



Harmonia axyridis (Coleoptera: Coccinellidae): Smelling the rat in native ladybird declines

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Abstract. In the last two decades a huge amount of research has focused on the invasive harlequin ladybird, *Harmonia axyridis*, particularly on potential or actual deleterious effects that have arisen after it has colonised new regions. A focus of this work has been real or anticipated declines in native ladybird abundance since the introduction of *H. axyridis*, for which it is deemed responsible. Scientists have generally painted a very bleak picture of the effects of *H. axyridis* on native species: in this paper I argue that the picture painted is often too bleak. I use the case of the 2-spot ladybird, *Adalia bipunctata*, the species most often invoked as threatened by *H. axyridis*, to illustrate my point. While there is little question that *H. axyridis* has led to a decline in *A. bipunctata* populations in Europe, it seems likely that prior to the invasive ladybird's arrival *A. bipunctata* occurred in artificially high numbers in the urban environments in which it was typically studied. Pollution in towns and cities led to enhanced numbers of prey aphids on plants there which initially favoured *A. bipunctata*, and later *H. axyridis*. Thus one species, *A. bipunctata*, that has benefitted from an association with humans has been replaced by another, *H. axyridis*, just as brown rats replaced black rats in Europe and North America. Viewed with a longer perspective, *A. bipunctata* has more likely declined back to pre-industrial levels: the artificially high level from which it has declined recently was not a 'natural' one, and thus its decline from this level does not imply that it is now threatened or endangered. More broadly, we need a wider perspective, encompassing other ladybirds, longer timeframes and better comparisons with other (non-ladybird) invasive species to more clearly assess whether *H. axyridis* really poses as much of a threat as is often proposed.

INTRODUCTION

In the last two decades, a huge amount of research has focused on just one species of ladybird, the invasive Asian species *Harmonia axyridis* (Pallas) (Sloggett, 2005, 2012; Roy et al., 2016). A lot of this research has documented its rapid spread outside its native range and potential or actual deleterious effects on other species in the areas it has colonised (reviewed in Koch, 2003; Majerus et al., 2006; Koch & Galvan, 2008; Sloggett, 2012; Roy & Brown, 2015; Roy et al., 2016). The ladybird has often appeared in a very bad light, both over its interactions with humans (e.g., McCutcheon & Scott, 2001; Goetz, 2009; Linder et al., 2009) and other organisms (e.g., Koch et al., 2006; Roy et al., 2012; Howe et al., 2015).

The effects of invasive *H. axyridis* on native ladybirds have received particular attention. The focus of this work has been actual or anticipated declines in native species abundance since the introduction of *H. axyridis* (e.g., Michaud, 2002; Martins et al., 2009; Adriaens et al., 2010; Roy et al., 2012, 2016; Grez et al., 2016), although the detailed picture is complex (Harmon et al., 2007; Bahlai et al., 2015). This focus has been coupled to numerous ex-

periments demonstrating strong intraguild predation of native species by *H. axyridis* in the laboratory and field (e.g., Cottrell & Yeargan 1998a, b; Yasuda et al., 2004; Ware & Majerus, 2008; Thomas et al., 2013; Rondoni et al., 2015), although competitive displacement could be more significant in explaining native species' declines (Harmon et al., 2007; Snyder, 2009; Bahlai et al., 2015).

In spite of the underlying complexity involved, the picture painted of the effects of *H. axyridis* on other coccinellids is generally bleak. This negative view has exerted an influence on the general public, often via the press (e.g., Roy et al., 2006), and on policy makers (Ehlers, 2011; Klapwijk, 2013). Gozlan et al. (2013) found that of five non-native species, *H. axyridis* was the most researched in Britain, although it was assessed by them as only the third-ranked ecological threat. All these observations argue for the best possible assessment of the threat posed by *H. axyridis*. In this paper, I argue that the picture painted is too bleak. To illustrate this point, I look at one case of an *H. axyridis*-associated native ladybird decline in detail, that of the 2-spot ladybird, *Adalia bipunctata* (L.). This species is often argued to be most at threat from *H. axyridis*. I use

personal observations and data from before and after the arrival of *H. axyridis* in its European range to argue that our perception of how dangerous *H. axyridis* is to *A. bipunctata*, and by implication other native ladybirds, might be greater than the threat it actually poses.

