|---|---|---|---|
| **Region** | ***C. septempunctata*** **(Oxfordshire n=317; Yorkshire n = 184)** | | ***H. axyridis*** **(Oxfordshire n=310; Yorkshire n = 179)** | | ***C. septempunctata*** **(Oxfordshire n=160; Yorkshire n = 100)** | | ***H. axyridis*** **(Oxfordshire n=145; Yorkshire n = 179)** | |
| | No. of *D. coccinellae* | % parasitism | No. of *D. coccinellae* | % parasitism | No. of *D. coccinellae* | % parasitism | No. of *D. coccinellae* | % parasitism |
| **Oxfordshire** | 2 | 0.63 | 0 | 0 | 4 | 2.50 | 0 | 0 |
| **Yorkshire** | 28 | 15.22 | 0 | 0 | 9 | 9.18 | 0 | 0 |

**Table 4.5**. Comparison table for GLMs of the semi-field survey of parasitism by *D. coccinellae* on overwintering aggregations of adult ladybirds (the native *C. septempunctata* and the IAS *H. axyridis*). Δ AIC is calculated as the AIC of each model in turn minus that of the null model; lower AIC values indicate better-fitting models. The best model is highlighted in bold.

| Explanatory variables within the model | AUC | AIC | Deviance | Model comparisons (to best model) | | |
|---|---|---|---|---|---|---|
| | | | | **ΔAIC** | **Δ deviance** | **p-value** |
| **Species, region** | **0.52** | **78.1** | **37.53** | **-** | **-** | **<0.001** |
| Species, region, treatment | 0.52 | 81.3 | 36.63 | 3.2 | -0.9 | <0.001 |
| Region, treatment | 0.52 | 94.4 | 51.75 | 16.3 | 14.22 | <0.001 |
| Species | 0.51 | 128.9 | 90.30 | 50.8 | 52.77 | <0.001 |
| Region | 0.53 | 130.0 | 91.36 | 51.9 | 53.83 | <0.001 |
| Species, treatment | 0.52 | 132.5 | 89.91 | 54.4 | 52.38 | <0.001 |
| Treatment | 0.52 | 143.6 | 102.99 | 65.5 | 65.46 | <0.001 |
| Null (intercept-only) | 0.53 | 173.7 | 137.03 | 95.6 | 99.5 | 1 |

**Table 4.6**. Coefficients for each explanatory variable retained within the best model (species (*C. septempunctata* or *H. axyridis*) and region (Leeds, Yorkshire or Crowmarsh Gifford, Oxfordshire)), with their individual significance levels.

| Explanatory variable | Coefficient (± SE) | z-value | p-value |
|---|---|---|---|
| Intercept | -1.56 (±0.18) | -8.623 | <0.001 |
| Species | -19.77 (±1856.92) | -0.011 | 0.992 |
| Region | -2.63 (±0.45) | -5.859 | <0.001 |

## 4.6. Discussion:

*Harmonia axyridis* in its introduced range is parasitised at a considerably lower rate than either *H. axyridis* in its native range, or populations of *C. septempunctata* native to the introduced range of *H. axyridis*. Pupae of the invasive alien ladybird *H. axyridis* were parasitised at an exceptionally low level across Britain (1.73%) and adults were not found to be parasitized at all in our study. This is in contrast to the co-occurring native species *C. septempunctata,* which experienced reasonably high parasitism (20.91% pupae, 5.67% adults). This is consistent with the predictions of the ERH that enhanced performance of an IAS in the introduced range may result from a reduction or absence of natural enemies (Elton, 1958, Torchin, Lafferty & Kuris, 2001). The aposematic colouration and chemical defences of ladybirds causes them to suffer low rates of attack by non-specialist natural enemies (Roy *et al.*, 2013), and consequently this discrepancy in the rate of parasitism by specialist parasitoids is likely to represent an advantage for *H. axyridis*. However, further research is required to explore the population-level effects of this difference in parasitism rates.

Less than two percent of the *H. axyridis* pupae succumbed to parasitism by phorids in our study whereas *C. septempunctata* experienced high phorid parasitism rates (18 percent) at the same sites. It is also notable that parasitism of *H. axyridis* by phorids in Japan is much higher than in Britain; indeed nearly 15 percent of *H. axyridis* were parasitized by the native phorid *P. philaxyridis* found in Japan by Osawa (1992). However, phorid parasitism rates are known to vary considerably, for example phorid parasitism of *H. axyridis* across the native range was between 2% and 67% (Disney, 1997, Osawa, 1992, Park, Park, Hong *et al.*, 1996, Maeta, 1969). The absence of *H. axyridis* parasitism by *D. coccinellae* was notable in the studied overwintering aggregations particularly when considering that nearly six percent of the *C. septempunctata* were parasitized. It should be noted that the mesocosms did not represent ideal overwintering conditions particularly for *H. axyridis* which often overwinters in buildings or at elevated positions (Roy *et al.*, 2013, Nalepa, Kidd & Ahlstrom, 1996). However the high proportion of *H. axyridis* and *C. septempunctata* retrieved from the mesocosm is encouraging.

Pupal *H. axyridis* were found to be successfully parasitised by three species of parasitoid, one more than was recovered from *C. septempunctata*. Although the additional species, *P. berolinensis*, is known to parasitise *C. septempunctata* (Disney, Majerus & Walpole, 1994, Hodek *et al.*, 2012), in the study area it was only recovered from *H. axyridis* and two conifer-specialist ladybird species, *Aphidecta obliterata* L. and *Anatis ocellata* L. (R. Comont, unpublished data). This suggests that *H. axyridis* is susceptible to the suite of parasitoids in the system. The lack of evidence for increased rates of parasitism on *H. axyridis* over time from colonisation suggests that there is little or no adaptation of parasitoids to the arrival of *H. axyridis* so far. Despite the potential resource presented by the presence of high numbers of this large ladybird species, it is perhaps unsurprising that the parasitism rate is low given the short period of time since arrival of this IAS.

This limited adaptation to the presence of an IAS is consistent with results from other range-expanding or invasive taxa (Girardoz, Kenis & Quicke, 2006, Cornell & Hawkins, 1993, Menéndez, Gonzalez-Megias, Lewis *et al.*, 2008), including parasitism and inquilinism (in which an animal characteristically lives commensally in the nest, burrow, or dwelling place of an animal of another species) in the alien gall-wasp *Andricus quercuscalicis* (Burgsdorf), which has been monitored in Britain since its arrival in the late 1950s (Schönrogge, Stone & Crawley, 1996). Very low levels of parasitism/inquilinism (one species, <0.01 inquilines per gall) were recorded up to 30 years after establishment at sites in southern England, but after an additional five years, another 12 species were recorded from the gall and the wasp larva, and the mean number of inquilines per gall had risen to 0.26 (Schönrogge *et al.*, 1996). Even after around 55 years in the invaded range, however, parasitism of the wasp remained low (<10%) (Schönrogge *et al.*, 1996, Schönrogge, Stone & Crawley, 1995).

By contrast, rapid responses of natural enemies to invaders of some taxa have been observed. For instance, parasitism of the moth *Phyllonorycter leucographella* (Zeller) reached similar levels in the introduced range (Britain) compared to the native range (Turkey) approximately 20 years after establishment (Gröbler & Lewis, 2008). The ladybird *Olla v-nigrum* (Mulsant) was assimilated even more quickly into a native ecosystem. A native of North America and Oceania (Gordon, 1985), the species was introduced to New Caledonia in early 1987, quickly becoming widespread and abundant (Chazeau, Bouyé & Bonnet de Larbogne, 1991). Parasitism by the native phorid fly *Phalacrotophora quadrimaculata* Schmitz was first recorded in the wild in 1988, and by March 1989, two years after introduction, parasitism rates of 79% were reported from some populations (15-79%, mean 39%) (Disney & Chazeau, 1990).

Previous studies (Koyama *et al.*, 2008, Hoogendoorn *et al.*, 2002, Berkvens *et al.*, 2010) found that *D. coccinellae* showed no oviposition preferences between *H. axyridis* and *C. septempunctata* but successfully eclosed significantly less often from the IAS, suggesting the species might act as a sink for the parasitoid (Berkvens *et al.*, 2010, Hoogendoorn *et al.*, 2002). Other studies have found that *H. axyridis* produces chemicals that attract *D. coccinellae* (Durieux, Fischer, Brostaux *et al.*, 2012, Richerson & DeLoach, 1972, Al Abassi, Birkett, Pettersson *et al.*, 2001). We found no evidence that the presence of *H. axyridis* affected the rate of parasitism of *C. septempunctata* by *D. coccinellae*, and hence no support for a role for apparent competition. We did find a strong site effect for parasitism of adult ladybirds by *D. coccinellae* and it is possible that high rates of parasitism of native species may lead to parasitoid spillover into *H. axyridis* populations, if the resulting large numbers of parasitoids are unable to find many native hosts after depleting the populations.  We only compared parasitism between *H. axyridis* and *C. septempunctata* and did not assess population-level effects on either host species. However, the low levels of parasitism found to date in *H. axyridis* populations suggests that the impacts of *H. axyridis* presence found by Roy *et al* (2012a) on common native ladybird species across Europe are likely to result entirely from direct interactions (predation and competition), rather than indirect interactions mediated by shared parasitoids.

*Harmonia axyridis* has aposematic colouration, strong morphological defences (spines) in the larval stage, and alkaloid-rich chemical defences at all life stages. Despite occasional observations of predation by birds, e.g. *Delichon urbicum* L. (R. Comont, personal observation) and mammals, e.g. *Rhinolophus ferrumequinum* (Shreber) (R. Comont, personal observation) and *Ursus arctos horribilis* Ord (Wang, Zhang & Zhang, 2007), predation is unlikely to have a regulatory effect on *H. axyridis* populations. Consequently, parasitism, which can reach 95% in populations of some species (Hodek *et al.*, 2012), is likely to be the dominant top-down factor regulating populations, and is effectively missing from *H. axyridis* populations in the introduced range at this early stage of invasion. The presence of several species of native parasitoid parasitising *H. axyridis* less than a decade after invasion does, however, suggest that the future recruitment of natural enemies to this abundant, albeit well-defended species is possible, particularly in the light of the documented time lags for recruitment of parasitoids to many invasive alien taxa (Cornell *et al.*, 1993, Schönrogge *et al.*, 1996, Schönrogge *et al.*, 1995, Girardoz *et al.*, 2006). Future research should focus on both the rate of parasitism and possible effects on the population dynamics of different species of ladybird.  Indeed continued monitoring of *H. axyridis*, native species of ladybird and the parasites associated with them is essential to unravelling the web of interactions around this invasive alien species.

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# Chapter 5. Assessing the relative importance of interspecific competition and intraguild interactions on invasion by the alien ladybird beetle *Harmonia axyridis.*

## 5.1. Abstract

Invasive alien species (IAS) are a major driver of biodiversity losses and environmental change. There is some evidence, however, that diverse native communities may be able to withstand or slow down invasion through impacts of competition, predation and parasitism, a phenomenon known as biotic resistance (the theory that community invasibility should increase as biodiversity decreases). The Asian harlequin ladybird *Harmonia axyridis* is a highly-successful IAS in Britain, and is thought to have detrimental effects on several native species.

