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Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives

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Abstract As an effective generalist predator of aphids and other hemipteran pests *H. axyridis* has been a successful biological control agent. However, the very functional traits that have contributed to its success in this regard also implicate it as an intraguild predator that poses a significant risk not only to the diversity of other natural enemies of Hemiptera (and their associated ecosystem services), but to biodiversity more widely. In this paper we will specifically review the existing data on intraguild predation involving *H. axyridis*, and consider the strength and symmetry of such interactions both within its native guild and within exotic guilds where it has established as an invasive alien. We will use these studies to interpret the observed population declines in predator diversity in the field, predict species at risk in regions not yet invaded and consider implications for resulting ecosystem services. We will also indicate gaps in our knowledge that require further study in order to identify opportunities for mitigation.

Keywords Coccinellidae · *Harmonia axyridis* · Aphidophagous guild · Intraguild predation · Predators · Parasitoids · Pathogens · Ecosystem services

Introduction

Terrestrial ecosystems support a diversity of species that are directly and indirectly linked to each other within food webs that span multiple trophic levels. Natural enemy species (in the context of this paper we will collectively call these ‘predators’ as they all have a trophic relationship with their hosts/prey) contribute to the population regulation of species in both

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the same and lower trophic levels (top-down pressure) and in this way influence the structure of the community as a whole. In the case of aphids these natural enemies (aphidophages) include specialist and generalist predators, parasitoids and pathogens (Völkl et al. 2007). Together they represent a 'guild', i.e., a community of species that share the same host/prey resource (Polis et al. 1989; Rosenheim et al. 1995). As aphids are often pests in managed ecosystems these natural enemies provide a valuable pest management ecosystem service that can be manipulated within biological control strategies (e.g., Barbosa 1998; Gurr et al. 2004; Losey and Vaughan 2006; Powell and Pell 2007; Pell 2008).

Different 'predator' taxa play different ecological roles within the guild (Rosenheim et al. 2004a). 'Intermediate predators' function from the third trophic level suppressing herbivores, whereas 'top predators' mainly operate from the fourth trophic level suppressing 'intermediate predators' and, consequently, releasing herbivore populations from control (Polis 1994; Rosenheim 1998). Intraguild predation occurs when one of two species competing for the same host/prey also consumes its competitor, and can be a strong force structuring communities. Omnivorous intraguild predation can be asymmetric when one of the two species (the intraguild predator) always preys on the other (the intraguild prey), or symmetric when both species prey on each other to a greater or lesser extent (Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995). The intraguild predator benefits not only from the nutritive value of the meal, but also from the removal of a competitor. Coincidental intraguild predation occurs when a parasitoid or pathogen is consumed while still developing within its herbivore host and, in this case, the herbivore and the intraguild prey are directly linked (Polis et al. 1989). Intraguild predators function as both 'intermediate' and 'top predators' by feeding on both herbivores and 'intermediate predators'.

The impact of intraguild predation on community structure and diversity can be extremely variable, complex and difficult to predict (Rosenheim et al. 2004a; Snyder and Evans 2006; Straub et al. 2008). Many studies have assessed the prevalence of intraguild predation in aphidophagous guilds (Polis et al. 1989; Rosenheim et al. 1995; Holt and Polis 1997; Müller and Brodeur 2002; Lucas 2005; Pell 2008) and reported it to be a widespread phenomenon with implications for both predator diversity within the guild and the pest management ecosystem services that the guild delivers.

As an effective generalist predator of aphids and other hemipteran pests *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) has been widely and repeatedly augmented or introduced for biological control. As such, it has contributed significantly to pest suppression in a wide variety of managed ecosystems including pecan, apple, sweet corn, alfalfa, cotton, tobacco, wheat and soybean (Tedders and Schaefer 1994; Buntin and Bouton 1997; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Wells and McPherson 1999; Wells et al. 2001; Musser and Shelton 2003; Koch 2003; Majerus et al. 2006; Roy et al. 2006). However, the very functional traits that have made *H. axyridis* an effective biological control agent, also implicate it as an intraguild predator that poses significant risk to the diversity of other natural enemies of Hemiptera and their ecosystem services. Although natural enemy diversity in its native range remains relatively stable in the presence of *H. axyridis* (Kuznetsov 1988, 1997), wherever it has established after introduction as an exotic species, it has been associated with declines in native natural enemies, particularly native coccinellids (Majerus et al. 2006; Roy et al. 2006; Snyder and Evans 2006). These declines have been attributed to direct interspecific competition for resources with less competitive/fecund natural enemies (Michaud 2002) but are also likely to be strongly influenced by its role as an intraguild predator.

There are a number of functional traits that determine the nature, symmetry and outcome of intraguild predation including: relative size (incidence of mortality is often inversely correlated with size) (Majerus 1994; Evans 2000), aggressive strategies and mandibular structure (Yasuda et al. 2001), degree of feeding and habitat specificity, mobility (sessile stages are particularly vulnerable), defence strategies and abundance of extraguild prey (Polis et al. 1989; Lucas et al. 1998; Roy et al. 2006; Straub et al. 2008). In this paper we will specifically review the existing, largely experimental, data on these traits for *H. axyridis*, and discuss their strength and symmetry both within its native guild and within exotic guilds where it has established as an invasive alien. We will use these studies to interpret the observed population declines in natural enemy diversity in the field, predict species at risk in regions not yet invaded and consider implications for resulting ecosystem services. We will also identify gaps in our knowledge that require further study in order to identify opportunities for mitigation.

Current knowledge

Intraguild predation between *H. axyridis* and coccinellids of other species

Eggs

The relative size and mobility of the intraguild predator and prey are known to influence the outcome of intraguild predation, both showing an inverse correlation with the incidence of mortality (Huey and Pianka 1981; Sengonca and Frings 1985; Rosenheim et al. 1995; Lucas et al. 1998). In coccinellids this equates to the immature stages being more vulnerable than adults, and eggs being particularly threatened (Sato and Dixon 2004; Cottrell 2007).

