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

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

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

23 **Introduction**

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

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28 the same and lower trophic levels (top down pressure) and in this way influence the  
29 structure of the community as a whole. In the case of aphids these natural enemies  
30 (aphidophages) include specialist and generalist predators, parasitoids and pathogens  
31 (Völkl et al. 2007). Together they represent a 'guild', i.e., a community of species that  
32 share the same host/prey resource (Polis et al. 1989; Rosenheim et al. 1995). As aphids are  
33 often pests in managed ecosystems these natural enemies provide a valuable pest man-  
34 agement ecosystem service that can be manipulated within biological control strategies  
35 (e.g., Barbosa 1998; Gurr et al. 2004; Losey and Vaughan 2006; Powell and Pell 2007; Pell  
36 2008).

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

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

60 As an effective generalist predator of aphids and other hemipteran pests *Harmonia*  
61 *axyridis* (Pallas) (Coleoptera: Coccinellidae) has been widely and repeatedly augmented or  
62 introduced for biological control. As such, it has contributed significantly to pest sup-  
63 pression in a wide variety of managed ecosystems including pecan, apple, sweet corn,  
64 alfalfa, cotton, tobacco, wheat and soybean (Teddars and Schaefer 1994; Buntin and  
65 Bouton 1997; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Wells and  
66 McPherson 1999; Wells et al. 2001; Musser and Shelton 2003; Koch 2003; Majerus et al.  
67 2006; Roy et al. 2006). However, the very functional traits that have made *H. axyridis* an  
68 effective biological control agent, also implicate it as an intraguild predator that poses  
69 significant risk to the diversity of other natural enemies of Hemiptera and their ecosystem  
70 services. Although natural enemy diversity in its native range remains relatively stable in  
71 the presence of *H. axyridis* (Kuznetsov 1988, 1997), wherever it has established after  
72 introduction as an exotic species, it has been associated with declines in native natural  
73 enemies, particularly native coccinellids (Majerus et al. 2006; Roy et al. 2006; Snyder and  
74 Evans 2006). These declines have been attributed to direct interspecific competition for  
75 resources with less competitive/fecund natural enemies (Michaud 2002) but are also likely  
76 to be strongly influenced by its role as an intraguild predator.



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

## 90 Current knowledge

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

### 92 Eggs

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

99 *Harmonia axyridis* adults and larvae find eggs of many insect species acceptable as  
100 prey; laboratory stocks are often maintained on eggs of the Mediterranean flour moth,  
101 *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Berkvens et al. 2008). Cottrell (2004)  
102 reports that *H. axyridis* adults attacked eggs of *Coleomegilla maculata* (De Geer)  
103 (Coleoptera: Coccinellidae) and *Olla v-nigrum* (Mulsant) (Coleoptera: Coccinellidae) more  
104 frequently than adults of these species attacked *H. axyridis* eggs, and attest that intraguild  
105 predation of eggs is a serious threat for these species. However, cannibalism and predation  
106 of coccinellid eggs are most often associated with larval stages (Dixon 2000; Cottrell 2007)  
107 and, for some species, may be affected by the relative abundance of extraguild prey (Sato  
108 et al. 2003); at low aphid or coccid densities, coccinellid larvae are more likely to engage  
109 in cannibalism or intraguild predation. In addition, the tendency for intraguild predation by  
110 larvae varies between species both as intraguild predators and intraguild prey. Cannibalism  
111 and intraguild predation by *H. axyridis* are commonly observed, both in the laboratory and  
112 the field, even when aphids or coccids are abundant (M.E.N. Majerus and R.L. Ware  
113 personal observation). A recent study concluded that *H. axyridis* larvae were more likely to  
114 engage in intraguild predation of the eggs of *C. maculata*, *Cycloneda munda* (Say)  
115 (Coleoptera: Coccinellidae), *Hippodamia convergens* Guérin-Méneville (Coleoptera:  
116 Coccinellidae) and *O. v-nigrum* than for *H. axyridis* eggs to be the intraguild prey of the  
117 larvae of these species (Cottrell 2007). This is in agreement with previous work of Cottrell  
118 (2004) demonstrating that neither *C. maculata* nor *O. v-nigrum* larvae can complete  
119 development on *H. axyridis* eggs whereas *H. axyridis* can complete development on a diet  
120 of either *C. maculata* or *O. v-nigrum* eggs.



