

Decline in native ladybirds in response to the arrival of *Harmonia axyridis*: early evidence from England

PETER M. J. BROWN,¹ ROBERT FROST, JULIAN DOBERSKI,¹ TIM SPARKS,² RICHARD HARRINGTON³ and HELENE . ROY⁴ ¹Animal and Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, Cambridge, U.K., ²Institute of Zoology, Poznań University of Life Sciences, Poznań, Poland, ³Department of Plant and Invertebrate Ecology, Rothamsted Research, Hertfordshire, U.K. and ⁴Biological Records Center, NERC Centre for Ecology & Hydrology, Wallingford, U.K.

Abstract. 1. *Harmonia axyridis* (Coleoptera: Coccinellidae) is an invasive non-native ladybird in Europe, where it was introduced as a biological control agent of aphids and coccids.

2. This study assesses changes to ladybird species assemblages, in arboreal habitats, over a 3-year period encompassing the invasion phase of *H. axyridis* in eastern England. The effects of *H. axyridis* and other factors (weather and prey availability) on native ladybirds are assessed.

3. *Harmonia axyridis* increased from 0.1% to 40% of total ladybirds sampled, whilst native aphidophagous species declined from 84% to 41% of total ladybirds. The actual number of native aphidophagous ladybirds per survey decreased from a mean of 19.7 in year 1, to 10.2 in year 3.

4. Three ladybird species in particular experienced declines: *Adalia bipunctata*, *Coccinella septempunctata*, and *Propylea quattuordecimpunctata*. *Harmonia axyridis* was the most abundant species by the end of the study.

5. The decline in native aphidophagous ladybirds could be attributed to competition for prey and intraguild predation of eggs, larvae, and pupae by *H. axyridis*. Physiological and behavioural traits of *H. axyridis* are likely to confer an advantage over native ladybird species.

Key words. *Adalia bipunctata*, biological control, Coccinellidae, harlequin ladybird, intraguild predation, invasive species, non-target effects.

Introduction

Harmonia axyridis Pallas (Coleoptera: Coccinellidae) is a predatory ladybird native to Asia (Dobzhansky, 1933; Kuznetsov, 1997). Although principally a semi-arboreal species (Hodek, 1973), *H. axyridis* occupies many habitats in its native and introduced ranges, including heathlands and riparian zones (Adriaens *et al.*, 2008), reed beds (Ware *et al.*, 2005), and crop systems (Colunga-Garcia & Gage, 1998; Jansen & Hautier, 2008). *Harmonia axyridis* has a long history of use as a classical biological control agent of aphids and coccids (scale insects) in North America, where it was first introduced in 1916 (Gordon, 1985). The species succeeded in controlling pest aphids on a wide range of crops (reviewed in Koch, 2003; Koch & Galvan, 2008).

Correspondence: Peter M. J. Brown, Animal and Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, Cambridge, U.K. E-mail: Peter.brown@anglia.ac.uk

In Western Europe, *H. axyridis* was first released as a biological control agent in 1990 in France and first marketed in 1995 (Coutanceau, 2006). It established in the late 1990s and expanded its range rapidly, especially from 2002 (Brown *et al.*, 2008a). The species has recently been recorded in other regions of the world, including South America (de Almeida & da Silva, 2002; Saini, 2004; Grez *et al.*, 2010), Central America (Koch *et al.*, 2006) and Africa (Ferran *et al.*, 2000; Stals, 2008). In Europe and elsewhere there is concern about the rapid increase in distribution and abundance of *H. axyridis*, and its impact on non-target species (Adriaens *et al.*, 2003; Majerus *et al.*, 2006; Roy *et al.*, 2006). *Harmonia axyridis* is a large ladybird and is well defended both physically (e.g. larvae possessing thick dorsal spines) (Ware & Majerus, 2008), and chemically (Sato & Dixon, 2004). There is evidence from Europe that the species is affected less by parasitoids (Koyama & Majerus, 2008) and fungal pathogens (Roy *et al.*, 2008) than are native coccinellids.

Table 1. Sites (A–G) surveyed for ladybirds from 2006 to 2008 in eastern England, including site name, grid reference, site description, vegetation type and vegetation species surveyed.

Site code	Site name	Grid reference	Site description	Vegetation type surveyed	Vegetation species surveyed (where mixed, shown in order of dominance)
A	St Ives churchyard	TL309716	Churchyard	Lime trees	<i>Tilia</i> × <i>europaea</i>
B	Fordham/Worlington churchyard	TL633707/TL691738	Churchyard	Lime trees	<i>T.</i> × <i>europaea</i>
C	Chippenham Fen 1	TL646698	Border of fenland National Nature Reserve and meadow	Plantation Scots pine trees	<i>Pinus sylvestris</i>
D	Brampton Wood	TL177698	Mixed woodland	Plantation Scots pine trees	<i>P. sylvestris</i>
E	Houghton Grange	TL296723	Mixed parkland	Mixed	<i>P. sylvestris</i> , <i>T.</i> × <i>europaea</i> and herbage (mainly grasses, <i>Urtica dioica</i> , <i>Cirsium</i> spp.)
F	Huntingdon	TL253725	Mixed parkland strip adjacent to suburban road	Mixed	<i>Acer pseudoplatanus</i> , <i>Sorbus intermedia</i> , <i>P. sylvestris</i> , <i>Fraxinus excelsior</i> , <i>Carpinus betulus</i> , <i>Hedera helix</i>
G	St Ives garden	TL306727	Suburban garden	Mixed	<i>A. pseudoplatanus</i> , <i>Prunus spinosa</i> , <i>Rhamnus cathartica</i> × <i>Frangula alnus</i> , <i>Ulmus glabra</i> , <i>H. helix</i>

The breadth of prey range of *H. axyridis* suggests that it may affect the food supply of a wide range of both generalist and specialist ladybirds in England. In Maine, U.S.A., aphids were substantially reduced after *H. axyridis* established in potato crops (Alyokhin & Sewell, 2004). The current study investigates changes to ladybird species assemblages in arboreal habitats, including deciduous and coniferous trees, as *H. axyridis* became established.

Studies in North America have shown declines in native ladybirds in response to the arrival of *H. axyridis* (Colunga-Garcia & Gage, 1998; Michaud, 2002), *Coccinella septempunctata* Linnaeus, (Elliott *et al.*, 1996; Turnock *et al.*, 2003; Evans, 2004), or both (Brown & Miller, 1998; Alyokhin & Sewell, 2004). Majerus (2008) presented the first evidence of decline in a population of *Adalia bipunctata* Linnaeus close to our study area, based on long-term overwintering records. The current study examines the structure of ladybird assemblages at a local scale, before and after the arrival of *H. axyridis*. The specific aims of the study were to: (i) assess changes over a 3-year period in ladybird species assemblages in habitat types suitable for *H. axyridis* in eastern England; (ii) assess the effects of *H. axyridis* and other factors (weather and prey availability) on native ladybirds.

