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Intraguild interactions implicating invasive species: *Harmonia axyridis* as a model species

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Understanding the mechanisms that result in the success of exotic species will contribute to predicting future invasions and managing invaded systems. Exotic animal species, whether introduced accidentally or deliberately, may impact communities of native species through different intraguild interactions. As an effective generalist predator of aphids and other soft-body pests the harlequin ladybird *Harmonia axyridis* Pallas has been a successful biological control agent. This species was deliberately introduced into several countries for biological control of different arthropods pests, but it was also introduced accidentally into several other countries. It became an invasive species, affecting the dynamic and composition of several guilds through direct or indirect interactions. In this paper we will specifically review the existing data on mechanisms of intraguild interactions, within exotic guilds, that result in the success of *H. axyridis* as an invasive alien. We will use these studies to interpret the observed population declines in predator diversity in the field, and predict species at risk in regions not yet invaded. Finally, we will review the available data on the impact of intraguild interactions implicating *H. axyridis* on pest biocontrol.
Keywords. *Harmonia axyridis*, native species, interspecific interactions, biological control, invasion, diversity decline.

Interactions intraguildes impliquant les espèces invasives : *Harmonia axyridis* en tant qu'espèce modèle. Comprendre les mécanismes conduisant à la réussite des espèces exotiques contribuera à prédire des invasions futures et à gérer les systèmes envahis. Les espèces animales exotiques, qu'elles soient introduites accidentellement ou délibérément, peuvent affecter les communautés des espèces natives à travers des compétitions pour la ressource, des interactions trophiques ou des interactions indirectes. En tant que prédateur généraliste de pucerons et d'autres ravageurs à corps mou, la coccinelle arlequin *Harmonia axyridis* Pallas est un agent effectif de la lutte biologique. Cette espèce a été délibérément introduite dans plusieurs pays pour la lutte biologique de différents ravageurs arthropodes, mais elle a également été introduite accidentellement dans plusieurs autres pays. Elle-même est devenue une espèce envahissante, affectant la dynamique et la composition de plusieurs guildes à travers des interactions directes et indirectes. Dans cet article, nous passerons particulièrement en revue les données existantes sur les mécanismes d'interactions intraguildes, au sein de guildes exotiques, conduisant à la réussite de *H. axyridis* en tant qu'espèce invasive. Nous nous servirons de ces études pour interpréter les déclins observés dans la diversité des prédateurs au champ et pour prédire les espèces en danger dans les régions non encore envahies. Enfin, nous examinerons les données disponibles sur l'impact des interactions intraguildes impliquant *H. axyridis* dans la lutte biologique contre les ravageurs.
Mots-clés. *Harmonia axyridis*, espèces natives, interactions interspecifiques, lutte biologique, invasion, déclin de diversité.

1. INTRODUCTION

Terrestrial ecosystems support a diversity of insect species that are directly and indirectly linked to each other within food webs that span multiple trophic levels. Natural enemies contribute to the population regulation of species in both 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, namely aphidophagous, 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 (Powell et al., 2007; Pell, 2008). However, aphid individuals represent limiting resources for the development of natural enemies, and provide ample opportunity for competition among these beneficials (Mills, 1999). Thus, when beneficial species share a pest species as their common prey, different intraguild interactions (IG) between them may take place. Following Mills (1999), consumers that share a prey may be subject to intraguild predation/parasitism, in which one species eats its competitor (Polis et al., 1989; Rosenheim et al., 1995), exploitative competition, in which competitors interact through the consumption of a diminishing supply of an essential resource (Grover, 1997), interference competition, in which the activity of one species reduces the access of a competitor to a limited but essential resource (Ridenour et al., 2001) or apparent competition, in which competitors share a common natural enemy (Abrams, 1998). Among these mechanisms of intraguild interactions, intraguild predation is the most common interaction between *H. axyridis* and other natural enemies.

The rapid increase in the introduction of exotic species throughout the world, and the potential of these species to become invasive, is a subject of much concern (Mack et al., 2000). The concept of biological invasion is, generally, used to refer to the arrival or introduction, establishment, geographical expansion and integration of a species into a region where it has never been before (Williamson, 1996; Shigesada et al., 1997). Biological invasions usually occur in three successive stages:

- transport of the invader to the target area,
- establishment and growth of invasive populations,
- dispersion of the invader into adjacent areas (Shea et al., 2002).

The complexity of trophic interactions in the recipient ecosystem is one of the main opposition factors of the ecosystem to the invasion. This is because it is more difficult to get established in a complex food web than in a simpler one (Hewitt et al., 2002; Shea et al., 2002). Based on the availability of plant resources and the limited number of trophic links, agro-ecosystems are highly susceptible targets for biological invasions.

The impact of some invaders is unquestionably negative and as such they are designated as invasive alien species. The harlequin ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), "the most invasive ladybird on Earth", is undoubtedly one such species (Roy et al., 2006). While the invading species may interact directly or indirectly with indigenous species, these invaders may affect the dynamics and composition of indigenous species guilds (Lucas et al., 2002; Evans, 2004). Following Reitz et al. (2002), if a superior competitor invades the habitat of an inferior species, the inferior species will be displaced (*i.e.* competitive displacement occurs). Introductions of exotic species for biological control have generated increasing threats for the conservation of native species, with major implications for biodiversity worldwide in both natural and managed (*e.g.* agricultural) habitats. Ecologists have long sought to identify key factors that determine why some exotic species turn invasive and damaging to native species while others fail to do so (Williamson, 1999). These topics have recently become of great interest in regards to the establishment and spread of introduced aphidophagous ladybirds (Coleoptera: Coccinellidae). Once introduced species become established, they have the potential to interact with indigenous species in a number of different ways, competition and intraguild predation (IGP) for example. Thus, recent species invasions, such as *Coccinella septempunctata* L. and *H. axyridis* into the North American continent (Alyokhin et al., 2004; Harmon et al., 2007), and *H. axyridis* into the Europe continent (Pell et al., 2008), leading to replacements of indigenous species have occurred across diverse taxa (Woodward et al., 2002). Major factors hypothesized to be important to the success of these two invaders are their tendency to engage in IGP with indigenous ladybirds (Michaud, 2002b; Snyder et al., 2004), and release from natural enemies (Torchin et al., 2003). Following Williamson (2006), the knowledge of processes and factors explaining the invasion success is still, however, rudimentary.