We used a Generalised Linear Mixed Model approach to investigate the *H. axyridis* invasion for two years in 16 habitat patches (eight *Tilia x europaea* and eight *Urtica dioica*) across Oxfordshire, southern Britain. We examined the effect of resource abundance, habitat type, abiotic factors, and the abundance and species richness of the ladybird community on abundance of the IAS, and we also explored the abundance of native species with respect to resource abundance, habitat type, abiotic factors, and the abundance of *H. axyridis*.

We found no evidence of biotic resistance: neither abundance nor diversity of the native ladybird community had any effect on abundance of *H. axyridis*. The IAS was more abundant in areas with high aphid numbers, but this relationship was not found for native species, suggesting that *H. axyridis* may be more likely to track aphid abundance across the landscape. We found a negative relationship between abundances of *H. axyridis* and the native *Subcoccinella vigintiquattuorpunctata*, but no other evidence of a detrimental effect of *H. axyridis* on native species. This may have been a result of sampling areas of high resource availability where native species and the IAS can coexist. Overall, however, the abundance of the native *Adalia bipunctata*, suggested to be worst-affected by *H. axyridis*, was strikingly low throughout the study period.

*Harmonia axyridis* is an opportunistic aphid predator which is not constrained by the biotic resistance offered by the community of native ladybirds. At least at a site level in the resource-rich systems we assessed, native ladybird species and the IAS co-occur.

**5.2. Keywords:** biotic resistance, Coccinellidae, Coleoptera, community, invasive species

## 5.3. Introduction

Invasive Alien Species (IAS) are a major cause of environmental change (Diamond, 1984; Millennium Ecosystem Assessment, 2005; Salafsky *et al.*, 2008; UK National Ecosystem Assessment, 2011), and are thought to drive significant losses in the biological diversity and function of invaded ecosystems (Wittenberg & Cock, 2001; Hulme *et al.*, 2009). Only a small proportion of the species introduced to an area establish, and only a subset of these become invasive (Williamson & Fitter, 1996; Jeschke, 2008; Jeschke *et al.*, 2012), that is, adversely affect biodiversity, society or the economy. Consequently, much effort has been expended on determining the traits of a species which convey invasiveness: the characteristics that allow a species to arrive, exploit a new environment sufficiently well to first establish and then spread (Jeschke & Strayer, 2008; Blackburn & Jeschke, 2009; Jeschke *et al.*, 2012). More recently, focus has shifted to the traits of invaded communities (invasibility) and the differential susceptibility of different functional groups of species to invasion by a new species (Stachowicz *et al.*, 1999; Xu *et al.*, 2004; MacDougall & Turkington, 2005; King & Tschinkel, 2008).

Invasibility has been defined as 'the susceptibility of an environment to the colonisation and establishment of individuals from species not currently part of the resident community' in Davis *et al* (2005), and it has been suggested that the invasibility of an area may be as important as traits of the IAS in determining the success of invasions (Drake *et al.*, 1989; Thebaud *et al.*, 1996; Lonsdale, 1999; Davis *et al.*, 2000). The theory of biotic resistance states that invasibility should increase as community biodiversity decreases, as reduced diversity and abundance of resident native species lowers the impacts of competition and predation on an invader (Elton, 1958; MacArthur, 1972). However, empirical studies indicate both positive and negative associations between the diversity of a community and the probability of it being invaded (Byers & Noonburg, 2003). There is also evidence to suggest that different aspects of community diversity (for example species richness, relative abundance, and which key competitor, predator, parasite, or host species are present) may have varying influences on invasion success (Crawley *et al.*, 1999; Stachowicz & Byrnes, 2006; Allington *et al.*, 2013).

Consequently, emphasis has shifted to stress the importance of productivity (Davis *et al.*, 2000; Levine, 2000; Byers & Noonburg, 2003) and the availability of empty niches (niche opportunity) (Shea & Chesson, 2002) on the invasibility of an area or habitat.  For example, native ants in New Caledonia underutilise both food and habitat resources, leaving an ecological niche opportunity which is exploited by the alien lesser fire ant *Wasmannia auropunctata* (Roger), allowing it to invade, establish and spread successfully (Breton *et al.*, 2005).

The Harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is a highly successful IAS (Roy *et al.*, 2006) native to temperate Asia but now established across Europe, Africa, and both North and South America after several introductions as a biocontrol agent of aphids (Brown *et al.*, 2011b).  The species established wild populations in Britain in 2004 (Majerus *et al.*, 2006b), quickly becoming the dominant ladybird species across much of Britain (Brown *et al.*, 2008; Brown *et al.*, 2011a),  invading 38% of the 10km grid cells in mainland Britain in the first six years of invasion (2004-2009).  Availability of suitable habitat and climate are significant predictors of the likelihood of invasion of given locations by *H. axyridis* at national scales (Poutsma *et al.*, 2008; Brown *et al.*, 2011b; Kessel, 2012).

The invasiveness of *H. axyridis* is thought to be facilitated by several ecological traits (Roy *et al.*, 2012). *Harmonia axyridis* is multivoltine in Britain, in contrast to the usually-univoltine native species (Brown *et al.*, 2008) possibly allowing this species to better exploit seasonally available resources such as aphids. This, along with high individual fecundity (Wang *et al.*, 2009), is also thought to have played a major role in the rate with which *H. axyridis* became the dominant species in Britain (Brown *et al.*, 2008).  The species is well-defended, with large larval spines and strong chemical defences (Ware & Majerus, 2008; Sloggett *et al.*, 2011).  It has good dispersal capabilities, both natural and anthropogenically-assisted, uses a broad range of habitats, climates, and diets, and, although the species primarily feeds on aphids, it can act as an intraguild predator within the aphidophagous guild (Ware *et al.*, 2005; Majerus *et al.*, 2006b; Roy & Wajnberg, 2008; Berkvens *et al.*, 2009; Brown *et al.*, 2011b).  In Britain, *H. axyridis* may also be better able to utilise disturbed habitats than other ladybird species, being particularly abundant in urban and suburban areas, where adults frequently overwinter in houses (Roy *et al.*, 2011).

In this study we aim to better understand the role of native biodiversity and the mechanisms of intraguild predation (IGP) versus competition for aphid prey in governing *H. axyridis* invasion success and impacts by quantifying local scale patterns in ladybirds and aphid communities in a region of Britain very recently invaded by *H. axyridis.* The arrival and spread of this large predatory ladybird has had detectable effects on native species. *Harmonia axyridis* has been linked to national declines in several native ladybird species (Brown *et al.*, 2011a; Roy *et al.*, 2012; Comont *et al.*, in press (Chapter 3)). The exact mechanism of impact is unclear, but *H. axyridis* is known to prey upon native ladybird species both in laboratory tests (Kajita *et al.*, 2006; Ware & Majerus, 2008; Ware *et al.*, 2009) and in the wild (Hautier *et al.*, 2008; Thomas *et al.*, 2013), but may also affect native species indirectly by outcompeting them for shared prey (Brown & Miller, 1998; Brown, 2003; Takizawa & Snyder, 2012).

By examining the community context that favours establishment of this IAS at a local scale, we may be able to unpick the role of direct intraguild predation versus competition with native species for aphid prey in governing *H. axyridis* invasion success and impacts. For example, if intraguild predation is key to invasion success, we predict that population abundance of *H. axyridis* will be positively affected by the diversity or abundance of all native ladybirds and the abundance of poorly defended native ladybirds would be negatively impacted by *H. axyridis*, with both effects being more pronounced when aphid abundance is low. If competition for aphid prey is a key constraint on invasion success, we would predict that *H. axyridis* abundance will have a strong positive association with aphid abundance and a negative association with either the total abundance of aphidophagous species or with the abundance of individual voracious aphidophagous species that represents a key competitor. If *H. axyridis* is constrained neither by competition for aphid prey or availability of ladybird prey for intra-guild predation, then we would expect only a positive association with aphid abundance.

Here we examine reciprocal relationships between abundance of native ladybirds and *H. axyridis* in sites with differing aphid availability and abiotic factors (sub-optimal herb layer versus optimal arboreal habitat, elevation). We aim to test the following hypotheses:

(1) *Harmonia axyridis* abundance is not affected by the diversity of the resident ladybird community but is determined by the availability of aphids and favourable abiotic factors.

(2) *Harmonia axyridis* abundance is affected to a greater extent by the abundance of species within the aphidophagous guild (suggesting competition for aphid prey) rather than the overall abundance of all native ladybird species (suggesting IGP as an important factor).

(3) Impacts of *H. axyridis* are more pronounced on species within the aphidophagous guild than on species from other guilds (suggesting competition for aphid prey).

## 5.4. Methods

### 5.4.1. Ladybird and aphid sampling

Sixteen field sites (eight patches of nettles, *Urtica dioica* L and eight patches of lime trees, *Tilia x europaea*) were surveyed in an area in the south of Britain measuring 16 km E-W and 22 km N-S, bounded by Marston, Oxford (SP529073), in the northwest and Nettlebed, Oxfordshire (SU677877), in the southeast. Elevation ranged from 44 to 209 metres above sea level. Field sites were visited between the 13th and 48th weeks of the year (the first week of April to the first week of December) in both 2010 and 2011. Eight sites (four *T. x europaea*, four *U. dioica*) were visited each week and the remaining eight sites (also four *T. x europaea*, four *U. dioica*) were visited the week after, so that each individual site was visited once every two weeks, 19 times per year. Elevation data was taken from the 1:50,000 Ordnance Survey map (sheets 164, 165, 174, 175).

At each site, adult ladybirds were sampled for 15 minutes either using a sweep-net (at *U. dioica* sites) or a beating tray (*T. x europaea* sites). Time spent identifying and recording the catch, which varied depending on the abundance and diversity of ladybirds at each site, was additional to the 15 minute survey time. The number of aphids present on 100 leaves was also recorded on each site visit, from branches and areas not surveyed for ladybirds, but in close proximity to them in the same patch of habitat.

Native ladybirds were aggregated into feeding guilds: primarily aphid-feeding (aphidophagous) species, primarily mildew-feeding (mycophagous), and the single phytophagous, *Subcoccinella vigintiquattuorpunctata* (L). For each site and year combination, mean weekly abundance was calculated for these guilds and for seven individual native ladybird species (*C. septempunctata*, *S. vigintiquattuorpunctata*, *Propylea quattuordecimpunctata* (L), *Adalia decempunctata* (L), *Calvia quatuordecimguttata* (L), *Halyzia sedecimguttata* (L), and *Psyllobora vigintiduopunctata* (L)) as well as *H. axyridis* and total aphids.

### 5.4.2. Analysis

Local-scale abundance models for each native ladybird species and guild and for *H. axyridis* were formulated as Generalised Linear Mixed Models (GLMMs) with a Poisson error distribution and a site random effect. Models were fitted using the statistical language R version 2.15.2 (R Development Core Team, 2012) and the LME4 package (Bates *et al.*, 2011). For each native species or guild, per-site counts were related to five predictors: year, elevation and habitat type (*U. dioica* or *T. x europaea*), (logged) aphid abundance and the abundance of *H. axyridis*. These models were compared to equivalent models with an added interaction between habitat type and aphid abundance, but these interaction models possessed less explanatory power so the non-interaction models were retained (data not shown).