The study was initiated at the start of the invasion process of *H. axyridis* in eastern England. *Harmonia axyridis* was first recorded in the vicinity of the study area in 2004, but in 2006 (year 1 of this study) it was not abundant and is unlikely to have had an effect on the coccinellid assemblage up to that time.

Materials and methods

Ladybird surveys

Surveys were carried out from 2006 (year 1) to 2008 (year 3) at seven sites (A–G) representing three arboreal

habitat types in Cambridgeshire and Suffolk, eastern England (Table 1). The target time of day for surveys was between 10.00 and 16.00, and the target weather was dry and preferably sunny, with air temperature of at least 14 °C (achieved for 87% of surveys – the remainder carried out when air temperature was 10.5–13.5 °C, most such surveys being early or late in the year). Each site was surveyed nine times per year between April and October (twice per month in May and June and once per month in other months). At sites A–D each survey was 20 min in duration. Sites E–G were larger and more diverse and the surveys were of longer duration (approximately 1 h), thus the data from them have been time-adjusted [i.e. species abundance in each survey at sites E–G was divided by a factor of (mean survey time for site divided by 20 min), so that the results represent an equivalent 20-min survey]. This was done for reasons of clarity, allowing direct comparison of abundance from sites E–G with sites A–D. On occasions when high numbers of ladybirds were found, additional time for identification was added, so that a standard sampling effort was maintained.

The surveyed vegetation is listed in Table 1. Different sampling techniques had to be used for surveying the different forms of vegetation. However, a standard sampling effort was maintained by the strict time allocation for each survey. For sampling trees, branches were beaten with a stick above a 110 cm × 86 cm white canvas beating tray, branch heights ranging from approximately 1–4 m above ground level. For sampling herbage, a 46-cm diameter sweep net was used. Before the start of recording in year 3, the trees at site B (Fordham) were pollarded, thus severely affecting the ladybird catch. Whilst the site continued to be surveyed, a substitute site (Worlington) was added and it is the data from there that have been used for year 3. Fordham and Worlington are approximately 7 km apart and are similar churchyard sites dominated by mature lime trees *Tilia* × *europaea* L. (Malvaceae).

In year 3, only seven surveys were carried out at sites E and F, so estimated data for these have been calculated using least square methods. This involved forming a site by survey data matrix for each species and using a two-way ANOVA to estimate the missing surveys, based on the seasonal patterns at the remaining sites and the records made at the incomplete sites in the remainder of the year.

Conspicuous coccinellid (i.e. sub-families Epilachninae, Coccinellinae, and Chilocorinae – ladybirds *sensu* Majerus, 1994) adults and larvae were recorded to species. Exceptions were first- and second-instar larvae (which could not be identified to species and have been excluded), *Adalia* larvae (*A. bipunctata* and *Adalia decempunctata* Linnaeus) could not reliably be separated so were recorded as *Adalia* spp., and third instar *Harmonia* larvae *H. axyridis* and *Harmonia quadripunctata* Pontoppidan could not be separated until fourth instar, so third instars were recorded as *Harmonia* spp. Inconspicuous coccinellid species such as *Rhyzobius litura* Fabricius, and *Scymnus suturalis* Thunberg, were found only in small numbers and have been excluded from further analyses. Ladybirds were re-released on-site.

For some analyses the ladybirds were subdivided into three groups: (i) *H. axyridis*; (ii) aphidophagous natives, i.e. *A. decempunctata*, *A. bipunctata*, *Anatis ocellata* Linnaeus, *C. septempunctata*, *Calvia quattuordecimguttata* Linnaeus, *H. quadripunctata*, *Myrrha octodecimguttata* Linnaeus, and *Propylea quattuordecimpunctata* Linnaeus; (iii) non-aphidophagous natives, i.e. *Aphidecta oblitterata* Linnaeus, *Chilocorus renipustulatus* Scriba, *Exochomus quadripustulatus* Linnaeus, *Halyzia sedecimguttata* Linnaeus, *Subcoccinella viginti-quatuor-punctata* Linnaeus, *Tythaspis sedecimpunctata* Linnaeus, and *Psyllobora vigintiduopunctata* Linnaeus.

Aphid data

Aphid data from the Rothamsted Insect Survey (Harrington & Woiwod, 2007) (www.rothamsted.ac.uk/insect-survey/) were used as a measure of aphid availability. Insects were sampled using 12.2-m tall suction traps (Macaulay *et al.*, 1988), drawing in 0.75 m³ air per s and running continuously. Currently the U.K. suction trap network comprises 16 traps. Weekly total aphid numbers (all species) collected from 2006 to 2008 in the two traps closest to the ladybird survey sites [Rothamsted (Ordnance Survey grid reference TL133134) and Broom's Barn (TL754656)] were used. The ladybird survey sites were situated between Rothamsted and Broom's Barn, which are approximately 80 km apart. The mean number of aphids from the two traps over 4 weeks (the ladybird survey week, plus the three preceding weeks) was used as a measure of aphid abundance to compare with ladybird numbers. The 4-week period was used to reflect that ladybird abundance in a habitat may be influenced by recent, as well as current, aphid supplies.

Weather data

Shade air temperature at the time of each survey was recorded on-site using a mercury thermometer. Additional weather data (monthly mean maximum temperature, and monthly total sunshine hours and rainfall) for NIAB Cambridge (TL432603) for 2006–2008 were obtained from the U.K. Meteorological Office (www.metoffice.gov.uk/climate/uk/stationdata/cambridgedata.txt). The NIAB Cambridge weather station is a maximum of 32 km from the ladybird survey sites. For statistical analyses, weather variables were used for both the calendar month of the survey and a mean for the three calendar month period ending in the month of the survey.

Statistical analyses

Differences between years in annual abundances of ladybird species at the seven sites were compared (Friedman test using SPSS 16.0 software). Pearson correlations were calculated between ladybird abundance (ladybirds grouped as outlined in Materials and methods) and aphid abundance, survey air temperature, monthly and 3-monthly mean maximum temperature, and monthly and 3-monthly total sunshine hours and rainfall. Pearson correlations were also calculated between individual ladybird species abundance and aphid abundance and between total weekly aphid abundance at the two suction trap sites. For Pearson correlations, mean ladybird abundances across sites A–G were used, with 27 survey periods (i.e. nine surveys in each of 3 years) assessed against corresponding aphid and weather data. Correlations were calculated using SPSS 16.0 software.