As an effective generalist predator of aphids and other soft-body pests, *H. axyridis* has been widely and repeatedly augmented or introduced for biological control worldwide. As such, it has contributed significantly to pest suppression in a wide variety of managed ecosystems including apple, alfalfa, cotton, wheat and soybean (*e.g.* 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 IG predator that poses significant risk to the diversity of native natural enemies and their ecosystem services. Although natural enemy diversity in the native range of *H. axyridis* remains relatively stable in the presence of *H. axyridis* (Kuznetsov, 1997), wherever it has been established after introduction as an exotic species, it has been associated with declines in indigenous natural enemies, particularly ladybirds (Majerus et al., 2006; Roy et al., 2006). These declines have been attributed to direct interspecific competition for resources with less competitive/fecund natural enemies (Michaud, 2002b) but are also likely to be strongly influenced by the role of *H. axyridis* as an IG predator.

In fact, most studies investigated on beneficial and negative impacts of *H. axyridis* in its exotic range were in USA and Europe. *H. axyridis* ''the most common invader among the ladybird community'' is known to have strong dispersal capacities (Koch, 2003; Roy et al., 2006) and studies in North America have shown that it can rapidly colonize large areas as an invader species (*e.g.* Michaud, 2002b; Cottrell, 2005). In Europe, it has spread very rapidly, particularly since 2002, and the species now exists as feral populations in 13 European countries involving Belgium, in which the expansion rate is decreasing in this later because it now colonized the whole country (Adriaens et al., 2008; Brown et al., 2008). In a risk assessment of 31 exotic natural enemies of pest species used in biological control in Europe, *H. axyridis* had a high environmental risk index. This was based on its wide host range (*i.e.* multiple prey species), ability to establish and disperse, and direct and indirect effects on non-target species (van Lenteren et al., 2003).

We will review, in this paper, the key mechanisms of interspecific competition that made the harlequin ladybird *H. axyridis* as the most invasive ladybird on Earth. Subsequently, we will review the existing data on the competitive displacement following *H. axyridis* invasion within exotic guilds where it has been 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. Finally, we will review the available data on the impact of intraguild interactions implicating *H. axyridis* on pest biocontrol.

2. MECHANISMS OF INTERSPECIFIC COMPETITION (IG INTERACTIONS) IMPLICATING *H. AXYRIDIS*

2.1. Exploitative competition

Exploitative competition is the most common mechanism of competition among arthropod insects in nature. It occurs among all natural enemies that share a common and limiting host, where the consumption of a limiting resource by one species makes that resource unavailable for consumption by another, and is characterized by an absence of direct interaction between competitors (Grover, 1997). This type of competition may occur intraspecifically (within species) or interspecifically (between species). For interactions between predators, more particularly in case of *H. axyridis* presence, it has proved difficult to separate the effects of exploitative competition from those of IGP. It appears that IGP among coccinellids has a stronger influence in the context of short-term laboratory experiments (Yasuda et al., 2004). Moreover, there is some evidence that a disparity in body size among coccinellid species may increase the likelihood of IGP (Yasuda et al., 2004). The strength of exploitative competition following *H. axyridis* presence, as a top predator, is often decreased by eating potential competitors (Polis et al., 1989).

Following Lucas et al. (2007), upon review of 24 studies on the impact of invader *H. axyridis* on competitors, 15 demonstrated a negative impact by exploitative competition or IGP. A superior ability (foraging efficiency) to acquire resources can strongly affect the survival and fecundity of the invader *H. axyridis*, and may confer a large competitive advantage *vs* other natural enemies in the invaded range (Koch, 2003). *H. axyridis* larvae and adults have been shown to have a higher predation and foraging efficiency than indigenous species, such as *C. septempunctata* (Yasuda et al., 2001), *Coleomegilla maculata* DeGeer (Labrie et al., 2006), *Hippodamia variegata* Goeze and *Adalia bipunctata* L. (Lanzoni et al., 2004), on which this competitive advantage could increase its population density *vs* these ladybird species.

2.2. Interference competition

Interference competition results from the direct interaction of competitors or from the modification of a resource by one competitor such that it becomes unusable by another. If we assume that ladybirds expend some time and/or matter and/or energy on competition or the avoidance of competition, then there are less of those resources available for maintenance and reproduction (Krebs, 1989). In the simplest case, interference among natural enemy species represents a contest between competitors where the victim is excluded from access to the host through direct fighting or conditioning of the host as a resource. Thus success in competition contest is often a specific characteristic of the biology of a natural enemy species although it can also be influenced by the relative timing of attack (Boivin et al., 2006). In addition, as with exploitative competition, interference competition can occur within species as well as between species. However, when interference occurs among predatory species (Rosenheim, 1998) or between a facultative hyperparasitoid and a primary parasitoid (Hunter et al., 2001) the contest frequently leads to IGP, a more complex case, in which the IG predator gains resources directly from its competitor (*e.g.* Janssen et al., 2006; Rosenheim et al., 2006).