For *H. axyridis*, five models were fitted each containing a different measure of native ladybird biodiversity, in addition to year, elevation, habitat type and aphid abundance. These measures were mean abundance of native ladybirds, mean abundance of aphidophagous native ladybirds, species richness of native ladybirds, species richness of aphidophagous native ladybirds, and mean abundance of the commonest native ladybird, *Coccinella septempunctata* (L). More complex measures of community diversity (Simpson’s diversity index, 1-D) possessed less explanatory power than did the equivalent species richness models.

The five models including native biodiversity terms were compared to a four-predictor model without such a term. The most parsimonious models amongst these six models was selected using an Akaike information criterion (AIC) approach (Akaike, 1974) where a drop in AIC of at least 2 was required to retain a native biodiversity term in the final model. Each of these models was also compared to an equivalent model with an added interaction between habitat type and aphid abundance, but the addition of this interaction term did not improve model fit.

The conformity of the models to the data was examined using adjusted deviance (Pierce & Schafer, 1986). Variance explained was calculated as the marginal $R^2$ (R2GLMM(m)) of Nakagawa and Schielzeth (2013). Spatial autocorrelation in the model residuals was examined in neighbourhoods ranging from 0.1 km to 25 km using the Moran's I test from the spdep package (Bivand *et al.*, 2013) and the correlog function from the ncf package (Bjornstad, 2012).

## 5.5. Results

There was considerable cross-site variation in the abundance of native ladybird species (Fig. 5.1) and ladybird guilds (Fig. 5.2). The mean number of ladybird individuals recorded per site in 2010 was 227 (range 47-612), of six species (3-9): in 2011, the figures were 305 (107-761) individuals of eight (5-10) species. In total 8503 ladybirds were found: of these, the most abundant species was the aphidophagous native *C. septempunctata* (3619 individuals, mean 113 individuals per site per year). It was one of only two species recorded at every site: the other was the IAS *H. axyridis* (2645 individuals, mean 83 species per site per year).

No effect of native ladybird biodiversity on *H. axyridis* abundance was detected. All models containing a measure of native ladybird biodiversity had higher AIC values than the models containing abiotic predictors and aphid abundance. The variance explained by the best model (environment-only, 1. in Table 5.1) was 0.793 (Table 5.1). The best performing measure of native ladybird diversity, the abundance of aphidophagous species, was not significantly related to abundance of *H. axyridis*, whereas site elevation, habitat type, and aphid abundance all were (Table 5.2). *Urtica dioica* sites contained fewer *H. axyridis* than did *T. x europaea* sites, and higher sites contained fewer *H. axyridis* than did lower sites, while aphid abundance was positively correlated with *H. axyridis* abundance (Table 5.2).

**Fig. 5.1. Boxplots of the variation in logged mean weekly abundance for the years 2010 and 2011 for each ladybird species** (*Harmonia axyridis, Halyzia sedecimguttata, Propylea quattuordecimpunctata, Psyllobora vigintiduopunctata, Subcoccinella vigintiquattuorpunctata, Adalia bipunctata, Adalia decempunctata, Calvia quatuordecimguttata, Coccinella septempunctata*), and for aphid abundance (aphids). Plotted whiskers extend to the minimum and maximum values, the box to the 25th and 75th percentiles, and the star is the median value.

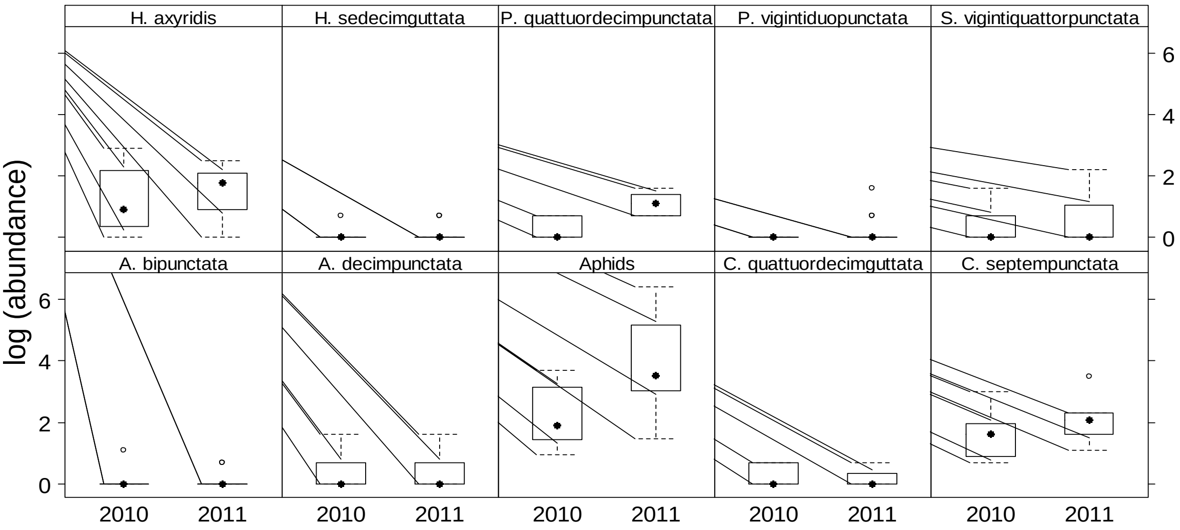

**Fig. 5.2. Boxplots of the variation in logged mean weekly abundance for the years 2010 and 2011 for aphid abundance and the two multi-species ladybird guilds (aphidophagous and mycophagous) guild**. Plotted whiskers extend to the minimum and maximum values, the box to the 25th and 75th percentiles, and the star is the median value.

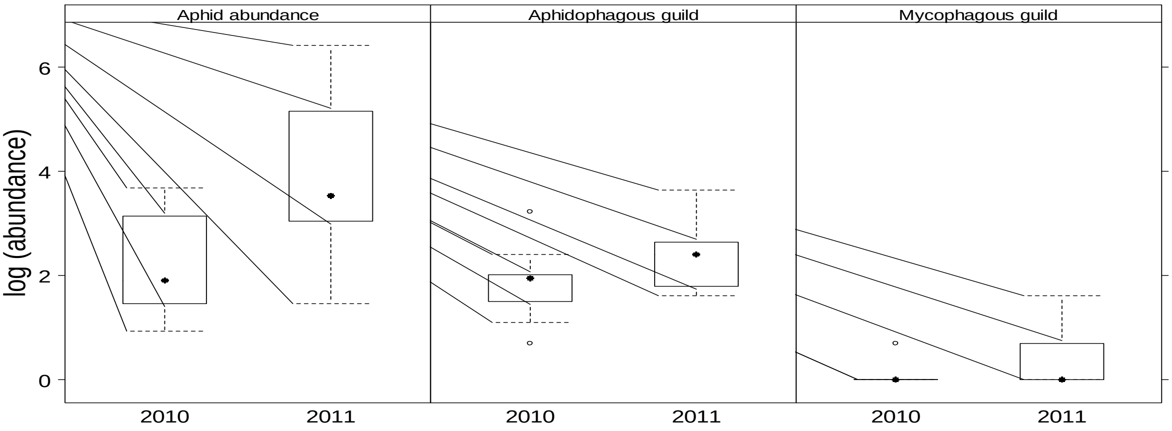

**Fig. 5.3. Boxplots of the logged values across sites of aphid abundance and the modelled measures of the biodiversity of the native ladybird community** (total abundance and species richness of aphidophagous and all native ladybirds, and abundance of *C. septempunctata*), used as potential explanatory variables for the abundance of *H. axyridis*. Plotted whiskers extend to the minimum and maximum values, the box to the 25th and 75th percentiles, and the star is the median value.

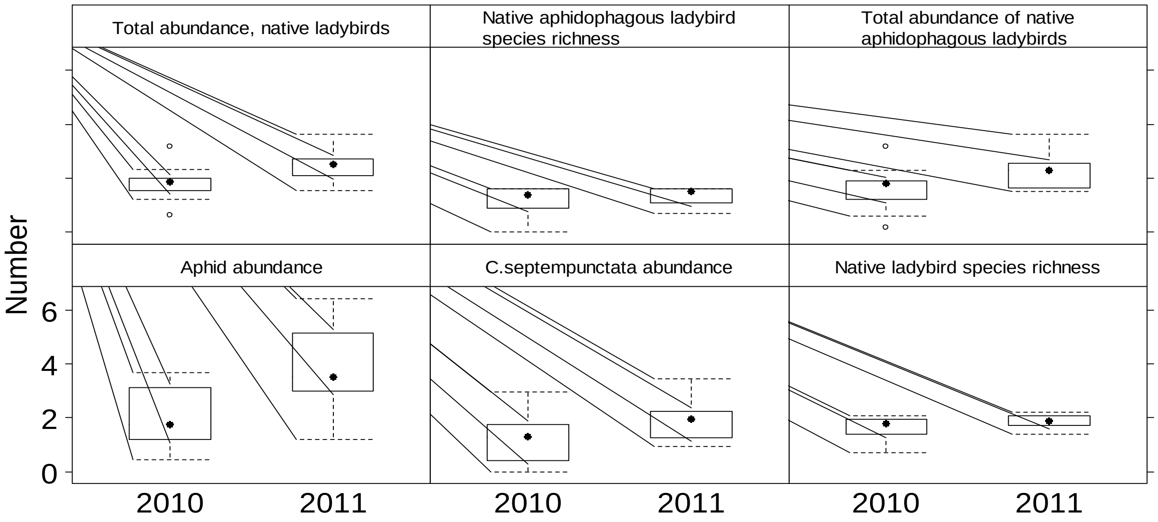

**Table 5.1. Goodness of fit of *Harmonia axyridis* abundance modelled against abiotic and biotic factors at 16 sites across Oxfordshire.** Model 1 (M1) contains elevation, habitat type, aphid abundance and year, while the bottom five models each contain one of five separate measures of the biodiversity of the native ladybird community (total abundance and species richness of aphidophagous and all native ladybirds, and abundance of *C. septempunctata*). Delta AIC values indicate the difference from AIC of the best model when the explanatory variable in question is dropped from it.

| Predictors in the model | AIC | ΔAIC from best model | Deviance | Variance explained | Moran's I | p-value of Moran test |
|---|---|---|---|---|---|---|
| M1. Elevation, habitat type, aphid abundance, year | 51.4 | - | 37.41 | 0.793 | -0.0057 | 0.314 |
| M1. + Total abundance of native aphidophagous ladybird species | 51.7 | 0.33 | 35.74 | 0.787 | -0.0036 | 0.276 |
| M1. + Total abundance of native ladybirds | 52.1 | 0.66 | 36.07 | 0.790 | -0.0025 | 0.257 |
| M1. + Native ladybird species richness | 52.9 | 1.51 | 36.92 | 0.793 | -0.0055 | 0.390 |
| M1. + *Coccinella septempunctata* abundance | 53.0 | 1.57 | 36.98 | 0.788 | -0.0054 | 0.307 |
| M1 + Species richness of native aphidophagous ladybirds | 53.2 | 1.77 | 37.18 | 0.792 | -0.0056 | 0.312 |

A close correspondence between observed and predicted abundance patterns from models was obtained for three native species (*P. quattuordecimpunctata*, *A. decempunctata*, and *S. vigintiquattuorpunctata*), and for the aphidophagous guild. The model for *C. septempunctata* was significantly better than the equivalent null model, but variance explained was low (0.268), and there was no significant impact of habitat type, site elevation or aphid abundance, only of year (Table 5.3).