Results

Lime tree sites (A and B)

In year 1 a single specimen of *H. axyridis* was recorded (a larva at site B). By year 2 *H. axyridis* was the most abundant ladybird species at sites A and B. It continued to dominate in year 3 and was the only species to increase over the 3 years (Fig. 1a). *Adalia bipunctata*, *C. septempunctata*, and *P. quattuordecimpunctata* declined between years 1 and 3.

Of 21 surveys in years 2 and 3 when *Adalia* spp. larvae and/or *H. axyridis* larvae were recorded, 11 (52%) of the surveys recorded both species, five (24%) had *Adalia* spp. only (all were between May and July), and five (24%) had *H. axyridis* only (four of the five were in September or October). Thus there was a fairly high degree of overlap of larval stages at the sites. *Adalia* spp. tended to breed earlier with a single peak in abundance; most larvae being recorded in June and July in years 1 and 3, but occurrence was more prolonged (late May to August) in year 2. In year 2 the larval peak for *Adalia* spp. and *H. axyridis* was in August. *Harmonia axyridis* exhibited two peaks in larval abundance, suggesting bi-voltinism, but the timing of the peaks changed: from August and October in year 2 to late June and September in year 3.

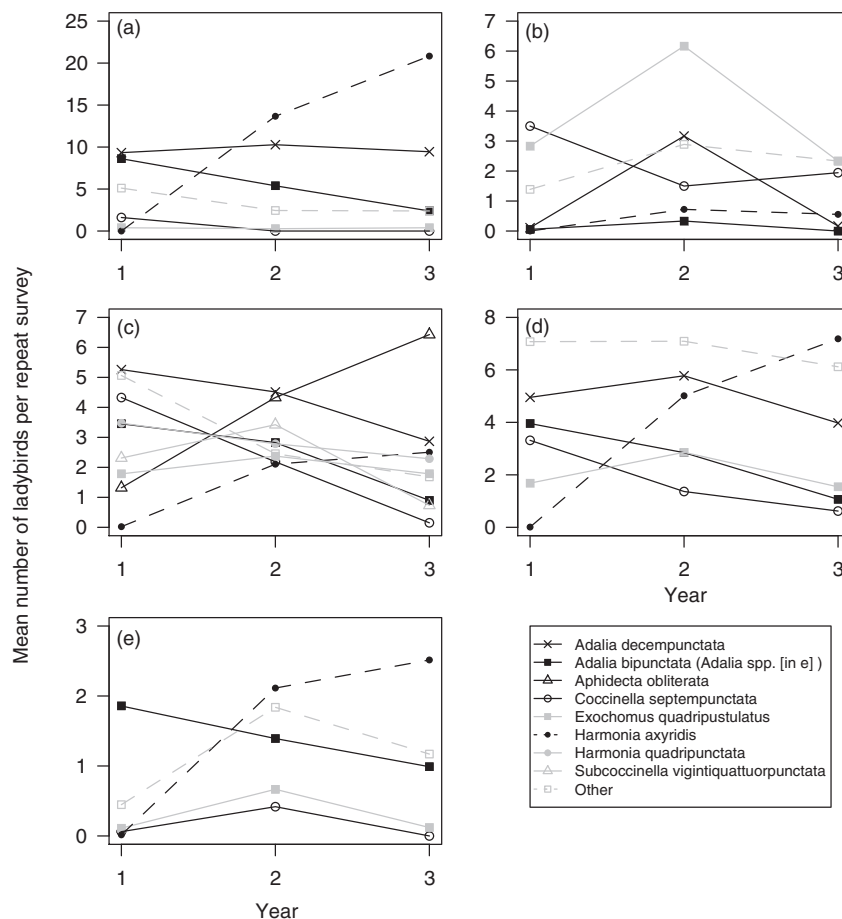


Fig. 1. Mean number of ladybirds per repeat survey, for each year (nine repeat surveys per site per year), grouped by habitat: (a) lime tree sites (sites A and B) adults; (b) pine tree sites (C and D) adults; (c) mixed sites (E–G) adults; (d) all sites adults; (e) all sites larvae. For standard errors see Appendix. Note difference in Y-axis scales.

Pine tree sites (C and D)

Years 1 and 3 appeared to be generally poor for ladybirds, with higher abundance of most species in year 2: this was the case for *A. decempunctata*, *A. bipunctata*, *E. quadripustulatus*, and *H. axyridis*, but not for *C. septempunctata* (Fig. 1b). Adults and larvae of *H. axyridis* were recorded at site C in year 2. However, in contrast to the lime tree sites, *H. axyridis* did not dominate and was less abundant than the conifer specialists *M. octodecimguttata* and *H. quadripunctata* and a third species commonly found on pines, *E. quadripustulatus*. *Harmonia axyridis* larvae were not recorded in year 3, and the species was not recorded at all at site D (although ladybirds in general were less abundant at this site).

Mixed sites (E–G)

Abundance of various species (including *A. decempunctata*, *A. bipunctata*, *C. septempunctata*, and *H. quadripunctata*) declined year-on-year, as *H. axyridis* increased in abundance, ending up as the third most abundant species in year 3

(Fig. 1c). The only other species to increase in abundance over the 3-year period was the adelgid and coccid feeder *A. oblitterata*, which became particularly abundant on the *Pinus sylvestris* trees at site F.

All sites (A–G)

Across all sites, from very low numbers in year 1, *H. axyridis* became the most abundant ladybird by year 3 (Fig. 1d). *Adalia bipunctata* and *C. septempunctata* were abundant in year 1 and decreased in each of years 2 and 3, whereas the abundance of *A. decempunctata* and *E. quadripustulatus* peaked in year 2, before declining in year 3.

Three species declined over the 3-year period and showed a significant difference in abundance between years: *A. bipunctata* ($\chi^2_2 = 9.333$, $P = 0.009$); *C. septempunctata* ($\chi^2_2 = 8.615$, $P = 0.013$); and *P. quattuordecimpunctata* ($\chi^2_2 = 7.000$, $P = 0.030$). One species increased over the 3-year period and showed a significant difference in abundance between years: *H. axyridis* ($\chi^2_2 = 9.000$, $P = 0.011$).