ADALIA BIPUNCTATA AND ITS INTERACTION WITH HARMONIA AXYRIDIS

Adalia bipunctata is a small aphidophagous member of the subfamily Coccinellinae, which contains most of the commonly recognised species of ladybirds. The ladybird is a habitat and dietary generalist, exhibiting something of a preference for deciduous trees, though also occurring on low-growing plants such as nettles and beans (e.g., Majerus, 1994; Honěk & Hodek, 1996). The species is of Holarctic distribution. Prior to the arrival of *H. axyridis*, it was an extremely common species in Europe. Its status as a native of North America is unclear although it is not a very recent arrival (Krafsur et al., 1996); furthermore, the possible roles of other invasive coccinellids, notably *Coccinella septempunctata* L., in its decline in North America (Harmon et al., 2007) make discussion of the situation there more complex. I therefore largely restrict my discussion in this paper to European populations of *A. bipunctata*.

Prior to the arrival of invasive *H. axyridis*, in Europe at least, *A. bipunctata* was one of the most extensively studied ladybird models (Sloggett, 2005). In large part this was due to numerous studies of its genetic colour pattern polymorphism (reviewed in Majerus, 1994; Sloggett & Honěk, 2012), but studies ranged widely over many other areas of ladybird biology including mating and reproduction, chemical defence, foraging and feeding, and host-parasite interactions (Majerus, 1994; Omkar & Pervez, 2005; Sloggett, 2005; Hodek et al., 2012).

There is no doubt that *H. axyridis* has had a strong deleterious effect on *A. bipunctata*, even though some populations had apparently been declining prior to its arrival (see discussion). Five years after the arrival of *H. axyridis*, *A. bipunctata* had declined by 30% in Belgium and by 44% in the UK, where previously it had been increasing (Roy et al., 2012). *Harmonia axyridis* shows a strong habitat overlap with *A. bipunctata*, being also a generalist with a preference for deciduous trees (Majerus et al., 2006; Adriaens et al., 2008). A number of studies have documented asymmetric intraguild predation in favour of *H. axyridis* over *A. bipunctata* in the laboratory (e.g., Ware & Majerus, 2008; Katsanis et al., 2013) and intraguild predation of *A. bipunctata* by *H. axyridis* has also been demonstrated in the field (e.g., Hautier et al., 2011; Thomas et al., 2013): this has been suggested as a cause for the decline of *A. bipunctata*.

The fate of *A. bipunctata* has drawn considerable attention beyond the research community. Based on IUCN Red List criteria, the species was classed as “Vulnerable” in Flanders (Belgium) due to its declining numbers (Adriaens et al., 2015). In France an economic evaluation of willingness to compensate for the effects of *H. axyridis*, suggested that individual households would be prepared to pay annually between €8.60 and €11.40 to preserve *A. bipunctata*;

this amounts to a total budget of €198 million to €266 million per year (Chakir et al., 2016).

URBANISATION AND LADYBIRDS

There is good, though scattered, evidence that man-made environments favour certain ladybirds. Such habitats include not only agricultural ecosystems (Honěk, 2012), but also urban and industrial habitats (e.g., Kozlov, 2015; Akkermans, 2016; Egerer et al., 2017). Aphids are known to benefit from the presence of humans, reaching high densities on plants suffering from the effects of pollution: this can lead to high aphid populations in urban areas (Bell et al., 1993), perhaps further exacerbated by higher temperatures in towns (Dale & Frank, 2014). Such resource availability increases the size of ladybird populations, especially of generalist species, which prefer high aphid densities (see Sloggett, 2008).