Harmonia axyridis adults and larvae find eggs of many insect species acceptable as prey; laboratory stocks are often maintained on eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Berkvens et al. 2007). Cottrell (2004) reports that *H. axyridis* adults attacked eggs of *Coleomegilla maculata* (De Geer) (Coleoptera: Coccinellidae) and *Olla v-nigrum* (Mulsant) (Coleoptera: Coccinellidae) more frequently than adults of these species attacked *H. axyridis* eggs, and attest that intraguild predation of eggs is a serious threat for these species. However, cannibalism and predation of coccinellid eggs are most often associated with larval stages (Dixon 2000; Cottrell 2007) and, for some species, may be affected by the relative abundance of extraguild prey (Sato et al. 2003); at low aphid or coccid densities, coccinellid larvae are more likely to engage in cannibalism or intraguild predation. In addition, the tendency for intraguild predation by larvae varies between species both as intraguild predators and intraguild prey. Cannibalism and intraguild predation by *H. axyridis* are commonly observed, both in the laboratory and the field, even when aphids or coccids are abundant (M.E.N. Majerus and R.L. Ware personal observation). A recent study concluded that *H. axyridis* larvae were more likely to engage in intraguild predation of the eggs of *C. maculata*, *Cycloneda munda* (Say) (Coleoptera: Coccinellidae), *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) and *O. v-nigrum* than for *H. axyridis* eggs to be the intraguild prey of the larvae of these species (Cottrell 2007). This is in agreement with previous work of Cottrell (2004) demonstrating that neither *C. maculata* nor *O. v-nigrum* larvae can complete development on *H. axyridis* eggs whereas *H. axyridis* can complete development on a diet of either *C. maculata* or *O. v-nigrum* eggs.

Defensive adaptations (chemical or physical) are often effective in reducing the susceptibility of sessile life stages, such as eggs, prepupae and pupae to intraguild predation and cannibalism. The chemical defences of coccinellid eggs have been well studied (Agarwala and Dixon 1992; Hemptinne and Dixon 2000). Indeed, while intrinsic toxicity or unpalatability is governed by de novo synthesis of species-specific alkaloids (Pasteels et al. 1973; King and Meinwald 1996), Hemptinne and Dixon (2000) demonstrated the existence of extrinsic chemicals on the surface of some species' eggs that act as deterrents against intraguild predation. Ware et al. (2007) have recently discussed the role of surface deterrents on eggs of the European species *Calvia 14-guttata* (L.) (Coleoptera: Coccinellidae) as a defence against intraguild predation by *H. axyridis*. A similar phenomenon has been speculated for the eggs of the Japanese species *Eocaria muiri* Timberlake (Coleoptera: Coccinellidae) (Ware et al. 2008). The defensive chemistry of *H. axyridis* eggs themselves has been implicated as pivotal to the observed resistance of *H. axyridis* eggs to predation by other aphidophages that appear to find them unpalatable (Alam et al. 2002; Sato and Dixon 2004). Interestingly, similar alkanes to those found on the surface of *H. axyridis* eggs are also present in larval tracks and act as oviposition deterring semiochemicals for other ladybirds, thus reducing egg cannibalism and intraguild predation (Magro et al. 2007).

Larvae and pupae

Ware and Majerus (2007) have comprehensively examined intraguild predation of immature stages of British and Japanese coccinellids by *H. axyridis*. A total of 12 species of coccinellid (Coleoptera: Coccinellidae) were included in this laboratory study: eight derived from British populations (*Coccinella 7-punctata* L., *Adalia 2-punctata* (L.), *Adalia 10-punctata* (L.), *Propylea 14-punctata* (L.), *C. 14-guttata*, *Anatis ocellata* (L.), *Harmonia 4-punctata* (Pontoppidan), *Coccinella 5-punctata* L.) and four from Japanese populations (*Coccinella 7-punctata brucki* Mulsant, *Cheilomenes 6-maculatus* (Fabricius), *Propylea japonica* Thunberg and *E. muiri*). In general, *H. axyridis* was an intraguild predator of all species, with the exception of *A. ocellata*. The important conclusions of this study were that there was no obvious difference between the susceptibilities of Japanese and British coccinellids to intraguild predation by *H. axyridis*, and intraguild predation by *H. axyridis* represents a serious threat for many species in Britain (Ware and Majerus 2007).

The relatively large size of *H. axyridis* throughout its life cycle undoubtedly contributes to its success as an intraguild predator following the 'size matters' hypothesis. In predatory interactions between coccinellid larvae it is generally the larger that eats the smaller, assuming both are mobile (Majerus 1994). Notably, in comparative tests between fourth instar larvae of *H. 4-punctata*, *H. axyridis* and *A. ocellata*, which have similar behavioural and physical defences, the level of intraguild predation was directly correlated to size. Larvae of the largest species, *A. ocellata*, won the majority of encounters with *H. axyridis*, while the smallest species, *H. 4-punctata*, lost most such encounters (Ware and Majerus 2007).

There are few reports of other larval coccinellids successfully attacking *H. axyridis*, and most evidence suggests that the immature stages of *H. axyridis* are resistant to reciprocal attacks. In a laboratory study assessing the interactions between *H. axyridis* and *C. 7-punctata*, Yasuda et al. (2001) attributed the greater success of the former to its higher attack rates and greater escape ability. Recent research is beginning to confirm the importance of chemical defence of *H. axyridis* larvae as a means of preventing counter-attacks (Ware and Majerus 2007), and larvae are known to produce similar defensive alkaloids to those present within eggs and released by adults (Pasteels et al. 1973; King and

Meinwald 1996). Further studies have also implicated the role of superior physical defences (spines rather than hairs) in larval stages of *H. axyridis* compared to other species (Ware and Majerus 2007).

In the field, coccinellid larvae tend to disperse from a plant when prey abundance is low (Sato 2001) and this reduces the incidence of cannibalism and intraguild predation by larger larvae and adults (Sato et al. 2003). However, emigration is a precarious strategy for an immature coccinellid, so there is a trade-off between emigrating or remaining on a plant with a low prey density and risking cannibalism or intraguild predation. *Harmonia axyridis* commonly co-occurs with *C. 7-punctata brucki* and *P. japonica* in their native Japanese range (Yasuda and Shinya 1997; Sato 2001). In a Japanese field study of these three coccinellid species co-occurring on shrubs both *C. 7-punctata brucki* and *H. axyridis* larvae emigrated in response to low prey density whereas *P. japonica* larvae did not (Sato 2001). The prevalence of intraguild predation and cannibalism of *C. 7-punctata brucki* and *H. axyridis* larvae was low whereas no *P. japonica* larvae completed their development on the shrubs and this was assumed to be as a consequence of intraguild predation. In further studies it was confirmed that the early emigration of *C. 7-punctata brucki* larvae enabled them to escape from intraguild predation by *H. axyridis* larvae (Sato et al. 2003) and that the late emigration of *P. japonica* larvae accounted for the high incidence of intraguild predation by *H. axyridis* larvae (Sato et al. 2003).