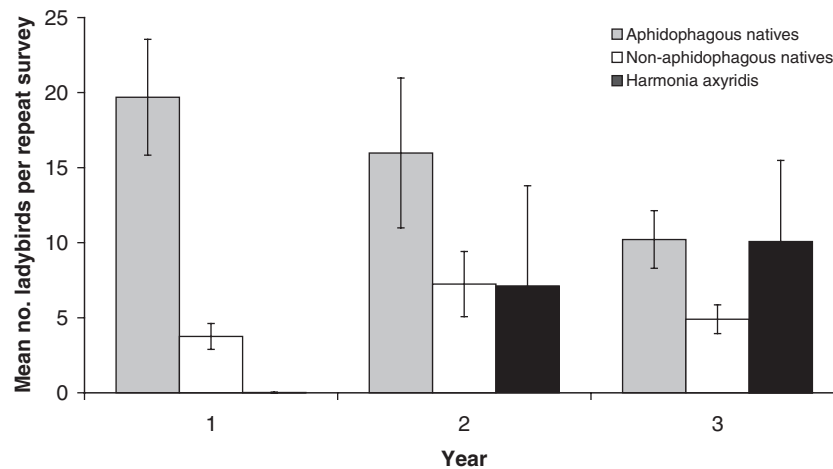


Fig. 2. Mean number of ladybirds (adults and larvae) per repeat survey, for each year (nine repeat surveys per site per year) at sites A–G. Error bars indicate 95% confidence intervals based on a sample of nine repeat surveys (i.e. sites A–G combined). Ladybirds grouped as follows: *Harmonia axyridis* only; Aphidophagous natives: *Adalia decempunctata*, *Adalia bipunctata*, *Anatis ocellata*, *Coccinella septempunctata*, *Calvia quattuordecimguttata*, *Harmonia quadripunctata*, *Myrrha octodecimguttata*, and *Propylea quattuordecimpunctata*; Non-aphidophagous natives: *Aphidecta oblitterata*, *Chilocorus renipustulatus*, *Exochomus quadripustulatus*, *Halyzia sedecimguttata*, *Subcoccinella vigintiquatuordecimpunctata*, *Tytthaspis sedecimpunctata*, and *Psyllobora vigintiduordecimpunctata*.

The only species that increased in larval abundance in both of years 2 and 3 was *H. axyridis* (Fig. 1e). Some of the other species (notably *C. septempunctata* and *E. quadripustulatus*) experienced an increase in larval abundance in year 2, followed by a major decline in year 3.

The abundance of *H. axyridis* in relation to all native ladybirds (aphidophagous and non-aphidophagous species grouped separately) is shown in Fig. 2. In year 1, *H. axyridis* was present but not abundant in the survey area and was recorded in very small numbers (0.1% of total ladybirds recorded; $n = 1480$). In year 3, *H. axyridis* was dominant (accounting for 40% of total ladybirds recorded; $n = 1586$). Conversely, native aphidophagous species declined from 84% of total ladybirds in year 1 to 41% in year 3.

The seasonal patterns of the three ladybird subgroups and aphids are shown in Fig. 3. This emphasises the decline in aphidophagous native species in year 3 and the corresponding rise in *H. axyridis*.

Relationships between ladybirds, aphids, and weather

Significant negative correlations were found for aphidophagous native adults with both *H. axyridis* adults and larvae. Significant positive correlations were found for non-aphidophagous native adults with both *H. axyridis* adults and larvae. A further significant positive correlation was found between aphidophagous native larvae and non-aphidophagous native larvae (Table 2).

The weekly aphid abundance totals between the two suction traps (Rothamsted and Broom's Barn) were strongly correlated over the 3-year survey period ($r_{154} = 0.820$, $P < 0.001$), suggesting a broad consistency in aphid abundance across the region. There were no significant correlations

between aphid abundance and abundance of the three ladybird subgroups (Table 2). Significant positive correlations between aphid abundance and only two ladybird species were found: *A. bipunctata* adults ($r_{25} = 0.431$, $P = 0.025$) and *P. quattuordecimpunctata* adults ($r_{25} = 0.576$, $P = 0.002$).

Neither the monthly or the 3-monthly rainfall totals were significantly correlated with any of the ladybird measures, whilst monthly total sunshine was significantly positively correlated with aphidophagous native larvae and significantly negatively correlated to *H. axyridis* adults (Table 2). Monthly mean maximum temperature was significantly positively correlated with the abundance of aphidophagous native larvae, and 3-monthly mean maximum temperature was significantly positively correlated with non-aphidophagous native adults (Table 2).

Discussion

Over a 3-year period encompassing the invasion phase of *H. axyridis* in eastern England, *H. axyridis* increased dramatically, whilst native aphidophagous species declined. The first year of this study represents a baseline year, with native ladybirds at the study sites presumably affected little, if at all, by *H. axyridis*, which was very low in abundance. However, by the third year *H. axyridis* was clearly the most abundant species and the data provide evidence that it had started to displace some native aphidophagous ladybirds; notably *A. bipunctata*, *C. septempunctata*, and *P. quattuordecimpunctata*. Conversely, there was a positive relationship between non-aphidophagous native adults and *H. axyridis*. This was probably caused by the most abundant non-aphidophagous species, *A. oblitterata*, increasing over the 3 years, plus low interaction of non-aphidophagous native

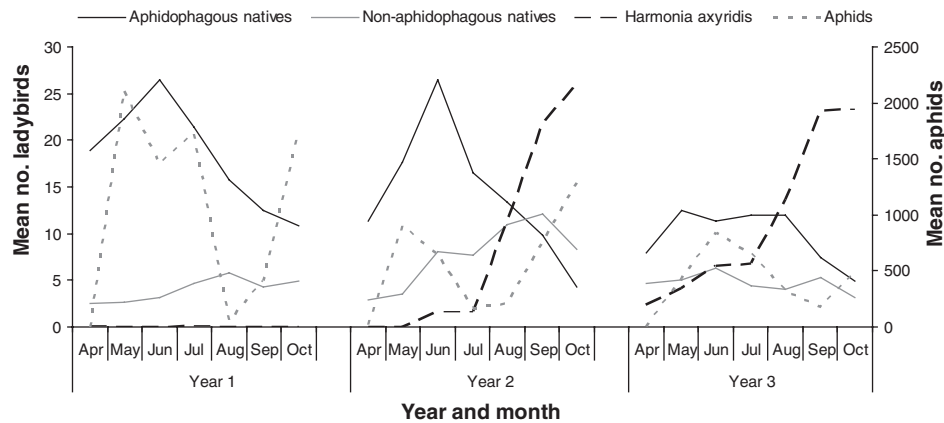


Fig. 3. Mean number of ladybirds (adults and larvae) per repeat survey for each month and year (nine repeat surveys per site per year), with corresponding mean number of aphids from the Rothamsted Insect Survey (Rothamsted and Broom's Barn suction traps). For details of species in aphidophagous native and non-aphidophagous native groups, see Fig. 2.

Table 2. Significance of Pearson correlations for ladybird abundance with aphid abundance and weather data.