Abundance of *S. vigintiquattuorpunctata* (the only phytophagous species found) was negatively associated with abundance of *H. axyridis*, while abundance of both *A. decempunctata* (aphidophagous) and the guild of native aphidophagous ladybirds was positively associated with *H. axyridis* abundance (Tables 5.4 and 5.5). No significant impacts of habitat type, site elevation or aphid abundance on the abundance of native ladybird species, or feeding guilds could be detected, although there was a significant positive effect of year for *C. septempunctata, P. quattuordecimpunctata* (both aphidophagous) (Table 5.4), and the aphidophagous ladybird guild (Table 5.4).

**Table 5.2. The effects of biotic (aphid abundance and habitat) and abiotic (year and elevation) explanatory variables on *Harmonia axyridis* abundance at 16 sites across Oxfordshire**. (a) Coefficients for the best model of *H. axyridis* ladybird abundance containing year, site elevation, habitat type, aphid abundance versus (b) coefficients for the second best model, containing all the variables of the best model plus the abundance of native aphidophagous ladybird species. Delta AIC values indicate the difference from AIC of the best model when the explanatory variable in question is dropped from it.

| Explanatory variables | (a) Coefficients | Z value | Δ AIC | p-value | (b) Coefficients | Z value | Δ AIC | p-value |
|---|---|---|---|---|---|---|---|---|
| (intercept) | 672.76 ± 391.94 | 1.716 | - | 0.086 | 977.90 ± 462.95 | 2.112 | - | 0.035 |
| Aphid abundance | 0.44 ± 0.10 | 4.247 | 17.23 | <0.0001 | 0.43 ± 0.10 | 4.185 | 17.30 | <0.0001 |
| Habitat (*U. dioica* compared to *T. x europaea*) | -1.42 ± 0.31 | -4.632 | 12.55 | <0.0001 | -1.30 ± 0.32 | -4.059 | 8.98 | <0.0001 |
| Year | -0.33 ± 0.20 | -1.713 | 0.95 | 0.087 | -0.49 ± 0.23 | -2.109 | 2.51 | 0.035 |
| Elevation | -0.013 ± 0.0058 | -2.194 | 4.77 | 0.028 | -0.012 ± 0.0059 | -1.971 | 3.12 | 0.049 |
| Total abundance of native aphidophagous ladybirds | - | - | - | - | 0.024 ± 0.019 | 1.301 | -0.30 | 0.1933 |

**Table 5.3. Native ladybird species abundances modelled against year, site elevation, habitat type, aphid abundance, and abundance of *H. axyridis*, at 16 sites across Oxfordshire**, monitored every two weeks for two years. Only models better than the equivalent null model are shown and variance explained is calculated as the marginal R2 (R2GLMM(m)) of Nakagawa and Schielzeth, 2013.

| **Species/group** | **AIC** | **ΔAIC from null model** | **Deviance** | **Variance explained** | **Moran's I** | **p-value of Moran's test** |
|---|---|---|---|---|---|---|
| *Coccinella septempunctata* | 67.81 | 3.45 | 51.81 | 0.268 | -0.00020 | 0.221 |
| *Propylea quattuordecimpunctata* | 29.13 | 15.53 | 13.13 | 0.644 | 0.034 | 0.011 |
| *Adalia decempunctata* | 18.93 | 20.24 | 2.93 | 0.990 | -0.0088 | 0.363 |
| *Subcoccinella vigintiquattuorpunctata* (phytophagous guild) | 34.35 | 12.55 | 18.35 | 0.988 | -0.025 | 0.769 |
| Aphidophagous guild (native species only) | 57.94 | 16.96 | 41.94 | 0.449 | -0.011 | 0.424 |

**Table 5.4.** Importance of individual explanatory variables for native ladybird species and guild abundances, modelled against year, site elevation, habitat type, aphid abundance, and abundance of *H. axyridis*, at 16 sites across Oxfordshire monitored every two weeks for two years. Delta AIC values indicate the difference from AIC of the best model when the explanatory variable in question is dropped from it. Rows in bold are significant at the 0.05 level. Only models better than the equivalent null model are shown.

| Species | Explanatory variables | Coefficients | Δ AIC | p-value |
|---|---|---|---|---|
| *Coccinella septempunctata* | **(intercept)** | **-1437.24 ± 416.86** | **-** | **0.00057** |
| | Aphid abundance | -0.11 ± 0.09 | -0.28 | 0.19 |
| | *Harmonia axyridis* | 0.073 ± 0.05 | 0.35 | 0.12 |
| | Habitat (*U. dioica*) | 0.43 ± 0.38 | | 0.26 |
| | Elevation | -0.0031 ± 0.0035 | -1.23 | 0.38 |
| | **Year** | **0.72 ± 0.21** | **7.55** | **0.00056** |
| *Propylea quattuorpunctata* | **(intercept)** | **-2920.18 ± 1052.078** | **-** | **0.0055** |
| | Aphid abundance | 0.19 ± 0.20 | -1.09 | 0.34 |
| | *Harmonia axyridis* | 0.076 ± 0.066 | -0.65 | 0.25 |
| | Habitat (*U. dioica*) | -0.19 ± 0.57 | -1.89 | 0.74 |
| | Elevation | 0.0042 ± 0.0048 | -1.26 | 0.39 |
| | **Year** | **1.45 ± 0.52** | **7.44** | **0.0055** |
| *Adalia decempunctata* | (intercept) | -409.033 ± 934.019 | - | 0.66 |
| | Aphid abundance | 0.23 ± 0.52 | -1.8 | 0.66 |
| | ***Harmonia axyridis*** | **0.12 ± 0.054** | **2.98** | **0.023** |
| | Habitat (*U. dioica*) | -22.01 ± 15537.085 | 11.07 | 0.99 |
| | Elevation | -0.019 ± 0.023 | -0.54 | 0.40 |
| | Year | 0.20 ± 0.46 | -1.81 | 0.66 |
| *Subcoccinella vigintiquattuorpunctata* (phytophagous guild) | (intercept) | 1250.55 ± 35463.50 | - | 0.97 |
| | Aphid abundance | 0.77 ± 0.42 | 1.04 | 0.068 |
| | ***Harmonia axyridis*** | **-0.59 ± 0.24** | **3.26** | **0.016** |
| | Habitat (*U. dioica*) | 22.72 ± 35399.62 | 5.3 | 0.99 |
| | Elevation | -0.0060 ± 0.0092 | -1.54 | 0.51 |
| | Year | -0.63 ± 1.059 | -1.65 | 0.55 |
| Aphidophagous guild (native species only) | **(intercept)** | **-1220.98 ± 339.71** | - | **0.00033** |
| | Aphid abundance | -0.021 ± 0.074 | -1.92 | 0.78 |
| | ***Harmonia axyridis*** | **0.081 ± 0.035** | **3.03** | **0.023** |
| | Habitat (*U. dioica*) | 0.099 ± 0.30 | -1.89 | 0.74 |
| | Elevation | -0.0025 ± 0.0029 | -1.24 | 0.38 |
| | **Year** | **0.61 ± 0.17** | **10.14** | **0.00032** |

Abundance patterns of *H. sedecimguttata*, *C. quattuordecimguttata*, *P. vigintiduopunctata*, and the mycophagous guild were unrelated to any of explanatory variables, and so these models are not discussed further. There was no significant spatial autocorrelation between sites or in model residuals.

## 5.6. Discussion:

The abundance of *H. axyridis* at a site appears to be driven by both habitat type and aphid abundance, rather than by the abundance or diversity of the native ladybird community. *Harmonia axyridis* was more abundant in trees (*T. x europaea*) than in low vegetation (*U. dioica*), at lower elevations, and at sites with high aphid abundance than at sites with fewer aphids present. Our study showed no evidence of a link between the abundance of *H. axyridis* and the native ladybird community, whether measured as abundance or richness of all native ladybirds present, just the aphidophagous species, or the abundance of an ecologically-equivalent competitor (*C. septempunctata*). Abundance of the aphidophagous guild, *C. septempunctata* and *P. quattuordecimpunctata* all had a significant relationship with year. This is likely to be the result of year-to-year variation in the wider environment, and to reflect the effect of an unmeasured abiotic variable, potentially climatic, as changes in the wider environment will affect both diversity and abundance of the local species pool.

We focused on two habitats which are favourable for several ladybird species, particularly *H. axyridis*, and which harbour high abundance of aphids. Resource-rich habitats have been suggested to favour invasion even in the continuing presence of a diverse native community (Byers & Noonburg, 2003). This is thought to be due to either competition between native species for resources indirectly facilitating the IAS (Levine, 1976; Levine & D’Antonio, 1999), or increased resource availability leading to under-exploitation by native species (McCann *et al.*, 1998; Breton *et al.*, 2005). There is some suggestion that aphid colonies may often not be regulated by top-down pressures such as predation for at least the growth phase of their existence (Kindlmann & Dixon, 1999; Kindlmann & Dixon, 2001) (but see Rutledge *et al.*, 2004; Ragsdale *et al.*, 2011), so may be under-exploited by native ladybirds, leaving a niche at least partially vacant for *H. axyridis* to exploit upon arrival.

In contrast to *H. axyridis*, the abundance of native species or guilds of ladybirds was not associated with aphid abundance. This indicates that *H. axyridis* is more likely than natives to be found in large numbers where aphids are abundant, suggesting that the species may be more opportunistic than natives, and possibly more likely than native species to track aphid abundance across the landscape.

The IAS is a habitat generalist species, and so is not restricted to the aphids present in any one habitat type (Majerus *et al.*, 2006a). This enhanced foraging behaviour may explain how the IAS is able to be regularly multivoltine in areas where native species are usually univoltine, as by tracking aphid abundance *H. axyridis* may be able to maximise its feeding rate, so taking in more energy more quickly than would be possible if not remaining in areas with high aphid abundance. This extra energy can then be used for reproduction.