Propylea japonica is also a smaller species than either *H. axyridis* or *C. 7-punctata brucki* and so this further supports the hypothesis that ‘size matters’ in intraguild predation. Ware and Majerus (2007) also report *P. japonica* larvae as highly palatable intraguild prey with little physical defence from attack by *H. axyridis*. It is interesting to note from field studies in Japan that *C. 7-punctata brucki* are active earlier in the spring than *H. axyridis* (Takahashi and Naito 1984; Sato 2001). Therefore, *H. axyridis* are more likely to experience a scarcity of aphids, which are abundant in spring and early summer, than *C. 7-punctata brucki*. Consequently, *H. axyridis* is likely to be more reliant on intraguild prey to complete their development than is *C. 7-punctata brucki* (Sato et al. 2003).

Adults

Adult coccinellids are generally less susceptible to predation than immature stages due to their protective elytra and aposematic colour patterns (Majerus 1994). However, they are exposed to a particularly vulnerable period just after eclosion, when their elytra are still soft. Ware and Majerus (2007) report observations of attacks made on eclosing or newly eclosed adults by larvae, when no other food was available. Fourth instar *H. axyridis* larvae were observed to attack and consume new adults of *A. 10-punctata*, *A. ocellata*, *C. 14-guttata*, *C. 7-punctata brucki* and *E. muiri*, after not having attacked them as pupae (Ware and Majerus 2007). However, the consumption of newly eclosed *H. axyridis* adults was rare, and only performed by conspecific larvae and larvae of the congeneric species *H. 4-punctata.* This supports the speculation that the defensive chemistry of *H. axyridis* adults may make them unpalatable to other coccinellids (Hough-Goldstein et al. 1996).

Intraguild predation between *H. axyridis* and non-coccinellid predators

Coccinellids are common within aphidophagous guilds and most studies considering the role of *H. axyridis* as an intraguild predator have focussed on interactions within the

Coccinellidae. However, *H. axyridis* interacts with many other predatory insects at the community level. Lacewings (Neuroptera) are both abundant as aphid predators in natural systems, and as components of biological control strategies. In a laboratory study, Phoofolo and Obrycki (1998) demonstrated that there was no difference in the development time or survival of *H. axyridis* (and also *C. maculata*) fed on a diet of pea aphids, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), or eggs of the lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). In contrast, *C. carnea* was unable to develop successfully when fed on *H. axyridis* eggs.

A further study examined the interactions between adult *H. axyridis*, *C. carnea* and the gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) in the presence of the soybean aphid, *Aphis glycines* Matsumara (Hemiptera: Aphididae), in microcosms and field cages (Gardiner and Landis 2007). *Harmonia axyridis* engaged in intraguild predation with both *C. carnea* and *A. aphidimyza* and was predicted to contribute to declines in both species in the field. Phoofolo and Obrycki (1998) and Gardiner and Landis (2007) both suggested the potential for *H. axyridis* to be an asymmetrical intraguild predator of *C. carnea*. However, *C. carnea* will consume *H. axyridis* eggs (Phoofolo and Obrycki 1998) and recent observations by Fremlin (2007) indicate that *C. carnea* will also attack *H. axyridis* pupae. Therefore, the interaction can be considered to be (weakly) symmetrical. Further research is required to expand our knowledge on interactions between neuropterans and *H. axyridis*.

The spined soldier bug, *Podisus maculiventris* Say (Heteroptera: Pentatomidae) is native to North America and has a broad prey range including over 100 species of insect, primarily soft-bodied, slow-moving larvae of Coleoptera and Lepidoptera, but also aphids (McPherson 1980; Herrick and Reitz 2004). Half of the species on which it preys are important crop pests (Herrick and Reitz 2004). *Podisus maculiventris* is therefore loosely linked with many trophic guilds, including that of aphids (McPherson 1980; Hough-Goldstein et al. 1996), and four species of predaceous coccinellid are listed as prey to this predatory bug (McPherson 1980). In laboratory studies, Hough-Goldstein et al. (1996) demonstrated that although *P. maculiventris* did not consume adult *H. axyridis* they did consume *H. axyridis* larvae in 'no choice' treatments. In this study, *H. axyridis* larvae were described as 'aggressive' and often noted to escape predation, whereas adult *H. axyridis* were rejected, presumably as unpalatable, by *P. maculiventris*. Indeed, *P. maculiventris* took four times longer to capture *H. axyridis* larvae compared to *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) larvae (Hough-Goldstein et al. 1996).

A further study demonstrated that interactions between *P. maculiventris* and *H. axyridis* in the presence or absence of extraguild prey (*Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae) or *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)) were asymmetric in favour of the bug (De Clercq et al. 2003). *Podisus maculiventris* fed on *H. axyridis* eggs and larvae but rarely on adults. As with interactions amongst coccinellids, this interaction was dependent on the life stage of the bug; fourth instar nymphs and adults were more aggressive in their interactions than second instars nymphs. In contrast, *H. axyridis* rarely attacked *P. maculiventris*. Intraguild predation by *P. maculiventris* on *H. axyridis* was reduced in the presence of *S. littoralis* but not *M. persicae*. De Clercq et al. (2003) interpreted this to infer that *H. axyridis* was a less preferred prey in comparison to *S. littoralis* and this was supported by the longer development time of the bug when fed on *H. axyridis* larvae compared to *S. littoralis*. There was a slight difference in the survival to adulthood of pentatomid nymphs fed on *H. axyridis* compared to *S. littoralis* (70% vs. 80–90% respectively) and no nymphs reached adulthood when fed on just aphids (De Clercq et al. 2003).

Intraguild predation between *H. axyridis* and parasitoids

Intraguild predation between predators and parasitoids is asymmetrical and can be described as both coincidental and omnivorous (Polis et al. 1989). In contrast to the literature on intraguild predation between *H. axyridis* and other predators, particularly coccinellids, there is very little information on such interactions between *H. axyridis* and parasitoids. Previous studies have reported the consumption of parasitized aphids by coccinellids (Wheeler et al. 1968; Ferguson and Stiling, 1996) and that the presence, or recent activity, of predatory coccinellids within an aphid colony can reduce the oviposition rate of aphid parasitoids (Taylor et al. 1998).