	<i>H. axyridis</i> adults	<i>H. axyridis</i> larvae	Aphidophagous native adults	Aphidophagous native larvae	Non-aphidophagous native adults	Non-aphidophagous native larvae
<i>H. axyridis</i> adults		0.351	-0.580	-0.315	0.406	-0.286
<i>H. axyridis</i> larvae		0.073	0.002	0.109	0.036	0.148
Aphidophagous native adults			-0.460	0.030	0.581	-0.109
Aphidophagous native larvae			0.016	0.883	0.001	0.587
Non-aphidophagous native adults				0.220	-0.310	0.308
Non-aphidophagous native larvae				0.269	0.116	0.119
Aphids					-0.079	0.578
Survey temperature					0.697	0.002
Monthly mean max. temperature						-0.089
3-monthly mean max. temperature						0.659
Monthly total sunshine	-0.144	-0.216	0.310	0.231	-0.275	0.147
3-monthly total sunshine	0.472	0.279	0.116	0.246	0.165	0.465
Monthly total rainfall	-0.364	-0.035	0.348	0.370	-0.054	0.218
3-monthly total rainfall	0.062	0.864	0.076	0.057	0.788	0.274
Monthly mean max. temperature	-0.257	0.048	0.248	0.407	0.102	0.271
3-monthly mean max. temperature	0.196	0.814	0.213	0.035	0.613	0.171
Monthly total sunshine	0.242	0.290	-0.191	0.078	0.397	0.043
3-monthly total sunshine	0.223	0.142	0.339	0.698	0.040	0.830
Monthly total rainfall	-0.448	-0.161	0.257	0.500	-0.098	0.172
3-monthly total rainfall	0.019	0.421	0.196	0.008	0.627	0.390
Monthly mean max. temperature	-0.194	0.061	0.048	0.304	0.219	0.179
3-monthly mean max. temperature	0.333	0.761	0.812	0.123	0.273	0.373
Monthly total sunshine	-0.048	-0.077	0.120	-0.195	-0.147	0.232
3-monthly total sunshine	0.812	0.703	0.552	0.329	0.464	0.245
Monthly total rainfall	0.125	0.194	-0.156	-0.019	0.327	0.272
3-monthly total rainfall	0.534	0.332	0.438	0.926	0.096	0.170

Correlations based on mean data across sites for each survey period (i.e. nine survey periods in each of 3 years). Degrees of freedom = 25. Significant values ($P < 0.05$) shown in bold. For details of species in Aphidophagous native and Non-aphidophagous native groups, see Fig. 2. NB with such a large number of comparisons, some significant results may arise by chance alone.

species with *H. axyridis*. The abundance of other specialist conifer ladybirds changed little at our study sites over the 3-year study period.

Aphid abundance is strongly associated with weather conditions (Masterman *et al.*, 1996; Zhou *et al.*, 1997; Dixon, 1998; Dixon & Kindlmann, 1999; Harrington *et al.*, 2007), although

the mechanism [e.g. winter temperature (Westgarth-Smith *et al.*, 2007) or winter precipitation (Estay *et al.*, 2009)] may vary depending on the aphid species and ecosystem. In eastern England, winter temperature correlated with the abundance of cereal aphids in early summer (Dixon, 1998). We found a positive correlation between *A. bipunctata* adults and aphid

abundance, but not between *H. axyridis* and aphids, suggesting that *A. bipunctata* was more reliant on aphids. *Adalia bipunctata* strongly prefers habitats with high aphid density (Honek, 1985); whilst *H. axyridis* successfully tracks prey seasonally within a heterogeneous habitat (Osawa, 2000). In the third year of our study, *H. axyridis* increased in abundance despite the presence of fewer aphids than in the preceding two years, in contrast to native aphidophagous species.

Whilst the suction trap data are the result of standardised sampling and represent the aphid population over a wide area, they are only a crude indicator of food availability to ladybirds, for a number of reasons. For example, they include only winged, dispersive individuals, whereas ladybirds will also feed on the wingless stages of aphids, which, in many species, form far denser colonies and represent a better food source. Ultimately, the number of winged forms is linked to the number of wingless aphids, but in highly complex, non-linear ways. Furthermore, not all aphid species recorded will be accessible to all ladybird species.

Monthly mean maximum temperature had a stronger positive correlation with the abundance of aphidophagous native ladybirds than with *H. axyridis*. This is partly explained by the high abundance of *H. axyridis* late in the year, when temperatures tended to be lower. Although aphids were recorded in October of each year, they were in decline by then; thus alternative food is assumed to have been utilised, particularly at the lime tree sites, with abundant *H. axyridis* causing high pressure on the limited number of aphids. This presumably included a significant level of cannibalism (which was observed at the lime tree sites, but not quantified). The high abundance of *H. axyridis* larvae very late in the year [larvae were sometimes present in November and December (P. Brown, personal observation)], with little chance of survival to adulthood, suggests that the species is not yet fully adapted to conditions in England. Similarly, larvae and pupae were observed in November in Denmark, where thousands of pupae that were alive in November did not survive the winter (Steenberg & Harding, 2009). Overwinter mortality in ladybirds is often very high (Majerus, 1994; Zhou *et al.*, 1994) but also very variable, and was low for *H. axyridis* in two studies: approximately 10% in Japan (Watanabe, 2002) and 32% in Italy (Bazzocchi *et al.*, 2004). The latter study showed much higher mortality (61%) for *A. bipunctata* and a higher post-overwintering rate of increase by *H. axyridis* (Bazzocchi *et al.*, 2004). In the current study, increasing abundance of *H. axyridis* in the final 2 years of the study suggests that overwinter survival of *H. axyridis* adults was high. Multi-voltinism in *H. axyridis* was a further advantage to its population growth in the current study; in England the species has two generations per year (Brown *et al.*, 2008b), whereas many native species (including *C. septempunctata* and *A. bipunctata*) are uni-voltine in most years (Majerus, 1994).

In England, the aphidophagous ladybirds occurring on deciduous trees tend to be rather generalist in terms of habitat and diet (Majerus, 1994). For example, *A. bipunctata*, *P. quatuordecimpunctata*, and *C. septempunctata* occur on a wide range of deciduous trees, plus herbage such as nettles. These species exhibit high niche overlap with *H. axyridis* in

England (P. Brown, unpublished data) and elsewhere in Europe (Adriaens *et al.*, 2008). The negative correlation between aphidophagous native adult ladybirds and *H. axyridis* add weight to the hypothesis that the latter was at least partially the cause of the observed decline in the former. Because of its particularly high niche overlap with *H. axyridis*, *A. bipunctata* faces the highest risk of further decline. There is already some evidence from England that *A. bipunctata* has declined as a consequence of the arrival of *H. axyridis* (Majerus, 2008) and strong evidence that *A. bipunctata* seriously declined in response to the arrival of non-native species *C. septempunctata*, and particularly *H. axyridis*, in North America (Colunga-Garcia & Gage, 1998; Harmon *et al.*, 2007).