There is considerable evidence that *H. axyridis* has negative effects on native ladybird species, both at a national (Roy *et al.*, 2012) and local (Brown *et al.*, 2011a) scales. Additionally, a similar study of ladybirds in arboreal habitats in Cambridgeshire recorded the impact of the arrival of *H. axyridis* as it increased from 0.1% of the ladybirds encountered to 40%, and native aphidophagous ladybirds decreased from a mean 19.7 individuals per survey in 2006 to 10.2 individuals per survey in 2008 (Brown *et al.*, 2011a). The IAS is known to be a strong intra-guild predator of most other ladybird species at the larval stage (Ware & Majerus, 2008; Thomas *et al.*, 2013). As the beneficiary of unidirectional intra-guild predation (IGP) (Ware & Majerus, 2008), it is possible that the presence of native ladybird species represents potential prey items, rather than competitors for *H. axyridis*. In our study system we were unable to detect an overall relationship between *H. axyridis* abundance and the abundance of native species, and only one species, *S. vigintiquattuorpunctata*, was found to be negatively associated with *H. axyridis* abundance. This is a small phytophagous ladybird species which does not compete for food with the IAS. It is probable that the negative relationship between abundance of the two species has arisen through niche separation caused by their different habitat and dietary requirements. *Subcoccinella vigintoquattuorpunctata* is largely a grassland species which feeds on grasses and clovers, whereas *H. axyridis* is a habitat and dietary generalist species, with preferences for arboreal habitats and aphid prey (Roy *et al.*, 2011; Hodek *et al.*, 2012). There are no records of predation between the two species in the literature, although it is entirely possible that this predation is occurring but has been overlooked, as *S. vigintiquattuorpunctata* is a very small species (Roy *et al.*, 2011).

One species which is known to be detrimentally affected by the presence of *H. axyridis* is *Adalia bipunctata* (L) (Roy *et al.*, 2012; Thomas *et al.*, 2013), and the low abundance of this species during the study period was also striking. Formerly one of the most widespread and abundant ladybirds in Britain (Roy *et al.*, 2011), it is possible that a decline in this species due to *H. axyridis* has preceded the study period. *Adalia bipunctata* has a high niche overlap with *H. axyridis* (77% on the plant use similarity index of Adriaens *et al* (2008)), and chemical and morphological defences which are ineffective against the IAS (Kajita *et al.*, 2006; Ware & Majerus, 2008; Ware *et al.*, 2009). Several previous studies, both in laboratory conditions (Ware & Majerus, 2008; Ware *et al.*, 2009) and in the field at the *H. axyridis* invasion front (Brown *et al.*, 2011a; Roy *et al.*, 2012) found the negative effects of *H. axyridis* were particularly pronounced on *A. bipunctata*, and the species has declined massively in terms of both abundance and distribution since the arrival of *H. axyridis* (Roy *et al.*, 2012). In our study it was only the 7th most abundant species, with just 140 individuals encountered (1.6% of the total) during 61 of the 560 site visits and 140 hours of sampling. By contrast, the two other common generalist native aphidophagous species, *C. septempunctata* and *P. quattuordecimpunctata*, were encountered during 370 site visits (3619 individuals, 42.6%) and 200 site visits (702 individuals, 8.3%), respectively.

The abundances of the aphidophagous ladybird *A. decempunctata*, and indeed the guild of aphidophagous native ladybirds as a whole, were positively correlated with *H. axyridis* abundance. This is probably a consequence of aphidophagous species aggregating within favourable areas (suitable habitat with high aphid abundance). Ladybirds have previously been shown to avoid potentially harmful areas for themselves and their offspring, such as leaves with high numbers of conspecific tracks (Agarwala & Dixon, 1992) or soil, leaves and cadavers with high levels of the pathogenic fungus *Beauvaria bassiana* (Balsamo) Vuillemin (Ormond *et al.*, 2011), but we found no evidence of avoidance of *H. axyridis* by aphidophagous native ladybirds.

Clearly, competing species (and those which prey on each other) can and do live alongside each other, and our findings show that native species do co-exist with *H. axyridis*. This may be because, in the resource-rich, favourable habitats we studied, aphid abundance is generally high enough to support several species, even with minimal niche separation. It would be interesting to examine whether this holds true in less resource-rich areas, and whether *H. axyridis* would be able to become a dominant species, perhaps via competitive exclusion. Alternatively, suboptimal areas might act as refugia for native species, as has been found in the USA (Evans, 2004).

Ladybirds in Britain occupy a wide range of habitat types with differing degrees of habitat specialisation, from species resident only on shingle riverbanks to habitat generalists found almost anywhere (Roy *et al.*, 2011). Consequently, we could only study the dynamics of a limited subset of the British ladybird fauna. This study was not carried out across the full range of available habitat types, and we did not examine occupancy of *H. axyridis*: we were only concerned with relative abundance of the different ladybird species in patches of two types of favourable habitat. It would be interesting to explore the effects of native ladybird community composition on invasion success by comparing sites within the invasion zone in which *H. axyridis* has and has not established populations some years after initial invasion. There are also many non-ladybird members of the aphidophagous guild, including syrphid (hover-fly) and neuropteran (lacewing) larvae, which may also influence biotic resistance to the *H. axyridis* invasion (Lucas *et al.*, 1998), and it would be desirable to assess these in future surveys. It would also be of interest to manipulate aphid abundance within the studied habitats in order to evaluate the role of resource richness in structuring the ladybird community.

In summary, *H. axyridis* is an opportunistic aphid predator which is not constrained by the biotic resistance offered by the community of native ladybirds, whether aphidophagous species, all species present, or the most ecologically-similar native species. At least at a site level and in the resource-rich systems we assessed, native ladybird species and the IAS co-occur, which may lay the foundations for the large-scale declines in native species found by Roy *et al* (2012).

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# Chapter 6. General discussion.

## 6.1. Introduction

Invasive alien species (IAS) have long been recognised as a significant component of environmental change worldwide, and their arrival has often been followed by a significant loss in the biological diversity and function of invaded ecosystems (Wittenberg & Cock, 2001; Millennium Ecosystem Assessment, 2005; Hulme *et al.*, 2009; UK National Ecosystem Assessment, 2011). The likelihood of establishment, rate of spread and magnitude of any effects of the IAS are partly mediated by the composition of the native communities affected, however, through processes including predation, parasitism, competition and biotic resistance (Stohlgren *et al.*, 1999; Davis *et al.*, 2000; Levine, 2000; Fridley *et al.*, 2007).

Therefore, a greater understanding of the community interactions between native species and IAS is important, particularly as rates of introduction of alien species are increasing rapidly (Pyšek *et al.*, 2009; Roy *et al.*, 2011a). Increased understanding of these processes enables better prediction of the species likely to establish and become invasive in different ecosystem contexts, and more accurate forecasting of the effects of IAS, feeding back into introduction risk assessments and watch-lists such as those maintained by the Great Britain Non-Native Species Information Portal (GB-NNSIP, www.nonnativespecies.org) and the European and Mediterranean Plant Protection Organisation (EPPO, www.eppo.int) (van Lenteren, 2006; van Lenteren *et al.*, 2006; Pyšek *et al.*, 2011).

## 6.2. Recent arrivals of new ladybird species in Britain

The British ladybird fauna has changed considerably over the last twenty years (Roy *et al.*, 2011b; Roy *et al.*, 2013). Five species have significantly increased in distribution, eleven have decreased significantly, and several species have become established (Roy *et al.*, 2011b). These include the herbivorous Mediterranean ladybird *Henosepilachna argus* (Geoffroy) (Menzies & Spooner, 2000) and two small, closely-related coccidophagous species, *Rhyzobius chrysomeloides* (Herbst) (Hawkins, 2000) and *R. lophanthae* (Blaisdell) (Booth, 2000). Most recently, the thirteen-spot ladybird, *Hippodamia tredecimpunctata* L. has possibly re-colonised the south coast (Comont & Willerton, 2012). By far the best-known arrival, however, is that of the harlequin ladybird *Harmonia axyridis* (Pallas). This species has become invasive across Europe, Africa and both North and South America since establishing in the southern USA in 1988 (Gordon & Vandenberg, 1991; Brown *et al.*, 2011). It became established in Britain during 2004, and spread rapidly across the country (Brown *et al.*, 2008).

*Harmonia axyridis* was documented as having detrimental effects on native species in North America (Snyder *et al.*, 2004), and this, coupled with the invasive traits of the species, meant its arrival within Britain was met with concern (Majerus *et al.*, 2006a). However, the establishment and spread of this species was also seen as a unique opportunity to track the spread of an IAS whilst also monitoring impacts on native ladybird species. Therefore, two on-line surveys were launched as part of the Biological Records Centre Coccinellidae Recording Scheme: the Harlequin Ladybird Survey, www.harlequin-survey.org, and the UK Ladybird Survey, www.ladybird-survey.org) (Brown *et al.*, 2008; Brown *et al.*, 2010). The tens of thousands of records submitted to these surveys from people across Britain have enabled the research within this thesis. This was to examine the responses of native UK ladybirds to the arrival of this IAS, to establish the effect of *H. axyridis* on native ladybird species when compared to other environmental drivers, and to investigate the possible facilitation of the *H. axyridis* invasion by natural enemy release.

## 6.3. Predicting ladybird distribution patterns from traits

Exploring the ecological traits of all species of ladybird in Britain, alongside the distribution patterns of these species, revealed a number of significant correlations (Chapter 2: Comont *et al.*, 2012). It was found that, in general, as largely predatory taxa, ladybird range size and fill are better-correlated with diet breadth than with measures such as habitat specificity (Chapter 2: Comont *et al.*, 2012). This has also been found in other taxa, e.g. Sphingidae (Lepidoptera) (Quinn *et al.*, 1997; Beck & Kitching, 2007; Garcia-Barros & Benito, 2010), suggesting that diet breadth may be a key niche-breadth determinant. This is particularly likely for predatory groups, where prey availability is a major determinant of patch suitability (chapter 2: Comont *et al.*, 2012).

Predatory ladybirds exploit a range of prey species (Mills, 1981; Hodek *et al.*, 2012). A distinction can be drawn between essential food sources, which are those on which the ladybird can feed solely while retaining the ability to mature and reproduce, and alternative food sources, which are those on which the ladybird can survive, but without reproducing (Hodek & Honek, 1996). In general, however, dietary generalists such as *H. axyridis* are likely to be able to persist for longer in less favourable areas than diet specialists, and so fill a larger range more completely (chapter 2). Climate envelope modelling also suggests that *H. axyridis* is unlikely to be majorly climatically-restricted in Britain, with the possible exception of the Scottish highlands (Poutsma *et al.*, 2008), so it seems likely that the IAS will continue to spread nationwide. It is worth noting, that even habitat- and dietary-generalist species such as *H. axyridis* are affected by many factors other than climate (for instance LaMana and Miller (1996) found the species to be abundant in arboreal habitats but infrequent in alfalfa, clover and peppermint in close proximity). This means that pure climate-envelope models should be taken as an estimate of the extent of the fundamental climatic niche rather than the eventual realised niche, which will depend on many other biotic and abiotic factors. The relatively slow spread of *H. axyridis* in Britain after 2006 when compared to the 2004-6 rate of spread (UK Ladybird Survey, unpublished data) may suggest that the species is nearing the full extent of its realisable niche in mainland Britain.