Takizawa et al. (2000) assessed whether the aphid *Aphis craccivora* Koch (Hemiptera: Aphididae), parasitized by *Aphidius colemani* Viereck (Hymenoptera: Braconidae), were suitable prey for three coccinellid species: *C. 7-punctata*, *P. japonica* and *H. axyridis*. The parasitoid was used at two life stages: 3-day-old larvae within living aphids (coincidental intraguild predation) and sessile aphid 'mummies' containing pupae (asymmetrical omnivorous intraguild predation). Consumption of parasitized aphids containing 3-day-old larvae did not reduce survival or increase development time of any of the coccinellids. In contrast, consumption of aphid 'mummies' increased the development time of all three species and reduced survival to adulthood of *C. 7-punctata* by 70% but did not affect the survival of *H. axyridis* and *P. japonica*. *Coccinella 7-punctata* is considered to be a more aphid-specific predator than *H. axyridis* (Hodek and Honek 1988). It is likely that parasitized 'mummies' are unsuitable prey and, hence, the low survival rates of *C. 7-punctata* fed on parasitized aphids could be attributed to their aphid-specific dietary requirements (Takizawa et al. 2000). In contrast, *H. axyridis* selectively preyed on pea aphids, *A. pisum*, rather than pea aphid 'mummies' parasitized by *Aphidius ervi* Haliday (Hymenoptera: Braconidae) (Snyder and Ives 2003). Although this would not change the impact of coincidental intraguild predation of larval parasitoids by *H. axyridis*, it does demonstrate that interactions are variable depending on the prey concerned. Similarly, in a study at larger spatial scales Snyder et al. (2004a) found that although *H. axyridis* did prey on 'mummies' of the aphid parasitoid *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae) (adult *H. axyridis* showed no discrimination between 'mummies' and aphids although larvae preferred aphids in feeding trials), the overall parasitism level was not affected.

Intraguild predation between *H. axyridis* and pathogens

Entomopathogenic fungi are common pathogens of aphids and can be involved in both coincidental and omnivorous, asymmetrical or symmetrical, intraguild interactions (Roy and Pell 2000; Völkl et al. 2007). The most common fungal pathogens are host-specific species from the Zygomycetes, order Entomophthorales, although other species from the Ascomycetes, order Hypocreales, some with wide host ranges, are used as biopesticides and could, therefore, be involved in intraguild interactions (Powell and Pell 2007; Pell 2008).

During the final stages of infection by entomopathogenic fungi the host dies and the fungus sporulates to produce more infective propagules (conidia) for transmission (Inglis et al. 2001; Pell et al. 2001). As the sporulating aphid cadaver is sessile, it is an easy prey item for generalist predators. In a laboratory study, Roy et al. (2008) assessed the predation of aphid cadavers sporulating with *Pandora neoaphidis* (Remaudière and Hennebert) Humber (Zygomycetes: Entomophthorales) by UK and Japanese-derived *H. axyridis* relative to that of the UK native species *C. 7-punctata*. Unlike *C. 7-punctata*, which showed a strong preference for aphids over sporulating fungal cadavers, *H. axyridis* showed little discrimination between the prey types and would consume whole, sporulating cadavers. The consumption of whole sporulating cadavers could remove a significant quantity of inoculum from the aphid population, which may result in a reduction in further transmission. As *P. neoaphidis* only infects aphids, this represents asymmetrical intraguild predation. The strength of intraguild predation by *H. axyridis* collected in the UK differed from those collected in Japan, with *H. axyridis* (UK) showing less discrimination between prey types compared to *H. axyridis* (Japan) (Roy et al. 2008). Whether feeding on infected cadavers has fitness consequences for *H. axyridis* is unknown.

Other entomopathogenic fungi have wider host ranges and may be infective towards both coccinellids and aphids, making the intraguild interaction potentially symmetrical. For example, isolates of the entomopathogenic fungi *Metarhizium anisopliae* (Metschnikoff) Sorokin (Ascomycete: Hypocreales), *Paecilomyces fumosoroseus* (Wise) Brown and Smith (Ascomycetes: Hypocreales) and *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycetes: Hypocreales) have been recorded infecting both aphids and coccinellids (e.g., Magalhaes et al. 1988; Keller and Zimmerman 1989; Butt et al. 1994; James and Lighthart 1994; Yeo 2000; Pell and Vandenberg 2002; Ormond et al. 2006). In particular, *B. bassiana* is a major overwintering mortality agent of *C. 7-punctata* (Majerus 1994; Ormond et al. 2006). Roy et al. (2007) assessed the susceptibility of *H. axyridis* derived from the UK and Japan to *B. bassiana* relative to that of the UK native species *C. 7-punctata* and *A. 2-punctata*. Only doses of 10^9 conidia ml^{-1} resulted in mortality of *H. axyridis*, in contrast, 80% of *C. 7-punctata* and 70% of *A. 2-punctata* exposed to 10^7 conidia ml^{-1} of *B. bassiana* succumbed to infection. In addition, the results suggested that the UK derived strain may be more resistant to infection than the Japanese derived strain. Interestingly, inoculation with *B. bassiana* at a concentration as low as 10^5 conidia ml^{-1} reduced the fecundity of *H. axyridis* (Roy et al. 2007). Whether any of these coccinellids feed on *B. bassiana*-infected cadavers and the implications of this on the symmetry of intraguild predation is unknown. However, in the study of Pell and Vandenberg (2002) the coccinellid *H. convergens* did consume living *Diuraphis noxia* Kurdjumov (Hemiptera: Aphididae) aphids infected by *P. fumosoroseus* but did not consume sporulating aphid cadavers.

In both studies by Roy et al. (2007, 2008), the interactions involving *H. axyridis* collected from the UK differed from those collected in Japan, with *H. axyridis* from the UK being a stronger intraguild predator of *P. neoaphidis* and more resistant to *B. bassiana* than the strain from Japan. These are the first studies to indicate fundamental differences between *H. axyridis* subpopulations and demonstrate the importance of assessing genetic and ecological variability amongst such subpopulations.

Intraguild predation involving *H. axyridis*: Conclusions to date

There is broad agreement, from the studies described above, that *H. axyridis* is a top predator as it is predominantly a strong asymmetrical intraguild predator of other guild members (Hironori and Katsuhiro 1997; Cottrell and Yeargan 1998; Phoofolo and Obrycki 1998; Yasuda and Ohnuma 1999; Michaud 2002; Sato et al. 2003, 2005; Felix and Soares 2004; Snyder et al. 2004b; Kajita et al., 2006; Pervez and Omkar 2006; Roy et al. 2006, 2007, 2008; Cottrell 2007; Ware and Majerus 2007) and as such can dominate in aggressive intraguild interactions and lead to a decline in guild diversity.