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

### 139 *Larvae and pupae*

140 Ware and Majerus (2008) have comprehensively examined intraguild predation of  
141 immature stages of British and Japanese coccinellids by *H. axyridis*. A total of 12 species  
142 of coccinellid (Coleoptera: Coccinellidae) were included in this laboratory study: eight  
143 derived from British populations (*Coccinella 7-punctata* L., *Adalia 2-punctata* (L.), *Adalia*  
144 *10-punctata* (L.), *Propylea 14-punctata* (L.), *C. 14-guttata*, *Anatis ocellata* (L.), *Harmonia*  
145 *4-punctata* (Pontoppidan), *Coccinella 5-punctata* L.) and four from Japanese populations  
146 (*Coccinella 7-punctata brucki* Mulsant, *Cheilomenes 6-maculatus* (Fabricius), *Propylea*  
147 *japonica* Thunberg and *E. muii*). In general, *H. axyridis* was an intraguild predator of all  
148 species, with the exception of *A. ocellata*. The important conclusions of this study were  
149 that there was no obvious difference between the susceptibilities of Japanese and British  
150 coccinellids to intraguild predation by *H. axyridis*, and intraguild predation by *H. axyridis*  
151 represents a serious threat for many species in Britain (Ware and Majerus 2008).

152 The relatively large size of *H. axyridis* throughout its life cycle undoubtedly contributes  
153 to its success as an intraguild predator following the 'size matters' hypothesis. In predatory  
154 interactions between coccinellid larvae it is generally the larger that eats the smaller,  
155 assuming both are mobile (Majerus 1994). Notably, in comparative tests between fourth  
156 instar larvae of *H. 4-punctata*, *H. axyridis* and *A. ocellata*, which have similar behavioural  
157 and physical defences, the level of intraguild predation was directly correlated to size. Larvae  
158 of the largest species, *A. ocellata*, won the majority of encounters with *H. axyridis*, while the  
159 smallest species, *H. 4-punctata*, lost most such encounters (Ware and Majerus 2008).

160 There are few reports of other larval coccinellids successfully attacking *H. axyridis*, and  
161 most evidence suggests that the immature stages of *H. axyridis* are resistant to reciprocal  
162 attacks. In a laboratory study assessing the interactions between *H. axyridis* and  
163 *C. 7-punctata*, Yasuda et al. (2001) attributed the greater success of the former to its higher  
164 attack rates and greater escape ability. Recent research is beginning to confirm the importance  
165 of chemical defence of *H. axyridis* larvae as a means of preventing counter-attacks (Ware and  
166 Majerus 2008), and larvae are known to produce similar defensive alkaloids to those present



167 within eggs and released by adults (Pasteels et al. 1973; King and Meinwald 1996). Further  
168 studies have also implicated the role of superior physical defences (spines rather than hairs) in  
169 larval stages of *H. axyridis* compared to other species (Ware and Majerus 2008).

170 In the field, coccinellid larvae tend to disperse from a plant when prey abundance is low  
171 (Sato 2001) and this reduces the incidence of cannibalism and intraguild predation by  
172 larger larvae and adults (Sato et al. 2003). However, emigration is a precarious strategy for  
173 an immature coccinellid, so there is a trade-off between emigrating or remaining on a plant  
174 with a low prey density and risking cannibalism or intraguild predation. *Harmonia axyridis*  
175 commonly co-occurs with *C. 7-punctata brucki* and *P. japonica* in their native Japanese  
176 range (Yasuda and Shinya 1997; Sato 2001). In a Japanese field study of these three  
177 coccinellid species co-occurring on shrubs both *C. 7-punctata brucki* and *H. axyridis*  
178 larvae emigrated in response to low prey density whereas *P. japonica* larvae did not (Sato  
179 2001). The prevalence of intraguild predation and cannibalism of *C. 7-punctata brucki* and  
180 *H. axyridis* larvae was low whereas no *P. japonica* larvae completed their development on  
181 the shrubs and this was assumed to be as a consequence of intraguild predation. In further  
182 studies it was confirmed that the early emigration of *C. 7-punctata brucki* larvae enabled  
183 them to escape from intraguild predation by *H. axyridis* larvae (Sato et al. 2003) and that  
184 the late emigration of *P. japonica* larvae accounted for the high incidence of intraguild  
185 predation by *H. axyridis* larvae (Sato et al. 2003).

186 *Propylea japonica* is also a smaller species than either *H. axyridis* or *C. 7-punctata*  
187 *brucki* and so this further supports the hypothesis that 'size matters' in intraguild predation.  
188 Ware and Majerus (2008) also report *P. japonica* larvae as highly palatable intraguild prey  
189 with little physical defence from attack by *H. axyridis*. It is interesting to note from field  
190 studies in Japan that *C. 7-punctata brucki* are active earlier in the spring than *H. axyridis*  
191 (Takahashi and Naito 1984; Sato 2001). Therefore, *H. axyridis* are more likely to expe-  
192 rience a scarcity of aphids, which are abundant in spring and early summer, than  
193 *C. 7-punctata brucki*. Consequently, *H. axyridis* is likely to be more reliant on intraguild  
194 prey to complete their development than is *C. 7-punctata brucki* (Sato et al. 2003).