## 6.4. Effects of *Harmonia axyridis* on other species

*Harmonia axyridis* became established in south-eastern England in late 2004 and spread rapidly, reaching Cornwall and Wales in the west and Yorkshire in the north by 2006, a rate of 144.5 km/yr westwards and 58 km/yr northwards. This spread is likely to have detrimental effects on native species. Laboratory experiments have found larvae of many native ladybird species to be susceptible to intraguild predation (IGP) by larvae of *H. axyridis* (Kajita *et al.*, 2006; Ware & Majerus, 2008), and in-field predation of at least two native species (*Adalia bipunctata* (L.) and *A. decempunctata* (L.)) by *H. axyridis* has been confirmed (Thomas *et al.*, 2013).

At a landscape scale, *H. axyridis* has been strongly linked to declines in both abundance and distribution (at a 1-km$^2$ grid-square level) of several of the commonest native species (Roy *et al.*, 2012). Chapter 3 expands this approach to consider local-scale (1-km$^2$ grid square) extinctions of native species in the context of habitat and climate factors, species-level traits, and spatial, temporal and niche overlap with *H. axyridis*. Dietary niche overlap with *H. axyridis* was one of two major correlates of local extinction in native species (the other was urbanisation), and so *H. axyridis* constitutes a key biotic environmental pressure on native ladybirds, with species-specific impacts dependent on overlap of resource use of individual species with the IAS (Chapter 3). However, the only environmental factor that both increased the likelihood of local extinction and reduced that of colonisation was the percentage of urban land cover. Despite the detrimental effects of *H. axyridis* on native species, and although gardens and parks in urban areas often seem to be favourable for some individual ladybird species (Roy *et al.*, 2011b), habitat destruction seems to be playing a major role in the decline of native ladybird species.  This is particularly concerning in light of predictions by the Department for the Environment, Food & Rural Affairs (Defra) that, in England alone, there will be a net 171,600 hectares converted from rural use to urban between 1991 and 2016, 2% of the land area of the country (Anon., 2006).

One species which is known to be detrimentally affected by the presence of *H. axyridis* is *A. bipunctata* (Roy *et al.*, 2012; Thomas *et al.*, 2013).  Formerly one of the most widespread and abundant ladybirds in Britain (Roy *et al.*, 2011b), the proportion of 1 km$^2$ grid squares this species has been recorded from in Britain has declined by 44% since the arrival of *H. axyridis* (Roy *et al.*, 2012).  In systematic surveys, the numbers of individuals of *A. bipunctata* has declined by 47% in Britain since the arrival of *H. axyridis* (Roy et al 2012). Perhaps unsurprisingly, this species was strikingly low in abundance during the field surveys described in Chapter 4.  *Adalia bipunctata* has a high niche overlap with *H. axyridis* (77% on the plant use similarity index of Adriaens *et al* (2008)), and the chemical and morphological defences of *A. bipunctata* appear to be ineffective against the IAS (Kajita *et al.*, 2006; Ware & Majerus, 2008; Ware *et al.*, 2009).  During the study period *A. bipunctata* was only the 7th most abundant species, with just 140 individuals recorded (1.6% of the total) during 61 of 560 site visits and 140 hours of sampling.  By contrast, the two other common generalist native aphidophagous species, *Coccinella septempunctata* (L.) and *Propylea quattuordecimpunctata* (L.), were noted during 370 site visits (3619 individuals, 42.6%) and 200 site visits (702 individuals, 8.3%), respectively.  This is in line with equivalent studies which found declines in abundance of *A. bipunctata* of 47.2% (eastern England), 57.1% (Switzerland), and 87.7% (Belgium) after the arrival of *H. axyridis* (Roy et al., 2012).

The importance of dietary niche overlap with *H. axyridis*, particularly compared to habitat niche overlap, suggests that competition for food could be the most important mechanism by which *H. axyridis* causes declines in native ladybird species.  Intra-guild predation may also play an important role, however, as within a given habitat, species exploiting the same food resource as *H. axyridis* are likely to come into contact with the invader more frequently, and so be at risk of predation, which correlates positively with encounter rate (Raak-van den Berg *et al.*, 2012).

## 6.5. Examining the effect of native communities on invasion by *Harmonia axyridis*

*Harmonia axyridis,* as a habitat generalist, is capable of surviving in the same habitat as many, if not all, native ladybird species (Adriaens *et al.*, 2008; Roy *et al.*, 2012). IAS are sometimes prevented from establishing in a particular area or habitat type by the species already resident, a process termed biotic resistance (Elton, 1958; MacArthur, 1972). However, in Chapter 4 the abundance of *H. axyridis* at a site was shown to be driven by habitat type and aphid abundance, rather than by the diversity or abundance of the existing community of native ladybirds. This remained the case whether the native ladybird community was modelled as all species present, just the aphidophagous species, or only the most ecologically-similar native species. The two habitats included in the field survey (lime trees, *Tilia x europaea* L., and nettles, *Urtica dioica* L.) harbour high abundance of aphids and are considered to be favourable for several ladybird species, particularly *H. axyridis*. Resource-rich habitats such as these have been suggested to favour invasion even in the continuing presence of a diverse native community (Byers & Noonburg, 2003). This is thought to be due to either competition between native species for resources indirectly facilitating the IAS (Levine, 1976; Levine & D'Antonio, 1999), or increased resource availability leading to under-exploitation by native species (McCann *et al.*, 1998; Breton *et al.*, 2005), leaving a niche at least partially vacant for *H. axyridis* to exploit.

The IAS *H. axyridis* is an opportunistic aphid predator with a broad dietary and habitat range, which perhaps enables it to track aphid abundance more effectively across the landscape than do native species. As the beneficiary of unidirectional IGP (Ware & Majerus, 2008), it is possible that the presence of native ladybird species represents potential prey items, rather than, or in addition to, competitors, for *H. axyridis*. At least at a per-site level, and in the resource-rich systems assessed in Chapter 5, there was no overall relationship between *H. axyridis* abundance and the abundance of native species. In North America, the invasion of *C. septempunctata* were found to have largely confined native species to native-habitat refugia rather than crop habitats (Evans, 2004), and it may be that the habitats sampled in Chapter 5 are the British equivalents of these refugia.

One native ladybird species, *Subcoccinella vigintiquattuorpunctata* (L.), was found to be negatively associated with *H. axyridis* abundance. This is a small phytophagous ladybird species which does not compete for food with the IAS, and it is probable that the negative relationship between abundance of the two species has arisen through niche separation caused by their different habitat and dietary requirements. *Subcoccinella vigintiquattuorpunctata* is largely a grassland species which feeds on grasses and clovers, whereas *H. axyridis* is a habitat and dietary generalist species, with preferences for arboreal habitats and aphid prey (Roy *et al.*, 2011b; Hodek *et al.*, 2012). The predatory relationship between the two species has not been formally assessed, but there are no casual records of predation between the two species in the literature, and it is probable that the negative relationship between abundance of the two species has arisen through niche separation caused by different habitat and dietary requirements (Roy *et al.*, 2011b). It is, however, entirely possible that this predation is occurring but has been overlooked, as *S. vigintiquattuorpunctata* is a very small species (Roy *et al.*, 2011b).

It would be interesting to examine whether the co-existence between *H. axyridis* and native ladybird species also occurs in less resource-rich areas and at different times post-invasion, by investigating different habitat types and by manipulating aphid abundance within favourable habitats. This would allow evaluation of the role of resource-richness in structuring the ladybird community, particularly whether *H. axyridis* would be able to become a dominant species, perhaps via competitive exclusion. Alternatively, suboptimal areas might act as refugia for native species, as has been found in the USA (Evans, 2004). There are also many non-ladybird members of the aphidophagous guild, including syrphid (hoverfly) and neuropteran (lacewing) larvae, which may also influence biotic resistance to the *H. axyridis* invasion (Lucas *et al.*, 1998), and it would be desirable to assess these in future surveys. Additionally, the effects of native ladybird community composition on invasion success could be further examined by comparing sites within the invasion zone in which *H. axyridis* has and has not established populations some years after initial invasion.

## 6.6. Parasitoids and the enemy release hypothesis

Biotic resistance is not the only way that a native community may resist the spread of an IAS, however. The enemy release hypothesis (ERH) states that IAS become invasive at least partially because alien species are released from the burden of co-evolved natural enemies such as parasitoids, and so are attacked less than either are populations of the IAS in their native ranges, or similar species native to the invaded range of the IAS (Elton, 1958; Torchin *et al.*, 2003). Britain has a range of parasitoid species which attack native ladybird species (Roy *et al.*, 2013), and Chapter 4 examined how these native parasitoids (particularly phorid flies, *Phalacrotophora fasciata* (Fallén) and *P. berolinensis* Schmitz, and the braconid wasp *Dinocampus coccinellae* (Schrank)) were adapting to the arrival of *H. axyridis,* compared to the ecologically-similar native species *C. septempunctata.*

Both pupae and adults (in overwintering aggregations) of *H. axyridis* were parasitised at a considerably lower rate than were British populations of *C. septempunctata*. Pupae of the IAS were parasitised at an exceptionally low level across Britain (1.7%) and adults were not found to be parasitised at all in our study. In contrast, *C. septempunctata* experienced reasonably high parasitism (20.9% pupae, 5.7% adults) when collected from the same areas at the same time. The aposematic colouration and chemical defences of ladybirds causes them to suffer low rates of attack by non-specialist natural enemies (Roy *et al.*, 2013), and consequently this discrepancy in the rate of parasitism by specialist parasitoids is likely to represent an advantage for *H. axyridis*, and may partly explain why the species is such a successful IAS. Previous studies of parasitism of *H. axyridis* in its native range found pupal parasitism of *H. axyridis* to be much higher in Japan than in Britain: approximately 15% of *H. axyridis* pupae were parasitised by the Japanese-native phorid *Phalacrotophora philaxyridis* Disney (Osawa, 1992). This is consistent with the predictions of the ERH that enhanced performance of an IAS in the introduced range may result from a reduction or absence of natural enemies (Elton, 1958; Torchin *et al.*, 2001).

Future research should focus on both the rate of parasitism and possible effects on the population dynamics of different species of ladybird. Indeed continued monitoring of *H. axyridis*, native species of ladybird and the parasites associated with them is essential to unravelling the web of interactions around this IAS. Within the invaded range, it may be possible to use molecular data to examine the population structure of *H. axyridis* and the parasitoid taxa found attacking it, along a gradient of time of arrival in the invasive range, as in Nicholls *et al.* (2010). It would also be fascinating to examine the interactions between *H. axyridis*, *C. septempunctata* and *D. coccinellae* within Britain, Japan, and the USA. The parasitoid is thought to be native to all three countries, *H. axyridis* is native to Japan but invasive in the USA (first established 1988) (Gordon & Vandenberg, 1991) and Britain (first established 2004) (Majerus *et al.*, 2006b), while *C. septempunctata* is native to Britain and Japan, but invasive in the USA (first established 1973) (Angelet & Jacques, 1975; Gordon, 1985). This would allow quantification of the rate of predation on both ladybird species by co-evolved populations of the parasitoid in areas where both host and parasitoid are native, and thus also evaluation of the degree to which the ERH explains a lack of predation on the same species in their invasive ranges, expressed as a drop-off in parasitism rate between regions.