Urban areas are suggested to be important in the establishment of new ladybird species (e.g., Kaneko, 2013; Kawakami et al., 2016), and this is certainly true for *H. axyridis* (e.g., Adriaens et al., 2008; Purse et al., 2015; Veran et al., 2016). Explanations for the effects of urbanisation include that *H. axyridis* finds suitable overwintering sites inside buildings and suitable foraging habitats or aphid host plants, such as lime (*Tilia* spp.) and sycamore (*Acer pseudoplatanus* L.) (Brown et al., 2008; Purse et al., 2015; Veran et al., 2016). It seems highly likely that human changes to the environment, resulting in higher aphid densities in urban and other anthropogenic habitats have favoured this large voracious ladybird (e.g., see Mukwehvo et al., 2017). Fig. 1a shows numbers of *H. axyridis* collected from lime trees in the Dutch city of Eindhoven and the surrounding region; limes support significant populations of aphids (*Eucallipterus tiliae* L.), which are increased in urban areas (Carter, 1992; Wilkaniec et al., 2013). Twice as many *H. axyridis* were recorded at the central site as in suburban and rural areas. Artificially long persistence of city aphid populations at high levels (e.g., see Wilkaniec et al., 2013) likely also leads to a long potential breeding season, favouring *H. axyridis*, which can produce several generations a year (e.g. Adriaens et al., 2008). In central Eindhoven, in 2016, *H. axyridis* larvae could still be found on limes into November.

However, the same was true for *A. bipunctata* before the arrival of *H. axyridis*. An extreme example was seen in London in the late 1990s. In 1999, I participated in a study of *A. bipunctata*, covering central London and its suburbs (Welch et al., 2001). Here, pollution or high temperatures favoured long-lasting aphid populations in the centre of the city, most notably *E. tiliae* on lime trees, which also harboured *A. bipunctata*. Like *H. axyridis*, *A. bipunctata* reached very high numbers in the central city and exhibited an altered phenology, breeding late into the year. In October 1999, I was able to collect abundant *A. bipunctata* adults and larvae from limes at Finsbury Park in North London (51.57°N, 0.10°W). Although perhaps less pronounced, the same appears to have been true for *A. bipunctata* in other

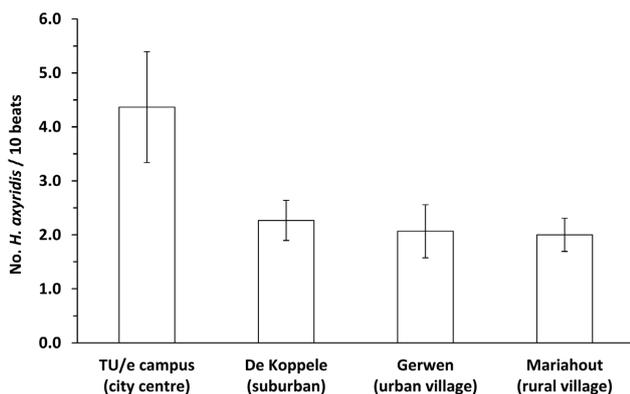
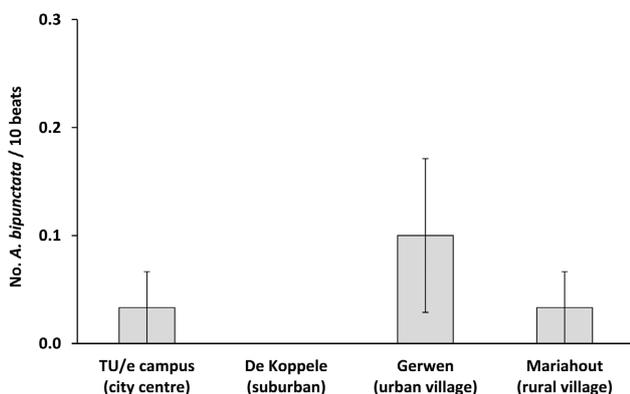
(a) *Harmonia axyridis*(b) *Adalia bipunctata*