## 195 Adults

196 Adult coccinellids are generally less susceptible to predation than immature stages due to  
197 their protective elytra and aposematic colour patterns (Majerus 1994). However, they are  
198 exposed to a particularly vulnerable period just after eclosion, when their elytra are still  
199 soft. Ware and Majerus (2008) report observations of attacks made on eclosing or newly  
200 eclosed adults by larvae, when no other food was available. Fourth instar *H. axyridis* larvae  
201 were observed to attack and consume new adults of *A. 10-punctata*, *A. ocellata*,  
202 *C. 14-guttata*, *C. 7-punctata brucki* and *E. muiri*, after not having attacked them as pupae  
203 (Ware and Majerus 2008). However, the consumption of newly eclosed *H. axyridis* adults  
204 was rare, and only performed by conspecific larvae and larvae of the congeneric species  
205 *H. 4-punctata*. This supports the speculation that the defensive chemistry of *H. axyridis*  
206 adults may make them unpalatable to other coccinellids (Hough-Goldstein et al. 1996).

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

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





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

218 A further study examined the interactions between adult *H. axyridis*, *C. carnea* and the  
219 gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) in the presence of  
220 the soybean aphid, *Aphis glycines* Matsumara (Hemiptera: Aphididae), in microcosms and  
221 field cages (Gardiner and Landis 2007). *Harmonia axyridis* engaged in intraguild predation  
222 with both *C. carnea* and *A. aphidimyza* and was predicted to contribute to declines in both  
223 species in the field. Phoofolo and Obrycki (1998) and Gardiner and Landis (2007) both  
224 suggested the potential for *H. axyridis* to be an asymmetrical intraguild predator of  
225 *C. carnea*. However, *C. carnea* will consume *H. axyridis* eggs (Phoofolo and Obrycki  
226 1998) and recent observations by Fremlin (2007) indicate that *C. carnea* will also attack  
227 *H. axyridis* pupae. Therefore, the interaction can be considered to be (weakly) symmet-  
228 rical. Further research is required to expand our knowledge on interactions between  
229 neuropterans and *H. axyridis*.

230 The spined soldier bug, *Podisus maculiventris* Say (Heteroptera: Pentatomidae) is  
231 native to North America and has a broad prey range including over 100 species of insect,  
232 primarily soft-bodied, slow-moving larvae of Coleoptera and Lepidoptera, but also aphids  
233 (McPherson 1980; Herrick and Reitz 2004). Half of the species on which it preys  
234 are important crop pests (Herrick and Reitz 2004). *Podisus maculiventris* is therefore  
235 loosely linked with many trophic guilds, including that of aphids (McPherson 1980;  
236 Hough-Goldstein et al. 1996), and four species of predaceous coccinellid are listed as prey  
237 to this predatory bug (McPherson 1980). In laboratory studies, Hough-Goldstein et al.  
238 (1996) demonstrated that although *P. maculiventris* did not consume adult *H. axyridis* they  
239 did consume *H. axyridis* larvae in 'no choice' treatments. In this study, *H. axyridis* larvae  
240 were described as 'aggressive' and often noted to escape predation, whereas adult  
241 *H. axyridis* were rejected, presumably as unpalatable, by *P. maculiventris*. Indeed,  
242 *P. maculiventris* took four times longer to capture *H. axyridis* larvae compared to *Spodoptera*  
243 *frugiperda* Smith (Lepidoptera: Noctuidae) larvae (Hough-Goldstein et al. 1996).

244 A further study demonstrated that interactions between *P. maculiventris* and *H. axyridis*  
245 in the presence or absence of extraguild prey (*Spodoptera littoralis* Boisduval (Lepidop-  
246 tera: Noctuidae) or *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)) were asymmetric in  
247 favour of the bug (De Clercq et al. 2003). *Podisus maculiventris* fed on *H. axyridis* eggs  
248 and larvae but rarely on adults. As with interactions amongst coccinellids, this interaction  
249 was dependent on the life stage of the bug; fourth instar nymphs and adults were more  
250 aggressive in their interactions than second instars nymphs. In contrast, *H. axyridis* rarely  
251 attacked *P. maculiventris*. Intraguild predation by *P. maculiventris* on *H. axyridis* was  
252 reduced in the presence of *S. littoralis* but not *M. persicae*. De Clercq et al. (2003)  
253 interpreted this to infer that *H. axyridis* was a less preferred prey in comparison to  
254 *S. littoralis* and this was supported by the longer development time of the bug when fed on  
255 *H. axyridis* larvae compared to *S. littoralis*. There was a slight difference in the survival to  
256 adulthood of pentatomid nymphs fed on *H. axyridis* compared to *S. littoralis* (70% vs.  
257 80–90% respectively) and no nymphs reached adulthood when fed on just aphids  
258 (De Clercq et al. 2003).