The key functional traits that make *H. axyridis* such an exceptional intraguild predator are its relatively large size, aggressive behaviour, extreme polyphagy and the possession of effective physical and chemical defence strategies. Together these traits provide the mechanism by which *H. axyridis* impacts on guilds and food webs in general (Tedders and Schaefer 1994; Hodek 1996; Yasuda and Shinya 1997; Yasuda and Ohnuma 1999; Kajita et al. 2000; Koch 2003). It therefore seems likely that *H. axyridis* could disrupt aphidophagous/coccidophagous community structure leading to declines in other species in the guild where it establishes as a non-native species. *Harmonia axyridis* has certainly become abundant and widely distributed as a non-native species throughout North America and Europe (Koch 2003; Brown et al. 2007) and field data from the USA has reported associated negative impacts on native coccinellid species in these regions (Elliott et al. 1996; LaMana and Miller 1996; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Lucas et al. 2002; Michaud 2002; Nault and Kennedy 2003). Interestingly, *C. 7-punctata* was also introduced and became established widely in North America prior to the establishment of *H. axyridis* (Gordon 1985). It too displaced native coccinellids and became the dominant predator. However, *H. axyridis* is a more aggressive predator than *C. 7-punctata*; larvae of *H. axyridis* consume those of *C. 7-punctata* but the reverse occurs considerably less frequently (Hironori and Katsuhiro 1997; Yasuda et al. 2004; Ware and Majerus 2007). Since the arrival of *H. axyridis* in the USA, it has displaced *C. 7-punctata* as the 'top predator' demonstrating the considerable dominance of *H. axyridis* as an intraguild predator of native and exotic coccinellids alike (Snyder et al. 2004b).

Similar evidence of declines in native coccinellid species after establishment of *H. axyridis* is accumulating in Europe. For example, evidence suggests that in London numbers of some, but not all, native coccinellids (particularly *A. 2-punctata*) have declined significantly since the arrival of *H. axyridis* in 2004 (Majerus, unpublished data). This is almost certainly due to its superior competitive ability and status as an intraguild predator. From the experimental studies of Ware and Majerus (2007), with consideration of the wider ecologies of *H. axyridis* and British ladybirds, and in the absence of control or mitigation, we anticipate that aphidophagous habitat generalists such as *C. 7-punctata, A. 2-punctata* and *P. 14-punctata* will be most at risk from the establishment of *H. axyridis* in the UK, followed by aphidophagous habitat specialists such as *Myzia oblongoguttata* (L.) (Coleoptera: Coccinellidae), *Myrrha 18-guttata* (L.) (Coleoptera: Coccinellidae) and *Anisosticta 19-punctata* (L.) (Coleoptera: Coccinellidae). The only species that may be relatively unaffected by invasive *H. axyridis* is *A. ocellata*, and indeed *H. axyridis* could actually be at risk from detrimental interactions with this species where they co-inhabit coniferous woodland. It is thought that the aphidophagous specialist *C. 5-punctata* would be particularly threatened if *H. axyridis* invades unstable river shingle, as it is already considered of conservation concern (Ware et al. 2005). Coccidophagous species such as *Exochomus 4-pustulatus* (L.) (Coleoptera: Coccinellidae) and *Chilocorus renipustulatus* (Scriba) (Coleoptera: Coccinellidae) and the *Erica*/*Calluna* heathland specialists *Chilocorus 2-pustulatus* (L.) (Coleoptera: Coccinellidae) and *Coccinella hieroglyphica* L. (Coleoptera: Coccinellidae) are thought to be less at risk, the latter because *H. axyridis* has yet to be recorded from such heathland. Mycophagous, phytophagous and myrmecophilous coccinellids, such as *Thea 22-punctata* (L.) (Coleoptera: Coccinellidae), *Subcoccinella 24-punctata* (L.) (Coleoptera: Coccinellidae) and *Coccinella magnifica* Redtenbacher (Coleoptera: Coccinellidae) respectively, are likely to be the least threatened by the establishment of *H. axyridis* in Britain.

There is clear evidence for declines in diversity of coccinellids in the USA and increasingly in Europe. However, there have been no studies to evaluate impacts on the diversity of other guild members or on biodiversity more widely. These are urgently required, particularly in areas undergoing invasion by *H. axyridis*, if the full implications of its presence are to be evaluated.

Knowledge gaps, future perspectives and implications for biodiversity and ecosystem function

Harmonia axyridis is also a dominant intraguild predator in its native range, as shown by Ware and Majerus (2007) who paired Japanese *H. axyridis* with Japanese native coccinellids in their laboratory interaction studies and found that *H. axyridis* was the successful intraguild predator in the majority of cases. It has also prevented the establishment of the introduced coccinellid *A. 2-punctata* in Japan (Sakuratani et al. 2000; Kajita et al. 2006). However, it appears to co-exist with most other guild members (Kuznetsov 1997) whilst causing declines and competitive exclusion of other coccinellid species in regions where it is an invasive exotic (e.g., Colunga-Garcia and Gage 1998; Michaud 2002). In co-evolved communities that utilise limited resources, species will be under selection to either ensure that they win any competitive interaction or that they avoid competition through resource-use complementarity and niche differentiation (Wilby and Thomas 2002a, b; Pell 2008). It is possible that, although *H. axyridis* is the top predator in its native range, other predator populations can escape intraguild predation through spatial or temporal niche differentiation. Studies to understand the mechanisms for co-existence with *H. axyridis* in its native range are essential if we are to mitigate existing effects in its invasive range.