Fig. 1. Numbers of adult *Harmonia axyridis* (a) and *Adalia bipunctata* (b) collected on lime trees (*Tilia* spp.) at four sites in and around the city of Eindhoven, The Netherlands, on 26th August 2016. From left to right, sites are at an increasing distance from central Eindhoven in a north-easterly direction, with distance from central Eindhoven (TU Eindhoven campus 51.4492°N, 5.4947°E): De Koppele (51.4810°N, 5.4910°E) 3.5 km; Gerwen (51.4885°N, 5.5645°E) 7 km; Mariahout (51.5410°N, 5.5705°E) 12 km. Tree branches were beaten using a one-metre long stick and beating tray ten times and ladybirds counted on the beating tray; this was carried out on three different areas of the reachable canopy (\leq approx. 3 m height) of each tree; ten trees were beaten at each site. Values given here are Mean \pm S.E. of mean values for the three areas of each tree. For *H. axyridis*, a one-way ANOVA across the four sites was carried out, using each of the three areas of each tree as repeated measures and Type III sum of squares in SPSS 24: $F_{3,36} = 3.362$, $P = 0.029$. No such analysis was carried out for *A. bipunctata* as the numbers of ladybirds were so low, being between a total of zero and three at each site (note that the y-axis is 1/20 the scale of the *H. axyridis* graph).

European urban areas (e.g., Timoféeff-Ressovsky, 1940; Czechowska & Bielawski, 1981; Brakefield, 1984).

This does not appear to be the case anymore. In spite of carrying out numerous collections of ladybirds on limes in the cities of Breda, Eindhoven and Maastricht in the south of the Netherlands since 2010, I have only observed numerous *A. bipunctata* on lime trees on a single occasion (Table 1). Fig. 1b shows data for *A. bipunctata* on limes collected in the same places and at the same time as the data for *H. axyridis* shown in Fig. 1a. Numbers are universally low and show none of the effects of urbanisation observed before the arrival of *H. axyridis*.

Table 1. Observations by the author of significant populations of *A. bipunctata* in the southern Netherlands in the period 2010–2016 after the invasion of *H. axyridis*. The (qualitative) criterion for inclusion here is that a sufficient number of adult ladybirds were observed over a number of plants in the same area not to be considered an isolated or chance occurrence, although exact numbers were not recorded. Immature stages are not considered here due to the problems of field differentiation between them and the same stages of the sibling species *Adalia decempunctata* (L.) (10-spot ladybird), although at some sites *A. bipunctata* immature stages appeared to be present. Only one observation was made on lime trees where *A. bipunctata* was hitherto abundant; others were made on a diversity of plants where *A. bipunctata* has been less regularly looked for. All observations were incidental, that is *A. bipunctata* was not being specifically searched for. Timing (e.g., an absence of observations in 2013–2014) is a reflection of periods when the author was or was not active in the field. It is also worth noting that only lime trees are regularly searched by the author, thus the observation of *A. bipunctata* on lime trees likely constitutes a much lower incidence of this species than on the other plants.

Date	Location	Plant
July–Aug 2011	Breda (centre) 51.5937°N, 4.7723°E	Tansy (<i>Tanacetum vulgare</i>)
July 2012	Eindhoven (centre) 51.4455°N, 5.4827°E	Tansy (<i>Tanacetum vulgare</i>)
July 2012	Maastricht (centre) 50.8406°N, 5.6960°E	Lime (<i>Tilia</i> sp.)
May–June 2015 May–June 2016	Eindhoven (centre) 51.4488°N, 5.4841°E	Hazel (<i>Corylus avellana</i>)
June–July 2016	Maastricht (suburban) 50.8375°N, 5.7095°E	Elder (<i>Sambuca nigra</i>)
July 2016	Eindhoven (suburban) 51.4333°N, 5.5225°E	Poplar (<i>Populus</i> sp.)

However, this picture is not complete. On other plants, I have observed a number of outbreaks of *A. bipunctata* (Table 1). In these cases, numbers of accompanying *H. axyridis* were often low, suggesting that on these plants *A. bipunctata* could have some form of competitive advantage. As a generalist, *A. bipunctata* has probably always occurred in these habitats: my own memories from before the arrival of *H. axyridis* suggest this was the case. However, it was less frequently observed or collected in these habitats due to the focus of researchers on hitherto large and abundant populations elsewhere, especially those easily collected on trees such as urban limes, and sycamores where *A. bipunctata* was also previously abundant (e.g., Dixon, 1970). More recent assessments of *A. bipunctata* have used the same urban trees (e.g., Roy et al., 2012 used urban limes and sycamores), likely overestimating the decline because other habitats have been underrepresented in surveys.