Recent studies of the magnitude, direction and symmetry of IGP between the different developmental stages of *H. axyridis* and *Coccinella undecimpunctata* L. revealed that *H. axyridis* was most often the IG predator (Felix et al., 2004). Although there is no IGP between adults of the two species, they may interact negatively by interfering with each other's foraging and oviposition (Lucas et al., 2002; Agarwala et al., 2003). Even when the resource is not in short supply, results of Soares et al. (2007) suggested that *H. axyridis* had a negative impact on *C. undecimpunctata* fitness, since fecundity was significantly affected in the presence of a heterospecific and predation of eggs occurred (an average of 21.6% of the eggs laid were eaten by *H. axyridis* adults). Interference competition was also detected between *H. axyridis* and the hoverfly *Episyrphus balteatus* DeGeer; results obtained by Alhmedi et al. (2009) suggested that the ladybird had a negative impact on *E. balteatus* oviposition, since ovipositional behavior was significantly affected in the presence of a heterospecific and predation of eggs occurred (an average of 79.1% of the eggs laid were eaten by *H. axyridis* larvae). Interference competition may cause ladybirds to fall off a plant, to switch from intensive to extensive search or to cease feeding (Ferran et al., 1993). It may also result in a decrease in fitness due to IGP (Michaud, 2002b; Felix et al., 2004) and competition for prey (Evans, 1991). It is difficult to speculate on the potential long-term impact of *H. axyridis* in the field (Lucas et al., 2002) because the other native species may respond differently. For example, *A. bipunctata* in Siberia avoids some species of plants, mainly *Salix* sp., where *H. axyridis* is present (Iablokoff-Khnzorian, 1982).

2.3. Apparent competition

Apparent competition results from the indirect interaction of two co-existent host species that share a common natural enemy, in which the victor is the host species that is more efficiently exploited by the natural enemy and supports the greatest natural enemy densities (Holt et al., 1993). For example, a more abundant host species can have a strong indirect negative impact on a less abundant host species by supporting a large natural enemy population that can use both hosts. In this way the less abundant host experiences a greater level of predation that it would in the absence of its competitor. Documentation of apparent competition among natural enemies appears to be more frequent among either parasitoid or phytophagous insects than among predators (reviewed by Mills, 1999). In fact, the competitive interaction among predatory communities has been often focused on IGP (Lucas, 2005). However, ladybird species that occur at differential levels of abundance, show differential susceptibility to commonly-occurring shared parasitoids.

Laboratory and field data already reported low levels of successful parasitism of *H. axyridis* adults by *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) in North America (Hoogendoorn et al., 2002; Firlej et al., 2005) or in Italy (Burgio et al., 2008). In this area, the indirect interactions recorded between *H. axyridis* and *C. maculata* may influence their populations in the field (Hoogendoorn et al., 2002). While both species are parasitized by the braconid wasp *D. coccinellae*, *C. maculata* was a more suitable host than *H. axyridis* for this parasitoid (Hoogendoorn et al., 2002), and this apparent competition increases the opportunities for *H. axyridis* to invade the native range of *C. maculata*.

The apparent competition is also greatly expected between the two co-existent species *H. axyridis* and *C. septempunctata*, where the later species is a preferential host of the parasitoid *D. coccinellae* (Geoghegan et al., 1998). In Japan, this wasp uses both *Coccinella septempunctata brucki* Mulsant and *H. axyridis* as hosts, but successfully parasitizes a higher proportion of the former species (Kawauchi, 1984; Koyama et al., 2008). This wasp usually prefers larger coccinellid species (Richerson et al., 1972), with recorded prevalence (proportion parasitized) being highest in *C. maculata* and *Hippodamia convergens* Guérin in North America (Obrycki, 1989), *C. septempunctata* in continental Europe (Iperti, 1964), and *Coccinella transversalis* Mulsant in Australia (Anderson et al., 1986). Several field and laboratory studies reported that the entomopathogen *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycota: Hypocreales) infects *H. axyridis*, *C. septempunctata* and *A. bipunctata*; however, the two later species were more suitable hosts for *B. bassiana* than *H. axyridis* (Roy et al., 2008a). This apparent competition may, as a consequence, increase the opportunities for *H. axyridis* to invade the native range of these ladybird species.

2.4. Intraguild predation

Intraguild predation (IGP) has become a major research topic in biological control and conservation ecology. It is assumed to be a widespread interaction within many communities of biocontrol agents (Rosenheim et al., 1995; Holt et al., 1997). IGP occurs when two predator species in a guild compete for the same prey (the extraguild prey), often limiting, and one (IG predator) of them also feeds upon its competitor (the IG prey) within the guild. IGP can be a strong force structuring beneficial insect communities (Polis et al., 1989). Its impact on community structure and diversity can be extremely variable, complex and difficult to predict (Snyder et al., 2006; Straub et al., 2008). IG predator mainly operates from the fourth trophic level suppressing both IG and extraguild preys. IG prey, by definition, is an intermediate predator or parasitoid that functions from the third trophic level suppressing herbivores, whereas the extraguild prey is the herbivore, aphids for example, that acts from the second trophic level.