Temporal niche differentiation

The co-existence of *H. axyridis* and sympatric species in Asia may, in part, be due to phenological differences that lead to temporal niche differentiation. For example, *C. 7-punctata brucki* is active earlier in the spring in Japan than *H. axyridis* and its larvae are therefore larger and more able to survive in intraguild combat with *H. axyridis* (Takahashi and Naito 1984; Sato 2001). Phenological studies of *H. axyridis* in its non-native range are essential if we are to predict the extent of intraguild predation and consequent impacts on biodiversity. Such studies are underway and in the UK, for example, early indications are that *H. axyridis* emerges from winter in synchrony with most native aphidophagous coccinellids, which contributes to the latter's inability to escape intraguild predation. *Harmonia axyridis* is also multivoltine and remains active for longer through the season, allowing numbers of individuals to build up rapidly. All life stages of *H. axyridis* have been recorded in November (early winter) in the UK (Majerus et al. 2006; Brown et al. 2007). In one study from the USA biological control literature, Flowers et al. (2006) considered intraguild interactions amongst three exotic predators attacking the hemlock woolly adelgid, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae) in hemlock stands in West Virginia. The species included were specialists, *Laricobius nigrinus* (Fender) (Coleoptera: Derodontidae) and the coccinellid *Sasajiscymnus tsugae* (Sasaji & McClure) (Coleoptera: Coccinellidae), and the generalist *H. axyridis*. The authors concluded that intraguild predation by *H. axyridis* was not common because they were phenologically separated and active during different seasons; *L. nigrinus* was most active in spring and *H. axyridis* in summer. This also has implications for the wider guild beyond other coccinellids, for which there is currently very little information.

Associations with ants

Other coccinellid species in *H. axyridis*' native range may escape intraguild predation through associations with ants. Although there are limited studies on myrmecophilous interactions in the native range of *H. axyridis*, it is well documented for some coccinellid species in Europe. Many aphids and coccids are myrmecophilous and gain benefits from being associated with ants, including protection from natural enemies, in exchange for food in the form of honeydew (e.g., Hölldobler and Wilson 1990; Jiggins et al. 1993; Majerus et al. 2007). There is considerable evidence to demonstrate that ants display ownership behaviour, whereby they behave more aggressively towards predators in the vicinity of tended colonies than elsewhere (Way 1963). In the case of coccinellids, this aggression may be directed toward both adults and larvae, the former being chased away (e.g., Itioka and Inoue 1996; Sloggett 1998), while the latter may be picked up and dropped off the plant, or killed (e.g., Jiggins et al. 1993; Sloggett and Majerus 2003). As a result of ant aggression, most coccinellids only feed on ant-tended prey when untended prey are scarce (Sloggett and Majerus 2000). Many coccinellids have defences against ant aggression, which may be behavioural, chemical or physical and lead to variation in tolerance to ants amongst different coccinellid species (Majerus et al. 2007). For example, Sloggett and Majerus (2000) showed a hierarchy in six species of coccinellid living in pine woodland in the UK to aggression from *Formica rufa* (L.) (Hymenoptera: Formicidae) from no tolerance (*M. 18-guttata* and *A. ocellata*) to high tolerance (*C. magnifica*). Unfortunately, the level of tolerance of *H. axyridis* to ant aggression in either its native or its invasive range is unknown. Should *H. axyridis* be found to be intolerant of ant presence, it is likely that those aphidophages that have a significant degree of ant tolerance, such as *M. oblongoguttata* and *C. 7-punctata*, will find a refuge from some of the effects of intraguild predation and competition imposed by *H. axyridis* in habitats occupied by ant-tended aphids. Experiments to investigate the level of tolerance of *H. axyridis* to common aphid tending ants, such as *F. rufa*, *Lasius niger* (L.) (Hymenoptera: Formicidae) and *Myrmica ruginodis* Nylander (Hymenoptera: Formicidae), are urgently needed. The small number of coccinellid species that are true myrmecophiles, i.e., have the closest relationships with ants and associated high tolerance, are likely to have the safest refuge from *H. axyridis*, unless *H. axyridis* is also highly tolerant to ants. These species include *C. magnifica* (Sloggett et al. 2002; Majerus et al. 2007) and *Platynaspis luteorubra* (Goeze) (Völkl 1995; Godeau 2000). It is possible that some species that have some tolerance of ants may come under additional selection pressures to improve their tolerance as a result of the presence of *H. axyridis*. In regions now occupied by *H. axyridis*, monitoring the coccinellid presence in the vicinity of nests of *F. rufa* over the next decade would be valuable.

Behavioural interactions

Further work is also required to acquire data on behavioural defence strategies of guild members in the presence of *H. axyridis*, such as dislodgement (dropping behaviour) and escape behaviours which could be extremely important for some species. For example, larvae of the coccinellid *P. 14-punctata* are consumed by *H. axyridis* in laboratory studies conducted in Petri dishes, but it is speculated that the highly mobile larvae of this species may have the capability to successfully escape from *H. axyridis* in field situations (Ware and Majerus 2007). We also know that parasitoids and predators can use volatile and chemical cues to avoid competition; both the coccinellid *C. 7-punctata* and the predatory bug *Anthocoris nemorum* (L.) (Heteroptera: Anthocoridae) can detect and avoid surfaces contaminated by the fungal pathogen *B. bassiana* to which they are susceptible (Meyling and Pell 2006; Ormond 2007). In addition, the aphid parasitoid *A. ervi* detects volatiles from the tracks of *C. 7-punctata* and avoids oviposition in nearby aphid populations (Nakashima et al. 2004). Such behavioural responses can ensure co-existence by reducing the risk of intraguild predation. They may contribute to co-existence of *H. axyridis* in its co-evolved native guild populations and are currently being evaluated for *H. axyridis* in the broader UK guild.

Other intraguild interactions, such as facilitation, have been recorded for some species and shown to mitigate the effects of intraguild predation on guild diversity and may also apply to *H. axyridis*. For example, although *C. 7-punctata* is an intraguild predator of the aphid-specific pathogenic fungus *P. neoaphidis*, it does not consume whole, fungal cadavers and transmission of the fungus is not reduced. Indeed, *C. 7-punctata* enhances transmission of the fungus and passively vectors it between aphid populations, thereby also aiding pathogen dispersal (Roy et al. 1998, 2001; Roy and Pell 2000). Some of these co-evolved behavioural traits may contribute to the maintenance of guild diversity in the native range of *H. axyridis* and may mitigate its effects on some species in the invasive range. In preliminary studies, *H. axyridis* did enhance transmission and dispersal of *P. neoaphidis* in the laboratory (J. Baverstock personal observation).