Thus our picture of *A. bipunctata* decline may be overly pessimistic. Certainly *A. bipunctata* has declined due to *H. axyridis* on certain urban trees. However, the decline in *A. bipunctata* has been from an artificially elevated level, the ladybird having previously risen to high numbers as a consequence of the same human-related environmental effects that subsequently favoured *H. axyridis*. In habitats elsewhere, *A. bipunctata* persists, probably as it did before

human interference, on sporadic outbreaks of aphids, relatively unthreatened by *H. axyridis*.

DISCUSSION

I have focused here on the effects of *H. axyridis* on *A. bipunctata*, as a way of examining in detail whether researchers' assessments of an acute threat posed by *H. axyridis* to other ladybird species are fully justified. *Adalia bipunctata* was for a long time a widely used research model and its apparent disappearance was likely for many researchers a personal manifestation of the effects of *H. axyridis*. Furthermore, *A. bipunctata* was a common species closely associated with man, thus highly visible. This made the effects of *H. axyridis* in such habitats very obvious. It was apparently clear that *A. bipunctata* was under threat.

But such a view is based on a very static view of the ladybird fauna that takes a 'before and after' view of invasive species, and sees their effects in isolation. The ladybird fauna prior to invasion was not a 'natural' one, but was already the product of many centuries of human influence, in agriculture and, as argued here, through other forms of development in cities, particularly those leading to pollution.

Certainly *A. bipunctata* has undergone habitat compression (sensu Evans et al., 2011); that is, the species has been forced back into habitat (aphid host plant) refugia. However, viewed in the longer term the threat posed by *H. axyridis* to *A. bipunctata* is neither so great nor so serious as has been proposed. The native ladybird appears to have been forced from urban trees particularly, where it only reached high numbers because of human effects enhancing aphid populations. Its presence there was not 'natural' but the product of human influence. During the 1999 study in London, Greg Hurst, the senior researcher, likened *A. bipunctata* to a "ladybird rat" in conversation. This is a fitting analogy, which may be taken further. It is analogous to the black rat (*Rattus rattus* L.). This human commensal was ultimately replaced in Europe and North America by the more aggressive, larger brown rat (*Rattus norvegicus* (Berkenhout)), another species closely related with humans (Hedrich, 2000; Feng & Himsworth, 2014). In this analogy, *H. axyridis* is the brown rat: a bigger, more rapacious human commensal replacing a smaller, pre-existing one.

The ideas developed here for European *A. bipunctata* receive support from other parts of the world where the two ladybirds also coexist. There is some evidence that *A. bipunctata* in North America have been subject to habitat compression by *H. axyridis*, in this case retreating from agricultural habitats, while persisting or appearing in arboreal ones (Obrycki et al., 2000; Hesler & Kieckhefer, 2008; Bahlai et al., 2015). Although the focus has been on anthropogenic urban ecosystems in this paper, the same considerations apply to agricultural ecosystems, where aphid and ladybird populations are also enhanced through human actions (e.g., Pimentel, 1971; Duffield et al., 1997). Furthermore, *A. bipunctata* has been slowly spreading in Japan, where it is an exotic, despite facing an abundant na-

tive population of *H. axyridis* (Toda & Sakuratani, 2006): this latter observation suggests that *H. axyridis* is unlikely to ever render *A. bipunctata* extinct.