Many studies have assessed the prevalence of IGP in aphidophagous guild (*e.g.* 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. IGP may be omnivorous or coincidental. Coincidental IGP occurs when a parasitoid or pathogen is consumed by IG predators, while still developing within its herbivore host and, in this case, the herbivore and the IG prey are directly linked (Polis et al., 1989). However, omnivorous IGP is defined in the food web theory as the act of feeding by one species on resources at different trophic levels (Pimm et al., 1978). One of the simplest conceivable examples of omnivory is a constellation of three species: a predator (top), a consumer (middle), and a resource (bottom) that is common to both consumer and predator. Thus, IGP is a combination of exploitative competition and predation interactions; it reduces however potential exploitative competition (Polis et al., 1989; 1992). Within a guild, omnivorous IGP can be asymmetric when one species (IG predator) is always the predator on the competitive species (IG prey), or symmetric when mutual predation occurs between both species (Polis et al., 1989; Rosenheim et al., 1995). The IG predator benefits not only from the nutritive value of the meal, but also from the removal of a competitor.

There are a number of functional traits that determine the nature, symmetry and outcome of IGP 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 (Roy et al., 2006; Straub et al., 2008). We will briefly outline the current knowledge on IGP implicating *H. axyridis*.

IGP is the most common interaction between *H. axyridis* and other natural enemies in comparison with other mechanisms of interspecific competition. Laboratory and field studies reviewed by Pell et al. (2008) indicate that *H. axyridis* engaged in IGP with many natural enemies (**Table 1**), and was predicted to contribute to declines in many of these species in the field. Coccinellids are common within aphidophagous guild and most studies considering the role of *H. axyridis* as an IG predator have focused on interactions within the Coccinellidae. However, *H. axyridis* interacts with many other non-coccinellid predatory insects. The relatively large size of *H. axyridis* throughout its life cycle undoubtedly contributes to its success as an IG predator. In predatory interactions between ladybird larvae it is generally the larger that eats the smaller, assuming both are mobile (Majerus, 1994). In fact, the relative size and mobility of the IG predator and prey are known to influence the outcome of IGP, both showing an inverse correlation with the incidence of mortality (Rosenheim et al., 1995; Lucas et al., 1998). Consequently, the immature stages of predators are more vulnerable to IGP than adults, and eggs are particularly threatened (Sato et al., 2004; Cottrell, 2007). Following these last authors, predation of ladybird eggs is most often associated with larval stages and, for some species, may be affected negatively by the relative abundance of extraguild prey. Recent studies concluded that *H. axyridis* larvae were more likely to engage in IGP of eggs of many predators than for *H. axyridis* eggs to be the IG prey of the larvae of these species (Phoofolo et al., 1998; Cottrell, 2007).

The chemical defences of coccinellid eggs have been implicated as central to the observed resistance to cannibalism (Hemptinne et al., 2000; Magro et al., 2007) or predation by other aphidophagous insects such as *A. bipunctata*, *C. septempunctata brucki* (Sato et al., 2004). Ware et al. (2008b) have recently discussed the role of surface deterrents on eggs of both the European species *Calvia quatuordecimguttata* L. and the Japanese species *Eocaria muiri* Timberlake as a defensive mechanism against IGP by *H. axyridis*. These last authors demonstrated the importance of chemical defence of *H. axyridis* larvae as a means of preventing counterattacks, where larvae are known to produce similar defensive alkaloids to those present within conspecific eggs and released by adults (King et al., 1996).

Morphological traits such as the relatively large body size of *H. axyridis* beetle compared to other aphidophagous species (Hodek, 1973; Michaud, 2002a), and the presence of spines on the back of third and fourth larval instars (superior physical defences) could provide a protection from IGP by other species (Ware et al., 2008b). Moreover, size, strength of the integument and distastefulness of its pupae make this stage less vulnerable to predation (Felix et al., 2004). 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 IGP by other predatory larvae and adults (Sato et al., 2003). However, this is not absolute safe strategy for an immature coccinellid, where there is always a risk of cannibalism or IGP. *H. axyridis* commonly co-occurs with *C. septempunctata* and *Propylea japonica* Thunberg in their native Japanese range (Sato, 2001). In a field study of these three coccinellid species co-occurring on shrubs, both *C. septempunctata* and *H. axyridis* larvae emigrated in response to low prey density whereas *P. japonica* larvae did not (Sato, 2001). In further studies it was confirmed that the early emigration of *C. septempunctata* larvae enabled them to escape from IGP by *H. axyridis* larvae and that the late emigration of *P. japonica* larvae accounted for the high incidence of IGP by *H. axyridis* larvae (Sato et al., 2003). *P. japonica* is also a smaller species than either *H. axyridis* or *C. septempunctata* and so this

Table 1. List of natural enemies implicated, to date, in predation interactions with the harlequin ladybird *Harmonia axyridis* — *Liste des ennemis naturels impliqués, jusqu'à présent, dans des interactions de prédation avec la coccinelle arlequin* Harmonia axyridis.