Natural enemy release and biotype variation

Differences in functional traits of invasive and non-invasive biotypes of *H. axyridis* may have exacerbated their impact in non-native ecosystems. Although direct comparisons between different biotypes of *H. axyridis* and other natural enemies found in its exotic range have only been made for a limited number of functional traits, they have all demonstrated that the UK invasive biotype is a stronger asymmetric intraguild predator than the Japanese biotype. Specifically Roy et al. (2007) demonstrated that *H. axyridis* from a culture derived from Japan were less likely to consume aphid cadavers supporting the beneficial aphid-specific fungal pathogen *P. neoaphidis* than those derived from the UK. They speculated that *H. axyridis* obtained from non-native populations were derived from biological control cultures and, through microevolution or founder effects, have been, perhaps unintentionally, selected for extreme polyphagy and an increased tendency towards intraguild predation compared to *H. axyridis* in its native range (Roderick and Howarth 1999; Hufbauer and Roderick 2005; Roy et al. 2008). It would be extremely interesting to compare the strength and symmetry of intraguild interactions between Japanese, UK and US derived *H. axyridis* for a wider range of guild members, from both native and non-native ranges to determine if they function differently in relation to all guild members with which they compete. In addition, UK-derived *H. axyridis* have greater resistance to some natural enemies, such as the fungus *B. bassiana* and the parasitoid wasp, *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) than do Japanese-derived *H. axyridis*, implying that they have also been released from their own population regulators (Koyama and Majerus 2007; Roy et al. 2007). Evolution of resistance to disease, parasitism and insecticides is not uncommon in insects and may be associated with trade offs in fitness (e.g., Foster et al. 2007; Völkl et al. 2007). For example, although UK-derived *H. axyridis* were less suceptible to infection they were also significantly less fecund when infected than *B. bassiana*-infected *H. axyridis* derived from Japan (Roy et al.

2007). Further research is needed to fully evaluate these interactions and determine whether any associated fitness costs could prove to be *H. axyridis*' weakness.

Going beyond managed ecosystems

The focus of research has largely been on interactions between *H. axyridis* and other coccinellids in managed ecosystems and, until recently, mainly in the USA, which has very different agricultural systems to Europe. However, it is clear from the studies described above that *H. axyridis* can have impacts on many other species and that this has implications beyond managed ecosystems to natural habitats. Such impacts require urgent investigation. *Harmonia axyridis* is dispersive and highly polyphagous and therefore likely to impinge on many foodwebs in many different ecosystems, with the potential to disrupt them all. Although native coccinellids with similar prey and habitat requirements are at greatest risk, other non-coccinellid guild members and non-target species beyond the guild, such as Hemiptera of no economic importance (Majerus et al. 2006), lepidopteran eggs and larvae (Koch 2003; Koch et al. 2006) and all the predators, hyperparasites and pathogens in the higher trophic levels (Roy et al. 2007) that may also be negatively affected. This represents a significant threat to biodiversity per se, particularly as some of these species are of considerable conservation concern (Koch et al. 2006).

What about scale?

We must also remember that many of the studies to date have been made on a small scale in the laboratory. This does not detract from their value in identifying key protagonists and 'worst case scenarios': certainly, a species that is not preyed on by *H. axyridis* in a Petri dish experiment is unlikely to be at risk in the field. However, they do not consider the importance of spatial scale and habitat complexity on niche differentiation and the outcome of contests. Testing hypotheses on these subjects requires experiments to move to larger spatial and temporal scales. The work of Snyder et al. (2004a) demonstrated that, although parasitoid 'mummies' of *A. asychis* were susceptible to intraguild predation by *H. axyridis*, overall parasitism rates were unaffected when experiments were done on a larger spatial scale. It is also important to consider more complex communities, i.e. not just pairs of protagonist species but a more representative guild, if we are to determine whether diversity will decline and what implications this will have for ecosystem services.

Potential implications for ecosystem services

Predators are part of the functional biodiversity in managed ecosystems and, while not the only contributor to herbivore population regulation, they are essential for sustainable pest management through the ecosystem services they provide and that we depend upon. While the abundance of particular species can be enhanced through biological control, the question of 'how many species are required to achieve the required service in the crop?' continues to be a matter of debate (e.g., Denoth et al. 2002; Pell 2008; Straub et al. 2008) and must be considered in the context of the arrival of *H. axyridis* and potential declines in guild diversity. The relationship between predator biodiversity and ecosystem function is poorly understood. From the studies described above, and field observations of declines in native aphidophages and coccidophages since the arrival of *H. axyridis*, we must consider whether *H. axyridis* as a top predator, will deliver the same ecosystem service when other guild species are excluded or whether this will reduce aphid regulation (prey release) and the reliability of biological control in the long term.

Straub et al. (2008) reviewed recent literature on the relative pest suppression function of multiple (more than two) compared to single predator species and found that the relationship between predator diversity and pest suppression was context-dependent and could be positive, negative or neutral. Theoretically, if increasing predator diversity encourages intraguild predation, or, as in the case of invasion by *H. axyridis*, an invasive intraguild predator is introduced to the system, then the prediction would be that the equilibrium density of the herbivore would increase and pest control function would be reduced (e.g., Polis et al. 1989; Finke and Denno 2004). Effectively, trophic cascades would be dampened and the herbivore would be released from predation. However, the experimental evidence to support this in a number of communities is mixed. Some studies have documented disruption of pest suppression and others have shown either no change or improved pest suppression in the presence of intraguild predation (Straub et al. 2008). Most recent meta-analysis by Rosenheim and Harmon (2006) and a literature review by Janssen et al. (2006) find no evidence that the presence of intraguild predation disrupts herbivore control. However, there was greater variation than expected between cases, suggesting that pest release depended on system-specific factors, such as the biological traits of the predators and prey, and extrinsic factors, such as the environment, i.e., there was no simple prediction relating intraguild predation to pest release (Straub et al. 2008).

However, Straub et al. (2008) have identified particular traits of relevance from the theoretical literature. The first relates to the life history of the intraguild prey. Coincidental intraguild predation of parasitoids and pathogens is likely to be less disruptive to herbivore suppression than omnivorous intraguild predation of other predators because predation of the herbivore and the parasitoid/pathogen are directly linked and intraguild predation will simultaneously result in predation of the herbivore (Rosenheim et al. 1995). However, this may not hold if several generations of the intraguild prey are considered (Snyder and Ives 2001). Secondly, the relative mobility and size (foraging mode) of the intraguild predator, intraguild prey and the herbivore can all influence the likelihood of prey release. A ‘sit and wait’ intraguild predator could disrupt suppression of a sedentary herbivore by a mobile intraguild prey species, although this will depend on the size of the intraguild prey species too. If it is large and highly mobile, it will have a large demand for prey, and if removed from the system by intraguild predation could result in release of the herbivore prey (Rosenheim and Corbett 2003). Furthermore, if the intraguild prey is a similar size to the herbivore then adding a larger intraguild predator will enhance herbivore suppression because predation of the herbivore by the intraguild predator would greatly outweigh the small release from predation achieved by the consumption of the intraguild prey (Diehl 1993). The opposite would be the case if the intraguild prey was much larger than the herbivore (Rosenheim and Corbett 2003). There is some experimental support for this second prediction (Rosenheim et al. 2004a, b) but for the most part they remain hypotheses that require experimental evaluation. In addition, they will be influenced by whether the top intraguild predator is co-evolved with the rest of the guild or whether it is an exotic alien species, as is the case with *H. axyridis*. Using the hypotheses above, one could predict from the biological traits of *H. axyridis* that it would release herbivores from control because it consumes intraguild prey that are large and mobile. However, it is itself large, mobile, well defended, multivoltine and highly voracious which could compensate for this, at least in the short term.