259 Intraguild predation between *H. axyridis* and parasitoids

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

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

290 Intraguild predation between *H. axyridis* and pathogens

291 Entomopathogenic fungi are common pathogens of aphids and can be involved in both  
292 coincidental and omnivorous, asymmetrical or symmetrical, intraguild interactions (Roy  
293 and Pell 2000; Völkl et al. 2007). The most common fungal pathogens are host-specific  
294 species from the Zygomycetes, order Entomophthorales, although other species from the  
295 Ascomycetes, order Hypocreales, some with wide host ranges, are used as biopesticides  
296 and could, therefore, be involved in intraguild interactions (Powell and Pell 2007; Pell  
297 2008).

298 During the final stages of infection by entomopathogenic fungi the host dies and the  
299 fungus sporulates to produce more infective propagules (conidia) for transmission (Inglis  
300 et al. 2001; Pell et al. 2001). As the sporulating aphid cadaver is sessile, it is an easy prey  
301 item for generalist predators. In a laboratory study, Roy et al. (2008a) assessed the pre-  
302 dation of aphid cadavers sporulating with *Pandora neoaphidis* (Remaudière and  
303 Hennebert) Humber (Zygomycetes: Entomophthorales) by UK and Japanese-derived



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304 *H. axyridis* relative to that of the UK native species *C. 7-punctata*. Unlike *C. 7-punctata*,  
305 which showed a strong preference for aphids over sporulating fungal cadavers, *H. axyridis*  
306 showed little discrimination between the prey types and would consume whole, sporulating  
307 cadavers. The consumption of whole sporulating cadavers could remove a significant  
308 quantity of inoculum from the aphid population, which may result in a reduction in further  
309 transmission. As *P. neophidius* only infects aphids, this represents asymmetrical intraguild  
310 predation. The strength of intraguild predation by *H. axyridis* collected in the UK differed  
311 from those collected in Japan, with *H. axyridis* (UK) showing less discrimination between  
312 prey types compared to *H. axyridis* (Japan) (Roy et al. 2008a). Whether feeding on  
313 infected cadavers has fitness consequences for *H. axyridis* is unknown.

314 Other entomopathogenic fungi have wider host ranges and may be infective  
315 towards both coccinellids and aphids, making the intraguild interaction potentially  
316 symmetrical. For example, isolates of the entomopathogenic fungi *Metarhizium*  
317 *anisopliae* (Metschnikoff) Sorokin (Ascomycete: Hypocreales), *Paecilomyces fumos-*  
318 *oroseus* (Wise) Brown and Smith (Ascomycetes: Hypocreales) and *Beauveria bassiana*  
319 (Balsamo) Vuillemin (Ascomycetes: Hypocreales) have been recorded infecting both  
320 aphids and coccinellids (e.g., Magalhaes et al. 1988; Keller and Zimmerman 1989; Butt  
321 et al. 1994; James and Lighthart 1994; Yeo 2000; Pell and Vandenberg 2002; Ormond  
322 et al. 2006). In particular, *B. bassiana* is a major overwintering mortality agent of  
323 *C. 7-punctata* (Majerus 1994; Ormond et al. 2006). Roy et al. (2008b) assessed the  
324 susceptibility of *H. axyridis* derived from the UK and Japan to *B. bassiana* relative to  
325 that of the UK native species *C. 7-punctata* and *A. 2-punctata*. Only doses of  $10^9$  conidia  
326  $\text{ml}^{-1}$  resulted in mortality of *H. axyridis*, in contrast, 80% of *C. 7-punctata* and 70% of  
327 *A. 2-punctata* exposed to  $10^7$  conidia  $\text{ml}^{-1}$  of *B. bassiana* succumbed to infection. In  
328 addition, the results suggested that the UK derived strain may be more resistant to  
329 infection than the Japanese derived strain. Interestingly, inoculation with *B. bassiana* at a  
330 concentration as low as  $10^5$  conidia  $\text{ml}^{-1}$  reduced the fecundity of *H. axyridis* (Roy et al.  
331 2008b). Whether any of these coccinellids feed on *B. bassiana*-infected cadavers and the  
332 implications of this on the symmetry of intraguild predation is unknown. However, in the  
333 study of Pell and Vandenberg (2002) the coccinellid *H. convergens* did consume living  
334 *Diuraphis noxia* Kurdjumov (Hemiptera: Aphididae) aphids infected by *P. fumosoroseus*  
335 but did not consume sporulating aphid cadavers.