Species	Overall IGP Status of *Harmonia axyridis*	References
Coleoptera: Coccinellidae		
Adalia bipunctata L.	IG predator	Sato et al., 2005; Ware et al., 2008b
Adalia decempunctata L.	IG predator	Ware et al., 2008b
Anatis ocellata L.	IG prey	Ware et al., 2008b
Calvia quatuordecimguttata L.	IG predator	Ware et al., 2008b
Cheilomenes sexmaculatus F.	IG predator	Ware et al., 2008b
Coccinella quinquepunctata L.	IG predator	Ware et al., 2008b
Coccinella septempunctata L.	IG predator	Yasuda et al., 2004; Ware et al., 2008b
Coccinella septempunctata brucki Mulsant	IG predator	Ware et al., 2008b
Coccinella transversoguttata Falderman	IG predator	Snyder et al., 2004; Yasuda et al. , 2004
Coleomegilla maculata DeGeer	IG predator	Cottrell et al., 1998; Cottrell, 2005
Cycloneda sanguinea L.	IG predator	Michaud, 2002b
Eocaria muiri Timberlake	IG predator	Ware et al., 2008b
Harmonia quadripunctata Pontoppidan	IG predator	Ware et al., 2008b
Hippodamia convergens Guérin-Méneville	IG predator	Snyder et al., 2004; Yasuda et al., 2004
Laricobius nigrinus Fender	IG predator	Flowers et al., 2005
Olla v-nigrum Mulsant	IG predator	Cottrell, 2005
Propylea japonica Thunberg	IG predator	Ware et al., 2008b
Propylea quatuordecimpunctata L.	IG predator	Ware et al., 2008b
Sasajiscymnus tsugae Sasaji and McClure	IG predator	Flowers et al., 2005
Neuroptera: Chrysopidae		
Chrysoperla carnea Stephens	IG predator	Phoofolo et al., 1998; Gardiner et al., 2007
Heteroptera: Pentatomidae		
Podisus maculiventris Say	IG prey	De Clercq et al., 2003
Diptera : Cecidomyiidae		
Aphidoletes aphidimyza Rondani	IG predator	Gardiner et al., 2007
Diptera: Syrphidae		
Episyrphus balteatus DeGeer	IG predator	Alhmedi et al., 2009
Hymenoptera : Braconidae		
Aphidius colemani Viereck	IG predator	Takizawa et al., 2000
Aphidius ervi Haliday	IG predator	Snyder et al., 2003
Hymenoptera: Aphilinidae		
Aphelinus asychis Walker	IG predator	Snyder et al., 2004
Zygomycetes: Entomophthorales		
Pandora neoaphidis (Remaudière and Hennebert) Humber	IG predator	Roy et al., 2008b
Ascomycota: Hypocreales		
Beauveria bassiana (Balsamo) Vuillemin	IG prey/predator	Roy et al., 2008a

further supports the hypothesis that "size matters" in IGP. Ware et al. (2008a) also reported *P. japonica* larvae as highly palatable IG prey with little physical defence from attack by *H. axyridis*.

Adult coccinellids are generally less susceptible to predation than immature stages due to their protective elytra, mobility and aposematic colour patterns (Majerus, 1994). However, they are exposed to a particularly vulnerable period just after emergence, when their elytra are still soft. Fourth instar *H. axyridis* larvae were observed to attack and consume new adults of *Adalia decempunctata* L., *Anatis ocellata* L., *C. quatuordecimguttata*, *C. septempunctata* and *E. muiri*, when no other food was available (Ware et al., 2008). In fact, the consumption of newly emerged *H. axyridis* adults was rare, and only performed by conspecific larvae and larvae of the congeneric species *Harmonia quadripunctata* Pontoppidan. This supports the speculation that the defensive chemistry of *H. axyridis* adults may make them unpalatable to other ladybirds (Hough-Goldstein et al., 1996). The ovoid shape of adults as well as bright color may also confer a protection from predators and competitors (De Clercq et al., 2003).

Regarding the predation interaction between *H. axyridis* and non-coccinellid predators, a further study examined the interactions between *H. axyridis* adults, the lacewing *Chrysoperla carnea* Stephens larvae and the gall midge *Aphidoletes aphidimyza* Rondani larvae in the presence of the soybean aphid *Aphis glycines* Matsumara (Homoptera: Aphididae) in microcosms and field cages (Gardiner et al., 2007); *H. axyridis* engaged in asymmetrical IGP with both *C. carnea* and *A. aphidimyza*. However, Phoofolo et al. (1998) then Fremlin (2007) found that *C. carnea* larvae attack *H. axyridis* eggs and pupae; therefore, the interaction between them can be considered to be (weakly) symmetrical.

The hoverfly *Episyrphus balteatus* DeGeer is known as aphidophagous predator at larva stadium. It is the most frequently encountered hoverfly species at aphid-infested sites in temperate regions, *e.g.* in central Europe, and one of the most efficient aphid-specific predators (Colignon et al., 2001). *H. axyridis* larvae engaged in an asymmetric IGP with immature stages (larvae and eggs) of *E. balteatus* even when aphids are available on host plant (Alhmedi et al., 2009). The heteropteran bug *Podisus maculiventris* Say is native to North America and has a broad prey range including over 100 species of insect, including larvae of Coleoptera and Lepidoptera, but also aphids (Herrick et al., 2004). 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 favor 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*. There was a slight difference in the survival to adulthood of pentatomid nymphs fed on *H. axyridis* compared to *S. littoralis* and no nymphs reached adulthood when fed on aphids only (De Clercq et al., 2003).

Regarding the IGP between predators and parasitoids, it is often asymmetrical in favor of predators and can be described as both coincidental and omnivorous (Polis et al., 1989). In fact, there is very little information in the literature on predation interactions between *H. axyridis* and parasitoids. Previous studies have reported the consumption of parasitized aphids by coccinellids (Ferguson et al., 1996) and that the presence 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 the bracond wasp *Aphidius colemani* Viereck, were suitable prey for three coccinellid species: *C. septempunctata*, *P. japonica* and *H. axyridis*. The parasitoid was used at two life stages: 3-day-old larvae within living aphids (coincidental IGP) and sessile aphid "mummies" containing pupae (omnivorous IGP). Consumption of parasitized aphids containing 3-day-old larvae did not reduce survival nor 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. septempunctata* by 70% but did not affect the survival of *H. axyridis* and *P. japonica*. It is likely that aphid "mummies" are unsuitable prey for these coccinellids. Snyder et al. (2003) found that *H. axyridis* selectively preyed on pea aphids, *Acyrthosiphon pisum*, rather than pea aphid "mummies" parasitized by *Aphidius ervi* Haliday. Snyder et al. (2004) found that although adult *H. axyridis* did not show discrimination between aphid "mummies" of *Aphelinus asychis* Walker and aphids, their larvae preferred aphids in feeding trials.