Within guilds of predators some species may be functionally redundant if they share traits and their function would be replaced by other species should they be lost (Wilby and Thomas 2002a, b; Ives et al. 2005; Casula et al. 2006). If there are many redundant species within a guild, then a decline in their diversity associated with the arrival of *H. axyridis* may not influence overall function. However, determining whether species are functionally redundant within a guild relies on the ability to divide them into functional groups with similar traits (e.g., prey preference, response to prey density, microhabitat use and phenology). Those with similar traits should compete strongly for resources and are, therefore, likely to be functionally redundant.

Within the aphidophagous guild there have been studies to demonstrate that increasing the number of species in the guild increases prey suppression, suggesting resource-use complementarity (Powell et al. 2006). However, other workers have shown no such effects and suggest significant redundancy of some guild members (Evans 1991; Chang 1996; Straub and Snyder 2006). The former may be more likely because the latter results could be due to negative and positive interactions between species counteracting each other (Snyder and Ives 2003) or because species that appear functionally redundant under some environmental conditions are functionally diverse when environmental conditions change (Naeem and Li 1997). This effect is encompassed in the 'insurance hypothesis' that maintains that different predators perform better or worse in particular environments and that by maintaining them all provides functional compensation and reliable pest suppression despite changing conditions (Loreau et al. 2003). This is essential in managed ecosystems that are fragmented and under constant change (Pell 2008). The multiplicity of responses to change that species from a single functional group are capable of, is critical to landscape scale ecosystem resilience (Elmquist et al. 2003). There are good examples of this in the aphid/predator system (Pell 2008). Key aphid mortality factors, which can be parasitoids on some occasions and syrphids, ground predators or entomopathogenic fungi on other occasions, demonstrate the need for diversity as insurance for function (Krauss and Poehling 1996; Hemmati 1999; Östman et al. 2001; Powell et al. 2003, 2004; Tscharntke et al. 2005; Pell 2008). Declines in guild diversity as a result of introduction of *H. axyridis* could, therefore, reduce the resilience of pest suppression in the long term.

A single prey type, or even species, can provide multiple feeding niches that a diversity of predators can use if there is niche complementarity rather than redundancy and this is achieved by resource partitioning and facilitation amongst predators. If their is complete complementarity then predator diversity should increase pest suppression (Wilby and Thomas 2002a, b; Casula et al. 2006). There is significant evidence for resource partitioning and facilitation within the aphid/predator system (Pell 2008). For example variation between aphid species, or within a species, provides an opportunity for preference amongst predators. The coccinellid *C. 7-punctata* exploited red morphs of the pea aphid more than green morphs whereas the parasitoid *A. ervi* only attacked green morphs, effectively partitioning the resource between them (Losey et al. 1997). Coccinellid species differ in their response to prey density, some being more effective at low densities and others at high densities, which effectively separates them into complementary niches (Evans 2004; Schellhorn and Andow 2005). A further example of complementarity can be seen for the interactions between *C. 7-punctata*, a foliar aphid predator, and the carabid beetle *Harpalus pennsylvanicus* (DeGeer) (Coleoptera: Carabidae), which is restricted to foraging on the soil surface. As the coccinellid forages, it dislodges aphids that are then consumed by the ground predator, enhancing overall aphid suppression (Losey and Denno 1998). Coccinellid predators and parasitoids also facilitate transmission and dispersal of the beneficial aphid pathogen *P. neoaphidis* (Pell et al. 1997; Fuentes-Contreras et al. 1998;

Roy et al. 1998, 2001; Baverstock et al. 2005). Avoidance behaviour of parasitoids and coccinellids in relation to other intraguild predators is common (Nakashima et al. 2004; Meyling and Pell 2006; Ormond 2007). As already described, coccinellid species can also be phenologically separated, thereby partitioning resources temporally and avoiding competition (Takahashi and Naito 1984; Sato 2001; Flowers et al. 2006) or they can have different patch-leaving times (Sato et al. 2003). As there are numerous examples of complementarity amongst aphidophagous species, it follows that the more species there are in the guild, the greater pest suppression will be. This confirms the hypothesis that declines in guild diversity as a result of introduction of *H. axyridis* could reduce effective pest suppression.

Conclusion

Overall, the evidence suggests that predator diversity is necessary for resilient pest suppression and that includes aphid and coccid control (Stiling and Cornelissen 2005; Cardinale et al. 2006; Pell 2008; Straub et al. 2008). Although intraguild predation does not necessarily interfere with the overall ecosystem service it can interfere with pest suppression in some systems, particularly when the intraguild prey are large compared to the extraguild prey and this is the case for *H. axyridis*. Niche complementarity is almost certainly the mechanism by which *H. axyridis* remains in equilibrium with its co-evolved native guild of predators. In its exotic range, the guild of predators are co-evolved with each other but not with *H. axyridis* and as such come into direct competition with *H. axyridis*. This has significant implications for predator diversity, biodiversity per se and also ecosystem services. Pest management strategies aimed at maintaining predator diversity through habitat manipulation and the diversification of our agricultural landscapes could help counter declines in predator diversity associated with the arrival of *H. axyridis* (e.g., Barbosa 1998; Landis et al. 2000; Gurr et al. 2004; Pell 2008). Although implications for biodiversity in natural habitats are of grave concern, it is perhaps through the manipulation of managed land, which, for example, represents 70% of land in the UK, that we have the greatest chance of optimising the environment to favour our native diversity in the presence of *H. axyridis*, thereby also protecting diversity in natural habitats. To achieve this we need robust research data to fill the gaps in knowledge identified in this paper and develop mitigation strategies.

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