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

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

343 There is broad agreement, from the studies described above, that *H. axyridis* is a top  
344 predator as it is predominantly a strong asymmetrical intraguild predator of other guild  
345 members (Hironori and Katsuhiko 1997; Cottrell and Yeargan 1998; Phoofolo and Obrycki  
346 1998; Yasuda and Ohnuma 1999; Michaud 2002; Sato et al. 2003, 2005; Felix and Soares  
347 2004; Snyder et al. 2004b; Kajita et al., 2006; Perez and Omkar 2006; Roy et al. 2006,  
348 2008a, b; Cottrell 2007; Ware and Majerus 2008) and as such can dominate in aggressive  
349 intraguild interactions and lead to a decline in guild diversity.





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350 The key functional traits that make *H. axyridis* such an exceptional intraguild predator  
351 are its relatively large size, aggressive behaviour, extreme polyphagy and the possession of  
352 effective physical and chemical defence strategies. Together these traits provide the  
353 mechanism by which *H. axyridis* impacts on guilds and food webs in general (Teddars and  
354 Schaefer 1994; Hodek 1996; Yasuda and Shinya 1997; Yasuda and Ohnuma 1999; Kajita  
355 et al. 2000; Koch 2003). It therefore seems likely that *H. axyridis* could disrupt  
356 aphidophagous/coccidophagous community structure leading to declines in other species in  
357 the guild where it establishes as a non-native species. *Harmonia axyridis* has certainly  
358 become abundant and widely distributed as a non-native species throughout North America  
359 and Europe (Koch 2003; Brown et al. 2008) and field data from the USA has reported  
360 associated negative impacts on native coccinellid species in these regions (Elliott et al.  
361 1996; LaMana and Miller 1996; Brown and Miller 1998; Colunga-Garcia and Gage 1998;  
362 Lucas et al. 2002; Michaud 2002; Nault and Kennedy 2003). Interestingly, *C. 7-punctata*  
363 was also introduced and became established widely in North America prior to the estab-  
364 lishment of *H. axyridis* (Gordon 1985). It too displaced native coccinellids and became the  
365 dominant predator. However, *H. axyridis* is a more aggressive predator than *C. 7-punctata*;  
366 larvae of *H. axyridis* consume those of *C. 7-punctata* but the reverse occurs considerably  
367 less frequently (Hironori and Katsuhiko 1997; Yasuda et al. 2004; Ware and Majerus  
368 2008). Since the arrival of *H. axyridis* in the USA, it has displaced *C. 7-punctata* as the  
369 'top predator' demonstrating the considerable dominance of *H. axyridis* as an intraguild  
370 predator of native and exotic coccinellids alike (Snyder et al. 2004b).

371 Similar evidence of declines in native coccinellid species after establishment of  
372 *H. axyridis* is accumulating in Europe. For example, evidence suggests that in London  
373 numbers of some, but not all, native coccinellids (particularly *A. 2-punctata*) have declined  
374 significantly since the arrival of *H. axyridis* in 2004 (Majerus, unpublished data). This is  
375 almost certainly due to its superior competitive ability and status as an intraguild predator.  
376 From the experimental studies of Ware and Majerus (2008), with consideration of the  
377 wider ecologies of *H. axyridis* and British ladybirds, and in the absence of control or  
378 mitigation, we anticipate that aphidophagous habitat generalists such as *C. 7-punctata*,  
379 *A. 2-punctata* and *P. 14-punctata* will be most at risk from the establishment of  
380 *H. axyridis* in the UK, followed by aphidophagous habitat specialists such as *Myzia*  
381 *oblongoguttata* (L.) (Coleoptera: Coccinellidae), *Myrrha 18-guttata* (L.) (Coleoptera:  
382 Coccinellidae) and *Anisosticta 19-punctata* (L.) (Coleoptera: Coccinellidae). The only  
383 species that may be relatively unaffected by invasive *H. axyridis* is *A. ocellata*, and indeed  
384 *H. axyridis* could actually be at risk from detrimental interactions with this species where  
385 they co-inhabit coniferous woodland. It is thought that the aphidophagous specialist  
386 *C. 5-punctata* would be particularly threatened if *H. axyridis* invades unstable river  
387 shingle, as it is already considered of conservation concern (Ware et al. 2005). Coccido-  
388 phagous species such as *Exochomus 4-pustulatus* (L.) (Coleoptera: Coccinellidae) and  
389 *Chilocorus renipustulatus* (Scriba) (Coleoptera: Coccinellidae) and the *Erica/Calluna*  
390 heathland specialists *Chilocorus 2-pustulatus* (L.) (Coleoptera: Coccinellidae) and  
391 *Coccinella hieroglyphica* L. (Coleoptera: Coccinellidae) are thought to be less at risk, the  
392 latter because *H. axyridis* has yet to be recorded from such heathland. Mycophagous,  
393 phytophagous and myrmecophilous coccinellids, such as *Thea 22-punctata* (L.) (Coleop-  
394 tera: Coccinellidae), *Subcoccinella 24-punctata* (L.) (Coleoptera: Coccinellidae) and  
395 *Coccinella magnifica* Redtenbacher (Coleoptera: Coccinellidae) respectively, are likely to  
396 be the least threatened by the establishment of *H. axyridis* in Britain.