Coniferous trees provide important habitats for some specialist ladybirds found in England (Majerus, 1994), e.g. *A. ocellata*, *M. octodecimguttata*, *A. oblitterata*, *Myzia oblongoguttata* (Linnaeus, 1758), and *H. quadripunctata*. Although *H. axyridis* sometimes dominates on pine trees in its introduced (Sloggett *et al.*, 2009) and native (McClure, 1986) ranges, it did not do so in our study and, based on the low number of larvae recorded, breeding in pines was limited. Pine trees are a secondary habitat of *H. axyridis* in Japan, where it coexists with the sympatric species *Harmonia yedoensis* Takizawa (Osawa & Ohashi, 2008) and may feed on coccids as well as aphids. Whilst *H. axyridis* may adapt better to the pine trees in England in the long term, it will similarly face competition from a sympatric species in *H. quadripunctata*, as well as from the largest and best-defended native ladybird, *A. ocellata*, which may be an intraguild predator of *H. axyridis* (Ware & Majerus, 2008).

Intraguild predation (IGP) can be an important factor shaping changes in species assemblage structure (Polis & Holt, 1992). This depends on the degree of niche overlap (i.e. temporal and spatial co-occurrence) of the species at different life stages, and the relative strengths (i.e. defence and attack capabilities) of the species that encounter each other. Many studies have investigated IGP involving *H. axyridis* and other ladybirds and have found asymmetric advantage in favour of *H. axyridis* (Burgio *et al.*, 2005; Soares & Serpa, 2007; Ware & Majerus, 2008). Specifically, *A. bipunctata*, *C. septempunctata*, and *P. quatuordecimpunctata* suffered 100% asymmetric IGP by *H. axyridis* in Petri dish confrontations of fourth-instar larvae (Ware & Majerus, 2008).

Adult female ladybirds are deterred from ovipositing by the presence of conspecific larval tracks (Doumbia *et al.*, 1998) to restrict cannibalism, but not by heterospecific tracks (Doumbia *et al.*, 1998; Yasuda *et al.*, 2000) to restrict IGP. Reasons to explain this apparent lack of adaptation include lack of habitat overlap by the species concerned (Doumbia *et al.*, 1998) or unpalatability in the case of two species that do coexist (Yasuda *et al.*, 2000). The latter scenario is suggested for *H. axyridis* in Japan, which is unpalatable to *C. septempunctata* (Yasuda *et al.*, 2000). *Harmonia axyridis* may enjoy a double benefit in England. Firstly, its own eggs have chemical defences and are unpalatable to species such as *A. bipunctata* and *C. septempunctata* (Sato & Dixon, 2004), whereas *A. bipunctata* and *C. septempunctata* eggs are more palatable (Sato & Dixon, 2004; Ware *et al.*,

2008). Secondly, the evidence of Doumbia *et al.* (1998) and Yasuda *et al.* (2000) suggests that *A. bipunctata* will not be deterred from ovipositing by the presence of *H. axyridis* larvae, thereby increasing the vulnerability of its eggs to IGP. Moreover, *A. bipunctata* tends to oviposit where there is high aphid density, leading to higher levels of egg predation (Schellhorn & Andow, 1999) as *H. axyridis*, attracted by the aphids, is likely also to exploit the eggs.

Intuitively, high aphid availability should lead to lower IGP, and vice versa, and this was observed for *H. axyridis* larvae acting as intraguild predators of American native ladybird larvae (Yasuda *et al.*, 2004); in the current study this may partly explain why, in contrast to the native aphidophagous species, *H. axyridis* continued to increase in abundance in the third year, despite low aphid abundance. *Harmonia axyridis* is a highly efficient intraguild predator (Sato *et al.*, 2008) and indications of a high level of IGP of native species, including *A. bipunctata* and *C. septempunctata*, has recently been shown in wild-caught *H. axyridis* larvae in Europe (Hautier *et al.*, 2008).

Whilst the mechanisms by which *H. axyridis* impacted on aphidophagous native species are not apparent from the data presented here, they likely include asymmetric competition for aphid prey and asymmetric IGP of eggs, larvae, and pupae, in favour of *H. axyridis*. Furthermore, physiological and behavioural traits of *H. axyridis*, including multi-voltinism and polyphagy, confer additional advantages over native species. Cannibalism is also likely to play a major role in the survival of *H. axyridis*, especially late in the year. However, whilst early changes are evident, 3 years is insufficient time for the full pattern of changing species assemblage dynamics to emerge; thus surveys are ongoing at some of our sites.

This study provides evidence that in Europe *H. axyridis* has the capacity to dominate ladybird assemblages in deciduous arboreal habitats within a few years of its arrival. Some native species, notably *A. bipunctata*, are at risk of further declines as a result of the arrival of *H. axyridis*.

Acknowledgements

We dedicate this paper to our colleague and friend Professor Michael Majerus of the University of Cambridge, who was instrumental in the set up of this study. Mike tragically died in 2009. We thank Dr Remy Poland (Clifton College), the National Biodiversity Network Trust and the Department for Environment Food and Rural Affairs, for their support. We also thank Alex Dittrich (Anglia Ruskin University) for his help in producing Fig. 1. Finally, we thank the reviewers for their helpful comments, which have improved the manuscript. PMJB is funded by the Animal and Environmental Research Group and Department of Life Sciences (Anglia Ruskin University) and was supported by the Natural Environment Research Council (NERC) Centre for Ecology & Hydrology. HER is funded through the NERC Centre for Ecology & Hydrology and the Joint Nature Conservation Committee.