Entomopathogenic fungi are common pathogens of aphids and can be involved in both coincidental and omnivorous intraguild interactions (asymmetrical or symmetrical) (Völkl et al., 2007). Asymmetrical IGP engaged by *H. axyridis* was recorded in case of the fungus *Pandora neoaphidis* (Remaudière and Hennebert) Humber (Zygomycetes: Entomophthorales), this last infects aphids only (Roy et al., 2008b). Whereas, symmetrical IG interactions were found between *H. axyridis* and the fungus *B. bassiana*, this last infects both aphids and coccinellids (Roy et al., 2008a).

3. MECHANISMS OF INTERSPECIFIC COMPETITION LEADING TO INVASION/ COMPETITIVE DISPLACEMENT

Negative impacts of introduced species include competitive suppression or displacement of native natural enemies and suppression or extinction of non-target prey species, some of which may be beneficial (Alyokhin et al., 2004). Competitive displacement is the most severe outcome of interspecific competition following *H. axyridis* invasion, in which competition for resources may lead to the competitive exclusion of one or more co-existent native species. The aggressive behavior of *H. axyridis* larvae possibly accounts for the replacements recorded particularly in ladybird communities (Yasuda et al., 2001; Agarwala et al., 2003). Based on the studies described above, it has proved difficult to separate the effects of either exploitative or interference competition from those of IGP on the natural enemy diversity following *H. axyridis* presence, where it appears that IGP among coccinellids has a stronger influence in the context of short-term laboratory experiments (Yasuda et al., 2004). There is clear evidence for declines in diversity of coccinellids in North America and increasingly in Europe following *H. axyridis* invasion. *H. axyridis* has certainly become abundant and widely distributed as an adventive species throughout North America and Europe and field data from the USA has reported negative impacts on native coccinellid species in these regions (Michaud, 2002b; Koch, 2003; Brown et al., 2008).

In addition to its intrinsic competitive advantages, as described above, over many other natural enemies, *H. axyridis* has other exceptional capacities allowing it to be successful in any new environment as invader, on which they may lead to the competitive displacement of one or more indigenous species (Soares et al., 2008). *H. axyridis* is a highly polymorphic species (Soares et al., 2001) and this could also help the species to be an efficient invader. The relative frequency of phenotypes seems to be related to geographical and seasonal factors (Iablokoff-Khnzorian, 1982; Osawa et al., 1992), suggesting that some phenotypes may be favorably selected in different parts of the ecosystem or at different times. Thus the genetic polymorphism in *H. axyridis* seems to be the strategy adopted for facing different habitats at different times.

Physiological characteristics, such as development, fecundity and low susceptibility to pathogens could allow its successful invasion in a new environment. A key factor in the invasion process is juvenile growth, as safe conditions in these vulnerable stages can ensure high population growth in the new environment (Marco et al., 2002). A shorter development time of younger larval instars of *H. axyridis* compared to the indigenous ladybird *Coleomegilla maculata lengi* Timberlake in Canada was observed in North America (Labrie et al., 2006). According to several studies, fecundity of *H. axyridis* is higher than other species, with between 703 and 3,800 eggs laid by a single female in laboratory studies (Iablokoff-Khnozorian, 1982; Stathas et al., 2001; Mignault et al., 2006). For example, fecundity of *H. axyridis* (2,008 eggs per female) reared on soybean aphids *A. glycines* was significantly higher than the invasive *P. quatuordecimpunctata* (593 eggs per female) or the indigenous *C. maculata* (390) in Québec, Canada (Mignault et al., 2006).

Reitz et al. (2002) documented, in their review, 42 cases of interspecific competition leading to competitive displacement, and of these 14 involved natural enemies used in the biological control of insect pests. Recent introductions of coccinellids into the North American environment have also led to competition with native coccinellids, causing a reduction in the abundance and habitat usage of the native species. The widespread release and establishment of *C. septempunctata* for aphid control has been associated with displacement of native Coccinellidae across North America, such as *Coccinella novemnotata* Herbst., *A. bipunctata*, *Coccinella transversoguttata richardsoni* Brown and *Hippodamia tredecimpunctata* L., where the relative abundance of the introduced *C. septempunctata* increased from 6% in 1980 to 100% in 1994 (Alyokhin et al., 2004; Harmon et al., 2007). The subsequent invasion by *H. axyridis* resulted in the displacement of *C. septempunctata* from its dominant position through IGP (Brown et al., 1998; Turnock et al., 2003). Evidence is now accumulating to suggest that the abundance of some other coccinellid species, including *Brachiacantha ursine* F., *Chilocorus stigma* Say, and *Cycloneda munda* Say, is declining concurrently in many ecosystems in USA (*e.g.* arboreal habitats and apple orchards) in the presence of dominated species *H. axyridis* (Brown et al., 1998).

Alyokhin et al. (2004) noted through their data set obtained from 1971-2001 that there was a significant decline in the abundance of aphids in the potato plots both in 1980 when *C. septempunctata* appeared and again after *H. axyridis* arrived in 1993-1995. These declines suggest that the exotic coccinellids may have been better exploiters of the aphids present on this exotic crop, and that exploitative competition may have played a role in the habitat displacement of native species by the exotic competitors (Evans, 2004). It is possible also that IGP advantage of exotic species may have contributed also in the competitive displacement of native species (Yasuda et al., 2004).