397 There is clear evidence of declines in diversity of coccinellids in the USA and  
398 increasingly in Europe. However, there have been no studies to evaluate impacts on the



399 diversity of other guild members or on biodiversity more widely; these are urgently  
400 required, particularly in areas undergoing invasion by *H. axyridis*, if the full implications  
401 of its presence are to be evaluated.

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

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

419 *Temporal niche differentiation*

420 The co-existence of *H. axyridis* and sympatric species in Asia may, in part, be due to  
421 phenological differences that lead to temporal niche differentiation. For example,  
422 *C. 7-punctata brucki* is active earlier in the spring in Japan than *H. axyridis* and its larvae  
423 are therefore larger and more able to survive in intraguild combat with *H. axyridis*  
424 (Takahashi and Naito 1984; Sato 2001). Phenological studies of *H. axyridis* in its non-  
425 native range are essential if we are to predict the extent of intraguild predation and  
426 consequent impacts on biodiversity. Such studies are underway and in the UK, for  
427 example, early indications are that *H. axyridis* emerges from winter in synchrony with  
428 most native aphidophagous coccinellids, which contributes to the latter's inability to  
429 escape intraguild predation. *Harmonia axyridis* is also multivoltine and remains active for  
430 longer through the season, allowing numbers of individuals to build up rapidly. All life  
431 stages of *H. axyridis* have been recorded in November (early winter) in the UK (Majerus  
432 et al. 2006; Brown et al. 2008). In one study from the USA biological control literature,  
433 Flowers et al. (2006) considered intraguild interactions amongst three exotic predators  
434 attacking the hemlock woolly adelgid, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae) in  
435 hemlock stands in West Virginia. The species included were: specialists, *Laricobius*  
436 *nigrinus* (Fender) (Coleoptera: Derodontidae) and the coccinellid *Sasajiscymnus tsugae*  
437 (Sasaji & McClure) (Coleoptera: Coccinellidae), and the generalist *H. axyridis*. The  
438 authors concluded that intraguild predation by *H. axyridis* was not common because they  
439 were phenologically separated and active during different seasons; *L. nigrinus* was most  
440 active in spring and *H. axyridis* in summer. This also has implications for the wider guild  
441 beyond other coccinellids, for which there is currently very little information.