The observations made here for *A. bipunctata* are not unique. Evans (2004) studying the effects of the European invasive *Coccinella septempunctata* in North America found that American native coccinellids displaced by *C. septempunctata* from alfalfa returned if the level of the prey pea aphid, *Acyrtosiphon pisum* (Harris), was artificially increased. He had previously observed that native species were more abundant in other, endemic vegetation (Evans, 2000). Further research using historical collections and literature suggested that at least one native species, *Coccinella novemnotata* Herbst, was previously more common in alfalfa in the 1950s as it exploited a population explosion of the invasive spotted alfalfa aphid *Therioaphis maculata* (Buckton) (Evans, 2013). Based on these observations it may be deduced that American native species at artificially high levels due to abundant aphids in crops were once again restricted to ancestral habitats in the face of an invader.

Not all observations support habitat compression (e.g., Finlayson et al., 2008) and certainly other factors are likely at play in the decline of *A. bipunctata*. Honek et al. (2016), using datasets extending over 39 years, have shown that *A. bipunctata* was already declining in Europe before the arrival of *H. axyridis*. It is tempting to suggest that this decline might have occurred because of decreasing air pollution or other anthropogenic effects, leading to lower aphid populations generally. In this case, it would not be an effect totally divorced from those discussed here. Such a study emphasises that the situation is not a simple one and a broader context is necessary than one narrowly focused on *H. axyridis*.

This broader context should certainly focus on a longer time perspective, as discussed above. Ladybird populations have been in flux since prehistory (Majerus, 1994) and will continue to be so with or without invasive species (Acorn, 2007). A better understanding of such changes is needed, including using entomological collections and literature in the manner of Evans (2013) for *C. novemnotata*. Collection specimens of *A. bipunctata*, for example, date back as far as the 17th century (Hammond, 1975). Hand-in-hand with this is a need to establish what other threats are posed to ladybirds. Loss of natural habitats may be a particularly influential factor. However this and other factors such as climate change (Roy & Majerus, 2010) are currently much less well researched than the effects of invasive ladybirds.

Because of its widespread nature and abundance, as well as its invasiveness, studies of *H. axyridis* are often in advance of studies of other members of the Coccinellidae. We frequently lack the context in which to assess which characteristics of *H. axyridis* make it so successful or pose a potential threat, because we lack studies of the same features of other non-invasive species (Sloggett, 2005, 2012). Thus a number of studies show that *H. axyridis* is an intraguild predator of *A. bipunctata* in the field (e.g., Hautier et al., 2011; Thomas et al., 2013; Rondoni et al., 2015).

However, we do not know if this poses a unique threat to *A. bipunctata* or not, because there is no work on intraguild predation of *A. bipunctata* in the field by native species of ladybirds: indeed there are relatively few laboratory studies (but see Hemptinne et al., 2000; Rondoni et al., 2012). It is perhaps ironic that the native species valued by so many *H. axyridis* researchers are so rarely studied themselves.

Underlying these issues is a lack of precision in defining the nature of the threat that *H. axyridis* poses. When we discuss a decline in native ladybirds are we implying that species will go extinct? Researchers may benefit from this association in the minds of policy makers or the general public but, in fact, we have no historical records of any ladybird ever going extinct (Honek et al., 2017). Could it be that *H. axyridis* poses an insufficient threat alone, but when combined with other threats, it will cause species extinctions? Or will similar levels of biodiversity be maintained, albeit with some species reduced to smaller numbers than before (as might be inferred from *A. bipunctata*)? This ambiguity needs to be resolved. Although often considered bad per se, a decline in numbers is not necessarily a catastrophe.

In conclusion, more care is required in assessing and describing the likely effects of ladybird invaders generally and *H. axyridis* in particular. Numerous papers have taken an uncompromising stance on the dire effects of the invader: a more nuanced view of its effects has been slow to emerge. Early on in its colonization of Europe, *H. axyridis* was given the title of the “most invasive ladybird on earth” (Roy et al., 2006). This title itself well illustrates the need for a wider perspective. For a ladybird researcher, it suggests that the ladybird is a serious environmental threat, but when coccinellids are viewed as a 6000-species strong single family compared to the likely millions of species in existence (Nedvěd & Kovář, 2012; Caley et al., 2014), the claim seems rather small. We need to ask ourselves if *H. axyridis* is as big a problem as initially it appeared to be, or whether other invasives pose a more serious threat.

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