The ladybird *C. maculata* is a native species in Québec, Canada (Mignault et al., 2006); it was less affected by the invasion of *H. axyridis* (Cottrell et al., 1998). Like *H. axyridis*, *C. maculata* is a polyphagous predator that feeds mainly on aphids, but also on insect eggs, pollen, and other prey (Hodek et al., 1996). The apparently low food requirements of *C. maculata* and its avoidance of interactions with *H. axyridis* may help this species in maintaining its population levels after the invasion of *H. axyridis* (Schellhorn et al., 2005). As reported by Musser et al. (2003), asynchronies in the temporal and spatial distributions of both species in the field are also likely to limit the effects of *H. axyridis* on *C. maculata* populations. On the other hand, *C. maculata* may also facilitate the invasion by *H. axyridis*. Shea et al. (2002) discussed invasions in relation to resource opportunities. Resource opportunities arise not only when resources are supplied at a high rate, but also when resident species that compete for these resources with the invader do not greatly reduce the resource densities. The low food requirements of *C. maculata* may help to create an environment that is easy for *H. axyridis* to invade.

The appearance of *H. axyridis* in Florida dates back to the early 1990s (M. Thomas, personal communication). Before 1996, *H. axyridis* was relatively rare in Florida citrus, possibly due in part to its inability to produce eggs on a diet of the spirea aphid, *Aphis spiraecola* Patch (Hemiptera: Aphididae), the dominant aphid prey in citrus before the invasion of the brown citrus aphid, *Toxoptera citricida* Kirkaldy (Hemiptera: Aphididae) (Michaud, 2000a). Following Michaud (2002b), the ladybird *C. sanguinea* was one of the most abundant coccinellids in various Florida agro-ecosystems including citrus ecosystem. The subsequent invasion by *H. axyridis* resulted in the competitive displacement of *C. sanguinea* from citrus ecosystems in Florida, USA (Michaud, 2002b). One potential mechanism of displacement is resource (exploitative) competition. In citrus groves, Michaud (2002b) showed that *H. axyridis* was a more voracious predator and had higher fecundity and fertility than *C. sanguinea*. A comparison of basic biology and life history parameters suggests that *H. axyridis* has many intrinsic advantages over *C. sanguinea*. Adult *H. axyridis* average two to three times the body weight of adult *C. sanguinea* when reared on aphids, *A. spiraecola* or *T. citricida* (Michaud, 2000b). In IGP experiments, Michaud (2002b) showed also that adults and larvae of *H. axyridis* had a greater tendency to prey on various life stages of *C. sanguinea* than vice versa. Following this author, it is notable that *C. sanguinea* larvae possess smooth dorsal surfaces lacking any defensive spines or waxy filaments such as those present in larvae of other coccinellid genera, whereas the dorsal surfaces of *H. axyridis* larvae are covered with short spines thought to provide some defense against predation (Dixon, 2000). The results presented by Michaud (2002b) indicate also that *H. axyridis* can complete development on a sole diet of *C. sanguinea* larvae with only a slight cost in terms of delayed development, whereas *C. sanguinea* could not develop successfully on *H. axyridis* larvae. Following this author, when sources of prey are exhausted in the field, the ability of *H. axyridis* to complete development on an exclusive diet of either heterospecific or conspecific larvae should translate into a substantial competitive advantage over species such as *C. sanguinea* that lack such capabilities. *H. axyridis* is also more resistant than *C. sanguinea* to fungicides (Michaud, 2001), acaricides (Michaud, 2002c) and insecticides (Michaud, 2002d) and more resistant than most native ladybirds to attacks by the red imported fire ant *Solenopsis invicta* Buren (Dutcher et al., 1999), a species that has the potential to disrupt biological control in citrus (Michaud et al., 1999).

Regarding the IG interactions with non-coccinellid predators, Gardiner et al. (2007) founded that a diverse guild of insect predators feeds on soybean aphid *A. glycines* in Michigan (USA) including the exotic coccinellid *H. axyridis*, the native gall midge *A. aphidimyza* and the native lacewing *C. carnea*. In laboratory and field studies, this adventive ladybird engaged in IGP with both predatory species (Gardiner et al., 2007). Moreover, in a laboratory study, Phoofolo et al. (1998) demonstrated that there was no difference in the development time or survival of *H. axyridis* fed on a diet of pea aphid *A. pisum* or eggs of the lacewing *C. carnea*; the last was unable to develop successfully when fed on *H. axyridis* eggs. These studies indicate that *H. axyridis* may contribute to local declines in these predatory species in the field (Gardiner et al., 2007).

H. axyridis has been documented to feed on various stages of many predatory species, and it can also complete development on sole diets of some of them (Yasuda, 1999; Gardiner et al., 2007). Phoofolo et al. (1998) showed that *H. axyridis* could develop on an exclusive diet of *C. carnea* eggs, whereas *C. septempunctata* could not. Yasuda (1999) showed also that *H. axyridis* could develop on a diet of larvae of *C. septempunctata*, whereas the reverse was not possible.