It is possible that the extreme polymorphism of *H. axyridis* may play a role in the species' invasional success, but limited work to date has focused on this. Studies on other taxa, e.g. Orthoptera, have found links between colour form, size and habitat selection (Ahnesjo & Forsman, 2003, 2006). Both *Chorthippus parallelus* (Zetterstedt) and *Tetrix undulata* (Sowerby), for example, have several different colour morphs which have been found to preferentially inhabit different habitat types, and which vary in fecundity (Ahnesjo & Forsman, 2003, 2006; Unsicker *et al.*, 2008). It may therefore be the case that the phenotypic variation of *H. axyridis* allows the species a wider niche than monomorphic species, thus allowing the IAS to colonise a wider range of areas and habitats. Additionally, the different colour forms may differ in the extent of their chemical defences, either because some colour forms require a greater energetic input (e.g. to produce the extra melanin needed for melanic forms), or because some colour forms are attacked more frequently, potentially because of greater conspicuousness to predators (Sloggett *et al.*, 2011). This in turn may have effects on invasional success: better-defended colour forms may be better able to resist attack by native natural enemies, so invade areas more successfully, or less-defended colour forms are able to devote more resources to reproduction and dispersal, and so they invade areas more successfully (Sloggett *et al.*, 2011).

## 6.7. The value of "citizen science"

What has been brought sharply into focus from this study of *H. axyridis* as an IAS is the value of long-term, large-scale datasets, and of citizen science data. Volunteer-recorded occurrence data are not perfect. There are potential data-quality issues, particularly with cryptic taxa, and recording-intensity issues associated with casual records rather than focused, intensive sampling: more apparent species are recorded more often, and records may be biased towards the distribution of recorders rather than the species in question (Dickinson *et al.*, 2010). Using volunteer-recorded data, however, allows much larger areas to be sampled than is possible using surveys by taxonomic experts, assuming equal time and costs. Recording-intensity issues can be minimised using statistical techniques and sub-setting of the data, e.g. Chapter 3 and Roy *et al* (2012), while data-quality issues have been found to be minimal in many citizen science schemes (Crall *et al.*, 2011; Gardiner *et al.*, 2012). More complex methods have also been developed to use citizen science data, for example extracting distribution patterns of liverworts and hornworts (Preston *et al.*, 2011), measuring relative change in range size (Telfer *et al.*, 2002), and interpreting atlas data in the absence of known recording effort (Hill, 2012).

Long-term citizen-science data have been used to produce distribution atlases for more than 11,000 species in Britain, from algae and bryophytes to mammals and birds (Preston *et al.*, 2012). The data have been used to monitor the spread of species, both native and alien, e.g. *Cameraria ohridella* Deschka & Dimić (Pocock *et al.*, 2011), to identify the traits of species changing distributions or abundances, e.g. in plant communities (Braithwaite *et al.*, 2006), and to evaluate the role of possible drivers of change and compare their effects between species groups such as birds, plants and butterflies (Thomas *et al.*, 2004; Wilson *et al.*, 2004).

Without data from volunteer recorders, there would at best be only a biased and incomplete record of the spread of the *H. axyridis* in Britain: with them, we have thousands of records of multiple species across the country, before and after the establishment and spread of *H. axyridis*. This allows evaluation of the impact of environmental changes such as the arrival of IAS, particularly through methods designed to use these data and which take their specific strengths and weaknesses into account. These include modelling approaches such as those used in Chapters 2, 3 and 5, a valuable approach as it can evaluate the comparative role of, and interactions between, biotic and abiotic drivers of distribution or population dynamics within the same framework, rather than independently.

## 6.8. Overall conclusions

Overall, *H. axyridis* is an extremely successful IAS. It is likely to continue spreading throughout the British Isles, and the detrimental effects that the species has on native species are likely to continue. The wide diet breadth of the IAS is likely to have played a critical role in the species' rapid spread, as species' diet breadth was the life-history or resource-use trait best correlated with range size: species predatory on a wide range of prey families had larger range sizes than those which ate fewer prey types (Chapter 2). Both urbanisation and the degree of dietary niche overlap between *H. axyridis* and native species show a strong positive correlation with the decline in recorded distribution of native species (Chapter 3). This indicates that the IAS is playing an important role in the declines of native species, but that habitat destruction is also playing a major part (Chapter 3).

There appears to be very little prospect that its spread will be slowed by biotic resistance of the native community (Chapter 4), or by top-down regulation from natural enemies native to the British Isles (Chapter 5), at least in the near future. This highlights the importance of the preventative principle with regards to the introduction of new species into the environment. The most effective way to prevent species becoming invasive is to prevent their initial establishment (Blackburn *et al.*, 2011). Horizon-scanning and risk assessments allow potential new arrivals such as *Vespa velutina nigrithorax* de Buysson to be evaluated pre-arrival, informed by examples such as *H. axyridis* (van Lenteren *et al.*, 2008). In turn, appropriate monitoring and control measures can be put in place to attempt to reduce the incidence and magnitude of future invasions.

The invasion of *H. axyridis*, particularly in Britain, has had an unusually high public profile, and has been possibly better-studied than any other invasive insect. It is to be hoped that this well-documented disaster for native wildlife will act as a warning to help prevent or control future invasions. The thousands of volunteer biological recorders in Britain who give up their spare time to monitor their local wildlife provide us with by far the best-studied flora and fauna anywhere in the world, an unrivalled opportunity to carry out in-depth ecological studies, and an observation network with the capability to pick up the earliest signs of invasion.

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# Appendix 1. Other publications & activities from the PhD period

## ISI papers:

- Haelewaters, D., **Comont, R.F.**, Zhao, S., Pfister, D. (in press). Hesperomyces virescens *(Fungi, Ascomycota, Laboulbeniales) attacking* Harmonia axyridis *(Coleoptera, Coccinellidae) in its native range.* Chinese Science Bulletin.
- Roy, H.E., Adriaens, T., Isaac, N.J.B., Kenis, M., Onkelinx, T., San Martin, G., Brown, P.M.J., Hautier, L., Poland, R., Roy, D.B., **Comont, R.**, Eschen, R., Frost, R., Zindel, R., van Vlaenderen, J., ***Nedvěd, O.***, Ravn, H.P., Grégoire, J-C., de Biseau, J-C., Maes, D. (2012). *Invasive arthropod predator causes rapid declines of native European ladybirds*. Diversity and Distributions 18 (7) p. 717-25
- Evans, E.W., **Comont, R.F.,** Rabitsch, W. (2011). *Alien arthropod predators and parasitoids: interactions with the environment*. Biocontrol 56 (4), p. 395-407

## Grey literature:

- **Comont, R.F.** (2013). The Garden Bioblitz: Citizen science meets social media. National Federation for Biological Recording Newsletter 46, p. 19-20
- Brown, P.M.J., **Comont, R.F.,** Roy, H.E. (2013). *Wildlife reports: Ladybirds*. British Wildlife, 24 (3), p. 208-209
- **Comont, R.F.** & Willerton, C. (2012). *The 13-spot ladybird,* Hippodamia tredecimpunctata *(Col: Coccinellidae) – a larval record from Britain*. British Journal of Entomology and Natural History 25 (1), p. 6
- Brown, P.M.J., **Comont, R.F.,** Poland, R.L, Roy, H.E. (2012). *Wildlife reports: Ladybirds*. British Wildlife, 23, p. 208-210
- Roy, H.E., Brown, P.M.J., **Comont, R.F.,** Lawson-Handley, L.J., Poland, R. (2012). *The UK Ladybird Survey: Engaging people in recording ladybirds*. Antenna 36(3), p. 186-193
- **Comont, R.F.**, & Roy, H.E. (2011). *The spread of the Harlequin ladybird in Britain.* Outlooks on Pest Management 22 (4), p. 152-5.
- Roy, H.E., Hesketh, H., McCracken, M., **Comont, R.F.**, Rondoni, G., Poland, R., Stentiford, G., Hails, R. (2010). *Living with the enemy: insects and their pathogens*. British Wildlife, 22. 94-100.

- Shaw, M.R., **Comont, R.F.,** McCracken, M., Hesketh, H., Roy, H.E., Hails, R.S. (2010). *The third modern British record of* Brachymeria tibialis *(Hymenoptera: Chalcididae), reared from* Zygaena filipendulae *(Lepidoptera: Zygaenidae)*. British Journal of Entomology and Natural History, 23. 170.
- **Comont, R.F**., McCracken, M., Hesketh, H., Hails, R.S., Roy, H.E. (2009). *Bivoltine Blues: A second generation in the British Chalkhill Blue* Polyommatus coridon *(Lepidoptera: Lycaenidae)*. British Journal of Entomology and Natural History, 22.
- Roy, H., Beckmann, B., **Comont, R.F.,** Hails, R., Harrington, R., Medlock, J., Purse, B., Shortall, C. (2009) *Nuisance insects and climate change*. Defra, 109pp. (http://www.defra.gov.uk/environment/quality/local/nuisance/odour/documents/insect-nuisance0903.pdf)

## Conference proceedings:

- **Comont, R.F.**, Roy, H.E., Lewis, O.T., Harrington, R., Shortall, C.R., Purse, B.V., (in press). *Does niche overlap with* Harmonia axyridis *correlate with population declines in the British ladybird fauna?* In: Sloggett, J.J.; Brown, P.M.J.; Roy, H.E., (eds.) *Proceedings of the second meeting on "Benefits and risks of exotic biological control agents".* International Organization for Biological and Integrated Control of Noxious Animals and Plants, West Palearctic Regional Section (IOBC/WPRS). (IOBC wprs Bulletin).
- **Comont, R.F.**, Harrington, R., Lewis, O.T., Purse, B.V., Roy, H.E. (2010). *Modelling* Harmonia axyridis *(Coleoptera, Coccinellidae) interactions within the aphidophagous guild*. In: Babendreier, Dirk; Aebi, Alexandre; Kenis, Marc; Roy, Helen, (eds.) *Proceedings of the first meeting on "*Harmonia axyridis *and other ladybirds"*. International Organization for Biological and Integrated Control of Noxious Animals and Plants, West Palearctic Regional Section (IOBC/WPRS), 27-28. (IOBC wprs Bulletin, Vol.58).

## Books:

- Roy, H.E., Brown, M.J., **Comont, R.F.,** Poland, R.L., Sloggett, J.J. (2013). *Ladybirds (Naturalist's Handbooks: Ecology and Identification 10).* Pelagic Publications, Exeter.