References

- Adriaens, T., Branquart, E. & Maes, D. (2003) The multicoloured Asian ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a threat for native aphid predators in Belgium? *Belgian Journal of Zoology*, **133**, 195–196.
- Adriaens, T., San Martín y Gomez, G. & Maes, D. (2008) Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. *Biocontrol*, **53**, 69–88.
- de Almeida, L.M. & da Silva, V.B. (2002) First record of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): a lady beetle native to the Palaearctic region. *Revista Brasileira de Zoologia*, **19**, 941–944.
- Alyokhin, A. & Sewell, G. (2004) Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, **6**, 463–471.
- Bazzocchi, G.G., Lanzoni, A., Accinelli, G. & Burgio, G. (2004) Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *Biocontrol*, **49**, 245–260.
- Brown, M.W. & Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143–151.
- Brown, P.M.J., Adriaens, T., Bathon, H., Cuppen, J., Goldarazena, A., Hagg, T. *et al.* (2008a) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *Biocontrol*, **53**, 5–21.
- Brown, P.M.J., Roy, H.E., Rothery, P., Roy, D.B., Ware, R.L. & Majerus, M.E.N. (2008b) *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native coccinellid. *Biocontrol*, **53**, 55–67.
- Burgio, G., Santi, F. & Maini, S. (2005) Intra-guild predation and cannibalism between *Harmonia axyridis* and *Adalia bipunctata* adults and larvae: laboratory experiments. *Bulletin of Insectology*, **58**, 135–140.
- Colunga-Garcia, M. & Gage, S.H. (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology*, **27**, 1574–1580.
- Coutanceau, J. (2006) *Harmonia axyridis* (Pallas, 1773): une coccinelle asiatique introduite, acclimatée et en extension en France. *Bulletin de la Société Entomologique de France*, **111**, 395–401.
- Dixon, A.F.G. (1998) *Aphid Ecology: An Optimization Approach*, 2nd edn. Chapman & Hall, London, U.K.
- Dixon, A.F.G. & Kindlmann, P. (1999) Population dynamics of aphids. *Insect Populations in Theory and in Practice* (ed. by J. P. Dempster and I. F. G. McLean), pp. 207–230. Springer, Dordrecht, Netherlands.
- Dobzhansky, T. (1933) Geographical variation in ladybeetles. *American Naturalist*, **67**, 97–126.
- Doumbia, M., Hemptinne, J.L. & Dixon, A.F.G. (1998) Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia*, **113**, 197–202.
- Elliott, N., Kieckhefer, R. & Kauffman, W. (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia*, **105**, 537–544.
- Estay, S.A., Lima, M. & Harrington, R. (2009) Climate mediated exogenous forcing and synchrony in populations of the oak aphid in the UK. *Oikos*, **118**, 175–182.
- Evans, E.W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology*, **85**, 637–647.
- Ferran, A., El-Arnauty, S.A., Beyssat-Arnaouty, V. & Galal, H. (2000) Introduction and release of the coccinellid *Harmonia axyridis* Pallas for controlling *Aphis craccivora* Koch on faba beans in Egypt. *Egyptian Journal of Biological Pest Control*, **10**, 129–136.

- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America North of Mexico. *Journal of the New York Entomological Society*, **93**, 1–912.
- Greze, A., Zaviezo, T., Gonzalez, G. & Rothmann, S. (2010) *Harmonia axyridis* in Chile: a new threat. *Ciencia e Investigación Agraria*, **37**, 145–149.
- Harmon, J.P., Stephens, E. & Losey, J. (2007) The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *Journal of Insect Conservation*, **11**, 85–94.
- Harrington, R. & Woiwod, I.P. (2007) Foresight from hindsight: the Rothamsted Insect Survey. *Outlooks on Pest Management*, **18**, 9–14.
- Harrington, R., Hulle, M. & Plantegenest, M. (2007) Monitoring and forecasting. *Aphids as Crop Pests* (ed. by H. F. van Emden and R. Harrington), pp. 515–536. CAB International, Wallingford, U.K.
- Hautier, L., Gregoire, J., de Schauwers, J., Martin, G.S., Callier, P., Jansen, J. *et al.* (2008) Intraguild predation by *Harmonia axyridis* on coccinellids revealed by exogenous alkaloid sequestration. *Chemoecology*, **18**, 191–196.
- Hodek, I. (1973) *Biology of Coccinellidae*. Dr W. Junk, The Hague, Netherlands.
- Honek, A. (1985) Habitat preferences of aphidophagous coccinellids [Coleoptera]. *Entomophaga*, **30**, 253–264.
- Jansen, J.P. & Hautier, L. (2008) Ladybird population dynamics in potato: comparison of native species with an invasive species, *Harmonia axyridis*. *Biocontrol*, **53**, 223–233.
- Koch, R.L. (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science*, **3**, 1–16.
- Koch, R.L. & Galvan, T.L. (2008) Bad side of a good beetle: the North American experience with *Harmonia axyridis*. *Biocontrol*, **53**, 23–35.
- Koch, R.L., Venette, R.C. & Hutchison, W.D. (2006) Invasions by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the Western Hemisphere: Implications for South America. *Neotropical Entomology*, **35**, 421–434.
- Koyama, S. & Majerus, M.E.N. (2008) Interactions between the parasitoid wasp *Dinocampus coccinellae* and two species of coccinellid from Japan and Britain. *Biocontrol*, **53**, 253–264.
- Kuznetsov, V.N. (1997) *Lady Beetles of the Russian Far East*. The Sandhill Crane Press, Gainesville, Florida.
- Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted Insect Survey 12 metre suction trap. *Bulletin of Entomological Research*, **78**, 121–129.
- Majerus, M.E.N. (1994) *Ladybirds*. HarperCollins, London, U.K.
- Majerus, M.E.N. (2008) First evidence of a decline in a native ladybird as a consequence of the arrival of the harlequin ladybird, *Harmonia axyridis*, in Britain. *Bulletin of the Amateur Entomologists' Society*, **67**, 142–147.
- Majerus, M.E.N., Strawson, V. & Roy, H.E. (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology*, **31**, 207–215.
- Masterman, A.J., Foster, G.N., Holmes, S.J. & Harrington, R. (1996) The use of the Lamb daily weather types and the indices of progressiveness, southerliness and cyclonicity to investigate the autumn migration of *Rhopalosiphum padi*. *Journal of Applied Ecology*, **33**, 23–30.
- McClure, M.S. (1986) Role of predators in regulation of endemic populations of *Matsucoccus matsumurae* (Homoptera: Margarodidae) in Japan. *Environmental Entomology*, **15**, 976–983.
- Michaud, J.P. (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, **31**, 827–835.
- Osawa, N. (2000) Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. *Population Ecology*, **42**, 115–127.
- Osawa, N. & Ohashi, K. (2008) Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae) and the roles of maternal investment through egg and sibling cannibalism. *European Journal of Entomology*, **105**, 445–454.
- Polis, G.A. & Holt, R.D. (1992) Intraguild predation – the dynamics of complex trophic interactions. *Trends in Ecology & Evolution*, **7**, 151–154.
- Roy, H.E., Brown, P. & Majerus, M.E.N. (2006) *Harmonia axyridis*: a successful biocontrol agent or an invasive threat? *An Ecological and Societal Approach to Biological Control* (ed. by J. Eilenberg and H. Hokkanen), pp. 295–309. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Roy, H.E., Brown, P.M.J., Rothery, P., Ware, R.L. & Majerus, M.E.N. (2008) Interactions between the fungal pathogen *Beauveria bassiana* and three species of coccinellid: *Harmonia axyridis*, *Coccinella septempunctata* and *Adalia bipunctata*. *Biocontrol*, **53**, 265–276.
- Saini, E.D. (2004) Presencia de *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) en la provincia de Buenos Aires: Aspectos biológicos y morfológicos. *Revista de Investigaciones Agropecuarias*, **33**, 151–160.
- Sato, S. & Dixon, A.F.G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology*, **6**, 21–24.
- Sato, S., Jimbo, R., Yasuda, H. & Dixon, A.F.G. (2008) Cost of being an intraguild predator in predatory ladybirds. *Applied Entomology and Zoology*, **43**, 143–147.
- Schellhorn, N.A. & Andow, D.A. (1999) Cannibalism and interspecific predation: role of oviposition behavior. *Ecological Applications*, **9**, 418–428.
- Sloggett, J.J., Obyrcki, J.J. & Haynes, K.F. (2009) Identification and quantification of predation: novel use of gas chromatography–mass spectrometric analysis of prey alkaloid markers. *Functional Ecology*, **23**, 416–426.
- Soares, A.O. & Serpa, A. (2007) Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. *Population Ecology*, **49**, 37–43.
- Stals, R. (2008) Invasive ladybird spreading in South Africa. *Biocontrol News and Information*, **29**, 24–26.
- Stenberg, T. & Harding, S. (2009) The harlequin ladybird (*Harmonia axyridis* Pallas) in Denmark: spread and phenology during the initial phase of invasion. *Entomologiske Meddelelser*, **77**, 27–39.
- Turnock, W.J., Wise, I.L. & Matheson, F.O. (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Canadian Entomologist*, **135**, 391–404.
- Ware, R.L. & Majerus, M.E.N. (2008) Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*. *Biocontrol*, **53**, 169–188.
- Ware, R.L., Majerus, M.E.N., Roy, H.E. & Symington, F. (2005) The harlequin ladybird arrives in Britain: a threat to our native species? *Bulletin of the Amateur Entomologists' Society*, **64**, 175–186.
- Ware, R.L., Evans, N., O'Farrell, K., Malpas, L., Michie, L.J. & Majerus, M.E.N. (2008) Intraguild predation of British and Japanese