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 native coccinellids (particularly *A. bipunctata*) 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 IG predator. However, with consideration of the wider ecologies of *H. axyridis* and British ladybirds, it is predicted that aphidophagous habitat generalists such as *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* will be most at risk from the establishment of *H. axyridis* in the UK, followed by aphidophagous habitat specialists such as *Myzia oblongoguttata* L., *Myrrha octodecimguttata* L., *C. quinquepunctata* and *Anisosticta novemdecimpunctata* L. (Ware et al., 2005; 2008b; Pell et al., 2008). The only species that may be relatively unaffected by the invader *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 (Ware et al., 2008b). Following Ware et al. (2008b), coccidophagous ladybird species such as *Exochomus quadripustulatus* L. and *Chilocorus renipustulatus* Scriba, *Chilocorus bipustulatus* L. and *Coccinella hieroglyphica* L. are thought to be less at risk, because *H. axyridis* has yet to be recorded from their specific habitats. Mycophagous, phytophagous and myrmecophilous ladybirds, such as *Thea vigintiduopunctata* L., *Subcoccinella vigintiquatuorpunctata* L. *and Coccinella magnifica* Redtenbacher respectively, are likely to be the least threatened by the establishment of *H. axyridis* in Britain. In

Belgium, modifications in ladybird communities have been reported through detailed monitoring studies in Brussels (Ottart, 2005). Following this author, prior to the invasion of *H. axyridis*, the native species *A. bipunctata* was the dominant ladybird on lime (*Tilia* sp.) and maple (*Acer* sp.), and was co-dominant with the native congeneric ladybird *Harmonia quadripunctata* Pontoppidan on Austrian pine (*Pinus nigra* Arn.). Only two years after its establishment, *H. axyridis* quickly became the predominant ladybird species in all habitats monitored. In addition, a significant decline in the abundance of two native ladybird species *A. bipunctata* and *A. decempunctata* was recorded between 2003 and 2005, while a simultaneous increase of the *H. axyridis* population was observed (Ottart, 2005). Due to its voracity and wide trophic niche, it was believed that *H. axyridis* would harm indigenous aphidophagous guild. 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 an adventive species.

4. INTRAGUILD INTERACTIONS IMPLICATING *H. AXYRIDIS*: BIOLOGICAL CONTROL CONTEST

As predators are essential parts of the functional biodiversity for sustainable pest management in managed ecosystems, a central question in biological control has been, thus, how potential declines in guild diversity following *H. axyridis* arrival affect the suppression of pest populations. In fact, 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 (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. septempunctata* 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 (Schellhorn et al., 2005). A further example of complementarity can be seen for the interactions between *C. septempunctata*, 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 et al., 1998). Coccinellid predators and parasitoids also facilitate transmission and dispersal of the beneficial aphid pathogen *P. neoaphidis* (Baverstock et al., 2005). Avoidance behavior of parasitoids and coccinellids in relation to other intraguild predators is common (Meyling et al., 2006). Coccinellid species can be phenologically separated, thereby partitioning resources temporally and avoiding competition (Sato, 2001; Flowers et al., 2005) 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 in the long-term (antagonistic effect).

However, the presence of *H. axyridis* in a system does not necessarily result in reduced pest suppression, particularly in a short-term (Lucas et al., 2002; Gardiner et al., 2007). While the competitive advantages of *H. axyridis* lead to a decline in many of native natural enemies, the high predation rate of *H. axyridis* on the pest appears to compensate for the resulting reduction in the abundance of other natural enemies (Gardiner et al., 2007). Losey et al. (1998) found synergistic (facilitation) effect when they studied the interactions between ladybirds and ground beetles both preying on pea aphids; by dropping from the plant in response to an attack by the ladybirds, aphids were more susceptible to predation by ground beetles. Additive effect was found also when predators engage in IGP with either parasitoids or pathogens, where the herbivore and the parasitoid/pathogen are directly linked (coincidental) and IGP will simultaneously result in predation of the herbivore (Rosenheim et al., 1995). For instance, Snyder et al. (2004) found, through different experimental conditions, that IG interactions between *H. axyridis* and the aphid parasitoid *A. asychis* did not disrupt aphid control. Gardiner et al. (2007) found also that despite the high asymmetric IGP engaging by *H. axyridis* against *A. aphidimyza* and *C. carnea*, the presence of these species together improved *A. glycines* aphid control on soybean. Following these last authors, biological control of soybean aphid would not likely be improved by removing *H. axyridis* from the system.

5. CONCLUSION

Based on the studies described above, interspecific competition was considered as a fundamental mechanism in structuring communities. There is a broad agreement that *H. axyridis* is an unparalleled top predator as it is predominantly a strong asymmetrical intraguild predator of other guild members (Sato et al., 2005; Cottrell, 2007; Ware et al., 2008b; Roy et al., 2008b) and as such can dominate in aggressive intraguild interactions and lead to a decline in guild diversity. In fact, several studies have stressed the functional traits that make *H. axyridis* a strong invader, among them, its aggressiveness (as an intraguild predator), polyphagy, voracity, fecundity and the fact that it is a less habitat and niche-specific coccinellid than native species. Key aphid mortality factors involving parasitoids and predators demonstrate that natural enemy diversity is necessary for resilient aphid suppression in agro-ecosystems (Straub et al., 2008). The decline recorded in natural enemy diversity following to *H. axyridis* invasion seems to be compensating by the high predation rate of this ladybird on the pest aphid for the declining of other natural enemies (Gardiner et al., 2007). However, its effectiveness as generalist predators in biological control may be reduced if increased availability of alternative prey causes individual predators to decrease their consumption of the target species. Pest management strategies aimed at maintaining beneficial insect diversity through natural and managed habitat manipulation (the diversification of our agricultural landscapes) could help counter declines particularly in native predator diversity associated with the arrival of *H. axyridis* and improve as a consequence pest biocontrol (Pell, 2008). To achieve this we need robust research data to fill the gaps in knowledge identified in this paper and develop efficient strategies.

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