## ID guides & keys:

- iRecord Ladybirds (ladybird ID and recording app for Android & iOS). https://play.google.com/store/apps/details?id=uk.ac.bris.ilrt.ladybird and https://itunes.apple.com/gb/app/irecord-ladybirds/id634591099?mt=8

- Roy, H.E., Brown, P.M.J., **Comont, R.F.** & Poland, R. (2012). Guide to the ladybird larvae of the British Isles, http://www.field-studies-council.org/publications/pubs/ladybird-larvae.aspx
- Rosewell, J., & **Comont, R.F.** (2011). Bayesian key to the adult ladybirds of Britain, http://www.ispot.org.uk/webkeys/keyintroduction.jsp?selectedKey=webkeys/ladybirds_with_melanics.1.2

## Presentations:

### 2013

- Ladybirds under threat: how can volunteers help? Oxford Conservation Society, Oxford, 6/6/2013
- The importance of biological recording. 'Bristol 99' project recording workshops for the Bristol Natural History Consortium, Bristol, 24 & 27/4/2013
- Ladybirds in a changing world. Royal Entomological Society Postgraduate Forum, Oxford, 5/2/2013
- Using traits to explain ladybird distribution patterns. British Entomology and Natural History Society annual Coleoptera Day, Oxford, 2/2/2013

### 2012

- Ladybirds in a changing world. British Ecological Society annual conference, Birmingham, 18/12/2012
- Ladybirds in a changing world. Centre for Ecology and Hydrology student meeting, Wallingford, 6/12/2012
- Ladybirds in a changing world. Ashmolean Natural History Society, Oxford, 4/4/2012
- Bioblitzes: a naturalist's perspective. National Bioblitz Conference, Bristol, 24/10/2012
- The 2012 Garden Bioblitz. National Bioblitz Conference, Bristol, 24/10/2012
- Hidden wildlife of Radley Lakes: a year in the life. Friends of Radley Lakes AGM, Abingdon, 12/10/2012
- Alien vs Predator: the harlequin ladybird in Britain. South and North Moreton Women's Institute, North Moreton, 12/9/2012
- Ladybirds in a changing world. Royal Entomological Society annual conference, Cambridge, 20/7/2012

- Ladybirds of Britain. Ladybird ID training course, Cambridge Wildlife Trust, Cambridge, 12/5/2012
- Ladybirds in a changing world. Centre for Ecology and Hydrology student seminar day, Wallingford, 20/4/2012
- The harlequin ladybird: interactions with British ecosystems. Anglia Ruskin Wildlife Conservation Society, Cambridge, 20/3/2012
- Using traits to explain ladybird distribution patterns. British Entomology and Natural History Society annual Hemiptera Day, Reading, 3/3/2012

### 2011

- The PhD: a student's perspective. Centre for Ecology & Hydrology student induction day, Wallingford, 15/11/2011
- The harlequin ladybird: biocontrol disaster. Conservation Biology MSc lecture, Reading University, 11/11/11
- Parasites and pathogens of the invasive alien *Harmonia axyridis*. Second meeting of the IOBC/WPRS working group 'Benefits and risks of exotic biocontrol agents', Hluboka, Czech Republic, 31/10/2011
- Does niche overlap with *Harmonia axyridis* correlate with population declines in the British ladybird fauna? Second meeting of the IOBC/WPRS working group 'Benefits and risks of exotic biocontrol agents', Hluboka, Czech Republic, 31/10/2011
- Ladybirds in the UK: can biological traits explain distribution patterns? British Ecological Society annual conference, Sheffield, 14/9/11
- Ladybirds in the UK: can biological traits explain distribution patterns? Centre for Ecology & Hydrology postgraduate conference, Wallingford, 5/4/2011
- The harlequin ladybird in the UK. Centre for Ecology & Hydrology open day for Bath Spa undergraduates, Wallingford, 24/3/2011
- Invasive species in Europe. Invasion Biology MSc, Warwick University, Warwick, 8/2/2011
- Modelling *Harmonia axyridis* interactions within the aphidophagous guild. Royal Entomological Society Postgraduate Forum, Hull, 3/2/2011

**2010**

- Ladybirds in the UK: can biological traits explain distribution patterns? Aphidophaga biannual conference, Perugia, Italy, 22/9/2010
- The harlequin ladybird in the UK. Centre for Ecology & Hydrology open day for the Women's Institute, Wallingford, 20/7/2010
- The harlequin ladybird: *Harmonia axyridis* in the UK. National Pest Technicians' Association annual conference, Surrey, 12/5/2010
- The harlequin ladybird in the UK. Centre for Ecology & Hydrology open day for Bath Spa undergraduates, Wallingford, 22/4/2010
- The harlequin ladybird in the UK. Milton Keynes Natural History Society, Milton Keynes, 2/2/2010

## Posters:

- Modelling *Harmonia axyridis* interactions within the aphidophagous guild. Royal Entomological Society postgraduate forum, Hull, 2-3/2/2011
- Modelling *Harmonia axyridis* interactions within the aphidophagous guild. Royal Entomological Society climate change special interest group, York, 22/10/2010
- Modelling *Harmonia axyridis* interactions within the aphidophagous guild. First meeting of the IOBC/WPRS working group '*Harmonia axyridis* and other invasive ladybirds', Engelberg, Switzerland, 6-10/9/2009

## Invited blog posts:

- What's on the van: 7-spot ladybird. The Oxford Museum of Natural History's Darkened not Dormant blog, 9/9/2013. http://darkenednotdormant.wordpress.com/2013/09/09/whats-on-the-van-7-spot-ladybird/
- Bioblitz your garden this June. The National Trust's Outdoor Nation blog, 21/5/2013. http://outdoornation.org.uk/2013/05/21/bioblitz-your-garden-this-june/
- The National Bioblitz Conference. Centre for Ecology & Hydrology science news blog, 28/10/2012. http://cehsciencenews.blogspot.co.uk/2012/10/national-bioblitz-conference.html
- Meet the UK Ladybird Survey. Bristol Natural History Consortium's Meet The Species blog, 2/9/2012. http://meetthespeciesdotorg.wordpress.com/2012/09/02/meet-the-uk-ladybird-survey/

- Meet the Species: the water stick-insect. Bristol Natural History Consortium's Meet The Species blog, 30/8/2012. http://meetthespeciesdotorg.wordpress.com/2012/08/30/richard-comont-on-the-water-stick-insect/
- Meet the Species: Roesel's bush-cricket. Bristol Natural History Consortium's Meet The Species blog, 29/8/2012. http://meetthespeciesdotorg.wordpress.com/2012/08/29/the-roesels-bush-cricket/
- Why ladybirds? (interview). Bristol Natural History Consortium's Meet The Species blog, 23/8/2012 http://meetthespeciesdotorg.wordpress.com/2012/08/23/richard-nature-wildlife-tycoon-comont-the-ladybird-survey/

## Media:

### 2013

- BBC Radio 4 – The Living World (Ivy Bees), recorded 23/09/2013
- BBC 1 – The One Show (One Show Bioblitz), recorded 12/06/2013. Insect expert
- BBC 1 – Springwatch Live (feature section on the Garden Bioblitz), 3/6/2013
- BBC 1 – Springwatch Live (feature section on the Garden Bioblitz), 30/5/2013

### 2012

- BBC Radio 4 – Saving Species, 29/10/2012. 'Bioblitzes'
- BBC Radio 4 – Saving Species, 21/10/2012. 'Where have all the ladybirds gone?'
- The Times, 18/5/2012. 'The ladybirds are coming'
- Channel 4 – Jimmy's Forest. Entomological consultant
- BBC 1 South – TV news, 7/2/2012. Interview about the impact of the harlequin ladybird on native ladybird species

### 2011

- BBC Radio 4 - The Living World (Winter Ladybirds), 27/11/2011
- Cryptozoology Online, 4/9/2011. 'Lost ladybird found in Devon' http://cryptozoologynews.blogspot.com/2011/09/lost-ladybird-found-in-devon.html
- Sydney Sun-Herald, 4/9/2011. 'Spot of luck for lady of extinction.'
- The Times, 3/9/2011. 'Extinct ladybird found'

- Daily Mail, 3/9/2011. ‘Ladybird with 13 spots is back – 60 years after being declared extinct’ http://www.dailymail.co.uk/news/article-2033235/Ladybird-13-spots-60-years-declared-extinct.html
- Digg, 3/9/2011. ‘Lost ladybird found in Devon’ http://digg.com/news/science/lost_ladybird_found_in_devon/who_dugg
- Western Morning News, 2/9/2011. ‘Beetle thought to be extinct found breeding in seaside resort’ http://www.thisisdevon.co.uk/Beetle-thought-extinct-seaside-resort/story-13251804-detail/story.html
- BBC News Online, 2/9/2011. ‘Extinct’ ladybird found breeding in Devon’ http://www.bbc.co.uk/news/uk-england-devon-14761809
- Planet Earth online, 2/9/2011. ‘Lost ladybird found in Devon’ http://planetearth.nerc.ac.uk/news/story.aspx?id=1048
- Guardian, 2/9/2011. ‘The week in wildlife – in pictures’ http://www.guardian.co.uk/environment/gallery/2011/sep/02/week-in-wildlife-in-pictures?CMP=twt_gu#/?picture=378506881&index=2
- Trinity Matters, 2/9/2011. ‘Long-lost ladybird back breeding near Axmouth’ http://www.trinitymatters.co.uk/trinity-broadband/fix-slow-broadband/333-long-lost-ladybird-back-breeding-near-axmouth
- BBC Radio Devon – Good Morning Devon, 2/9/2011. Interview, ‘The rediscovery of the 13-spot ladybird’
- Exmouth Midweek Herald, 26/8/2011. ‘Beetles make comeback at Seaton’ http://www.midweekherald.co.uk/news/beetles_make_comeback_at_seaton_1_1006401
- Guardian, 31/8/2011. ‘Long-lost ladybird species discovered breeding in UK’ http://www.guardian.co.uk/environment/2011/aug/31/rare-ladybird-breeding-uk
- Humanitarian News, 31/8/2011. ‘Long-lost ladybird species discovered breeding in UK’ http://humanitariannews.org/20110831/long-lost-ladybird-species-discovered-breeding-uk
- Exeter Express & Echo, 1/9/2011. ‘Estuary’s ‘bio-blitz’ finds rare ladybird’ http://www.thisisexeter.co.uk/Estuary-s-bio-blitz-finds-rare-ladybird/story-13244838-detail/story.html

- Exmouth Journal, 1/9/2011. ‘Extinct 13-spot ladybirds found in East Devon nature reserve’ http://www.exmouthjournal.co.uk/home/extinct_13_spot_ladybirds_found_in_east_devon_nature_reserve_1_1015161
- BBC Radio Lincoln – 25/8/2011. Interview, ‘Why are there so many ladybirds about?’
- BBC Radio 4 – Saving Species (The UK Ladybird Survey), 26/7/2011
- BBC 1 – Natural World ('Butterflies: A Very British Obsession'), 17/12/2011. Entomological consultant

## Science & natural history communication events:

Bioblitzes attended (as expert entomologist & guided walk leader): 19

Moth-trapping evenings led: 42

Children’s nature club events led: 20

Other public events attended: 16, including York Insect Festival, BBC Gardener’s World Live, Royal Society Summer Science Exhibition, Open Farm Sunday, National Insect Week, and the Wilderness festival (as part of the Bristol Natural History Consortium’s Cultural Olympiad event ‘Meet The Species’)

## Events organised:

- Garden Bioblitz 2013. Nationwide two-day garden survey, 1-2/6/2013. www.gardenbiolitz.org
- Garden Bioblitz 2012. Nationwide two-day garden survey, 21-22/7/2012