- coccinellid eggs by the invasive ladybird *Harmonia axyridis*. *Neobiota*, **7**, 263–275.
- Watanabe, M. (2002) Cold tolerance and myo-inositol accumulation in overwintering adults of a lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **99**, 5–9.
- Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F. & Harrington, R. (2007) Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming. *Quaternary International*, **173**, 153–160.
- Yasuda, H., Takagi, T. & Kogi, K. (2000) Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **97**, 551–553.
- Yasuda, H., Evans, E.W., Kajita, Y., Urakawa, K. & Takizawa, T. (2004) Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia*, **141**, 722–731.
- Zhou, X., Carter, N. & Powell, W. (1994) Seasonal distribution and aerial movement of adult coccinellids on farmland. *Biocontrol Science and Technology*, **4**, 167–175.
- Zhou, X., Perry, J.N., Woiwod, I.P., Harrington, R., Bale, J.S. & Clark, S.J. (1997) Temperature change and complex dynamics. *Oecologia*, **112**, 543–550.

Accepted 7 January 2011

Appendix. Means and standard errors of numbers of ladybirds per repeat survey, for each year, grouped by habitat, as shown in Fig. 1.

Associated letter from Fig. 1, site codes and ladybird life stage	Species	Year 1 mean	Year 1 SE	Year 2 mean	Year 2 SE	Year 3 mean	Year 3 SE
(a) Lime tree sites (sites A and B) Adults	<i>Adalia decempunctata</i>	9.33	3.00	10.28	2.50	9.44	3.00
	<i>Adalia bipunctata</i>	8.61	3.06	5.39	1.61	2.39	0.06
	<i>Coccinella septempunctata</i>	1.61	0.83	0.00	0.00	0.00	0.00
	<i>Exochomus quadripustulatus</i>	0.39	0.06	0.28	0.17	0.39	0.17
	<i>Harmonia axyridis</i>	0.00	0.00	13.67	5.56	20.83	5.06
(b) Pine tree sites (C and D) adults	Other	5.11	1.00	2.44	1.33	2.39	0.50
	<i>Adalia decempunctata</i>	0.11	0.00	3.17	2.61	0.17	0.17
	<i>Adalia bipunctata</i>	0.06	0.06	0.33	0.33	0.00	0.00
	<i>Coccinella septempunctata</i>	3.50	0.50	1.50	1.17	1.94	1.06
	<i>Exochomus quadripustulatus</i>	2.83	1.83	6.17	5.50	2.33	2.22
(c) Mixed sites (E–G) adults	<i>Harmonia axyridis</i>	0.00	0.00	0.72	0.72	0.56	0.56
	Other	1.39	0.94	2.89	2.11	2.33	2.22
	<i>Adalia decempunctata</i>	5.26	2.49	4.51	2.07	2.87	1.12
	<i>Adalia bipunctata</i>	3.45	1.44	2.83	1.02	0.90	0.44
	<i>Aphidecta oblitterata</i>	1.32	1.32	4.33	4.33	6.43	6.38
	<i>Coccinella septempunctata</i>	4.33	0.39	2.19	1.71	0.15	0.05
	<i>Exochomus quadripustulatus</i>	1.78	1.14	2.38	1.52	1.78	1.12
	<i>Harmonia quadripunctata</i>	3.47	1.83	2.79	1.47	2.29	1.30
(d) All sites adults	<i>Harmonia axyridis</i>	0.02	0.01	2.11	0.85	2.50	0.72
	<i>Subcoccinella vigintiquatuorpunctata</i>	2.31	1.39	3.42	3.15	0.73	1.10
	Other	5.06	0.57	2.45	0.37	1.68	0.80
	<i>Adalia decempunctata</i>	4.95	1.83	5.78	1.62	3.98	1.82
	<i>Adalia bipunctata</i>	3.96	1.59	2.85	0.94	1.07	0.43
	<i>Coccinella septempunctata</i>	3.31	0.53	1.37	1.02	0.62	0.55
	<i>Exochomus quadripustulatus</i>	1.68	0.70	2.86	1.62	1.54	0.72
	<i>Harmonia axyridis</i>	0.01	0.01	5.01	2.58	7.18	3.72
(e) All sites larvae	Other	7.08	2.15	7.09	2.92	6.12	3.20
	<i>Adalia</i> spp.	1.86	1.19	1.39	0.62	0.99	0.66
	<i>Coccinella septempunctata</i>	0.06	0.06	0.42	0.39	0.00	0.00
	<i>Exochomus quadripustulatus</i>	0.11	0.09	0.67	0.53	0.12	0.09
	<i>Harmonia axyridis</i>	0.02	0.02	2.11	1.56	2.51	1.69
	Other	0.45	0.12	1.84	0.65	1.17	0.49