442 *Associations with ants*

443 Other coccinellid species in *H. axyridis*' native range may escape intraguild predation  
444 through associations with ants. Although there are limited studies on myrmecophilous  
445 interactions in the native range of *H. axyridis*, it is well documented for some coccinellid  
446 species in Europe. Many aphids and coccids are myrmecophilous and gain benefits from  
447 being associated with ants, including protection from natural enemies, in exchange for food  
448 in the form of honeydew (e.g., Hölldobler and Wilson 1990; Jiggins et al. 1993; Majerus  
449 et al. 2007). There is considerable evidence to demonstrate that ants display ownership  
450 behaviour, whereby they behave more aggressively towards predators in the vicinity of  
451 tended colonies than elsewhere (Way 1963). In the case of coccinellids, this aggression  
452 may be directed toward both adults and larvae, the former being chased away (e.g., Itioka  
453 and Inoue 1996; Sloggett 1998), while the latter may be picked up and dropped off the  
454 plant, or killed (e.g., Jiggins et al. 1993; Sloggett and Majerus 2003). As a result of ant  
455 aggression, most coccinellids only feed on ant-tended prey when untended prey are scarce  
456 (Sloggett and Majerus 2000). Many coccinellids have defences against ant aggression,  
457 which may be behavioural, chemical or physical and lead to variation in tolerance to ants  
458 amongst different coccinellid species (Majerus et al. 2007). For example, Sloggett and  
459 Majerus (2000) showed a hierarchy in six species of coccinellid living in pine woodland in  
460 the UK to aggression from *Formica rufa* (L.) (Hymenoptera: Formicidae) from no toler-  
461 ance (*M. 18-guttata* and *A. ocellata*) to high tolerance (*C. magnifica*). Unfortunately, the  
462 level of tolerance of *H. axyridis* to ant aggression in either its native or its invasive range is  
463 unknown. Should *H. axyridis* be found to be intolerant of ant presence, it is likely that  
464 those aphidophages that have a significant degree of ant tolerance, such as *M. oblongo-*  
465 *guttata* and *C. 7-punctata*, will find a refuge from some of the effects of intraguild  
466 predation and competition imposed by *H. axyridis* in habitats occupied by ant-tended  
467 aphids. Experiments to investigate the level of tolerance of *H. axyridis* to common aphid  
468 tending ants, such as *F. rufa*, *Lasius niger* (L.) (Hymenoptera: Formicidae) and *Myrmica*  
469 *ruginodis* Nylander (Hymenoptera: Formicidae), are urgently needed. The small number of  
470 coccinellid species that are true myrmecophiles, i.e., have the closest relationships with  
471 ants and associated high tolerance, are likely to have the safest refuge from *H. axyridis*,  
472 unless *H. axyridis* is also highly tolerant to ants. These species include *C. magnifica*  
473 (Sloggett et al. 2002; Majerus et al. 2007) and *Platynaspis luteorubra* (Goeze) (Völkl  
474 1995; Godeau 2000). It is possible that some species that have some tolerance of  
475 ants may come under additional selection pressures to improve their tolerance as a result of  
476 the presence of *H. axyridis*. In regions now occupied by *H. axyridis*, monitoring the  
477 coccinellid presence in the vicinity of nests of *F. rufa* over the next decade would be  
478 valuable.

479 *Behavioural interactions*

480 Further work is also required to acquire data on behavioural defence strategies of guild  
481 members in the presence of *H. axyridis*, such as dislodgement (dropping behaviour) and  
482 escape behaviours which could be extremely important for some species. For example, larvae  
483 of the coccinellid *P. 14-punctata* are consumed by *H. axyridis* in laboratory studies con-  
484 ducted in Petri dishes, but it is speculated that the highly mobile larvae of this species may  
485 have the capability to successfully escape from *H. axyridis* in field situations (Ware and  
486 Majerus 2008). We also know that parasitoids and predators can use volatile and chemical



487 cues to avoid competition; both the coccinellid *C. 7-punctata* and the predatory bug  
488 *Anthocoris nemorum* (L.) (Heteroptera: Anthocoridae) can detect and avoid surfaces con-  
489 taminated by the fungal pathogen *B. bassiana* to which they are susceptible (Meyling and Pell  
490 2006; Ormond 2007). In addition, the aphid parasitoid *A. ervi* detects volatiles from the tracks  
491 of *C. 7-punctata* and avoids oviposition in nearby aphid populations (Nakashima et al. 2004).  
492 Such behavioural responses can ensure co-existence by reducing the risk of intraguild pre-  
493 dation. They may contribute to co-existence of *H. axyridis* in its co-evolved native guild  
494 populations and are currently being evaluated for *H. axyridis* in the broader UK guild.

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

#### 506 *Natural enemy release and biotype variation*

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



532 2008b). Further research is needed to fully evaluate these interactions and determine  
533 whether any associated fitness costs could prove to be *H. axyridis*' weakness.

534 *Going beyond managed ecosystems*

535 The focus of research has largely been on interactions between *H. axyridis* and other  
536 coccinellids in managed ecosystems and, until recently, mainly in the USA, which has very  
537 different agricultural systems to Europe. However, it is clear from the studies described  
538 above that *H. axyridis* can have impacts on many other species and that this has impli-  
539 cations beyond managed ecosystems to natural habitats. Such impacts require urgent  
540 investigation. *Harmonia axyridis* is dispersive and highly polyphagous and therefore likely  
541 to impinge on many foodwebs in many different ecosystems, with the potential to disrupt  
542 them all. Although native coccinellids with similar prey and habitat requirements are at  
543 greatest risk, other non-coccinellid guild members and non-target species beyond the guild,  
544 such as Hemiptera of no economic importance (Majerus et al. 2006), lepidopteran eggs and  
545 larvae (Koch 2003; Koch et al. 2006) and all the predators, hyperparasites and pathogens  
546 in the higher trophic levels (Roy et al. 2008b) that may also be negatively affected. This  
547 represents a significant threat to biodiversity per se, particularly as some of these species  
548 are of considerable conservation concern (Koch et al. 2006).

549 *What about scale?*

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

562 *Potential implications for ecosystem services*

563 Predators are part of the functional biodiversity in managed ecosystems and, while not the  
564 only contributor to herbivore population regulation, they are essential for sustainable pest  
565 management through the ecosystem services they provide and that we depend upon. While  
566 the abundance of particular species can be enhanced through biological control, the  
567 question of 'how many species are required to achieve the required service in the crop?'  
568 continues to be a matter of debate (e.g., Denoth et al. 2002; Pell 2008; Straub et al. 2008)  
569 and must be considered in the context of the arrival of *H. axyridis* and potential declines in  
570 guild diversity. The relationship between predator biodiversity and ecosystem function is  
571 poorly understood. From the studies described above, and field observations of declines in





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572 native aphidophages and coccidophages since the arrival of *H. axyridis*, we must consider  
573 whether *H. axyridis* as a top predator, will deliver the same ecosystem service when other  
574 guild species are excluded or whether this will reduce aphid regulation (prey release) and  
575 the reliability of biological control in the long term.

576 Straub et al. (2008) reviewed recent literature on the relative pest suppression function  
577 of multiple (more than two) compared to single predator species and found that the rela-  
578 tionship between predator diversity and pest suppression was context dependent and could  
579 be positive, negative or neutral. Theoretically, if increasing predator diversity encourages  
580 intraguild predation, or, as in the case of invasion by *H. axyridis*, an invasive intraguild  
581 predator is introduced to the system, then the prediction would be that the equilibrium  
582 density of the herbivore would increase and pest control function would be reduced (e.g.,  
583 Polis et al. 1989; Finke and Denno 2004). Effectively, trophic cascades would be damp-  
584 ened and the herbivore would be released from predation. However, the experimental  
585 evidence to support this in a number of communities is mixed. Some studies have docu-  
586 mented disruption of pest suppression and others have shown either no change or improved  
587 pest suppression in the presence of intraguild predation (Straub et al. 2008). Most recent  
588 meta-analysis by Rosenheim and Harmon (2006) and a literature review by Janssen et al.  
589 (2006) find no evidence that the presence of intraguild predation disrupts herbivore control.  
590 However, there was greater variation than expected between cases, suggesting that pest  
591 release depended on system-specific factors, such as the biological traits of the predators  
592 and prey, and extrinsic factors, such as the environment: i.e., there was no simple  
593 prediction relating intraguild predation to pest release (Straub et al. 2008).

594 However, Straub et al. (2008) have identified particular traits of relevance from the  
595 theoretical literature. The first relates to the life history of the intraguild prey. Coincidental  
596 intraguild predation of parasitoids and pathogens is likely to be less disruptive to herbivore  
597 suppression than omnivorous intraguild predation of other predators because predation of  
598 the herbivore and the parasitoid/pathogen are directly linked and intraguild predation will  
599 simultaneously result in predation of the herbivore (Rosenheim et al. 1995). However, this  
600 may not hold if several generations of the intraguild prey are considered (Snyder and Ives  
601 2001). Secondly, the relative mobility and size (foraging mode) of the intraguild predator,  
602 intraguild prey and the herbivore can all influence the likelihood of prey release. A 'sit and  
603 wait' intraguild predator could disrupt suppression of a sedentary herbivore by a mobile  
604 intraguild prey species, although this will depend on the size of the intraguild prey species  
605 too. If it is large and highly mobile, it will have a large demand for prey, and if removed  
606 from the system by intraguild predation could result in release of the herbivore prey  
607 (Rosenheim and Corbett 2003). Furthermore, if the intraguild prey is a similar size to the  
608 herbivore then adding a larger intraguild predator will enhance herbivore suppression  
609 because predation of the herbivore by the intraguild predator would greatly outweigh the  
610 small release from predation achieved by the consumption of the intraguild prey (Diehl  
611 1993). The opposite would be the case if the intraguild prey was much larger than the  
612 herbivore (Rosenheim and Corbett 2003). There is some experimental support for this  
613 second prediction (Rosenheim et al. 2004a, b) but for the most part they remain hypotheses  
614 that require experimental evaluation. In addition, they will be influenced by whether the  
615 top intraguild predator is co-evolved with the rest of the guild or whether it is an exotic  
616 alien species, as is the case with *H. axyridis*. Using the hypotheses above, one could  
617 predict from the biological traits of *H. axyridis* that it would release herbivores from  
618 control because it consumes intraguild prey that are large and mobile. However, it is itself  
619 large, mobile, well defended, multivoltine and highly voracious which could compensate  
620 for this, at least in the short term.



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

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

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



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

## 680 Summary

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

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