B A S E *Biotechnol. Agron. Soc. Environ.* 2012 **16**(4), 553-563 **Focus on:**

Habitat diversity of the Multicolored Asian ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in agricultural and arboreal ecosystems: a review

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The Multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas), native to Asia, is an invasive species in many European and American countries. Initially introduced as a biological control agent against aphids and coccids in greenhouses, this alien species rapidly invaded many habitats such as forests, meadows, wetlands, and agricultural crops. This paper reviews the habitats (forests, crops, herbs, gardens and orchards) where *H. axyridis* has been observed, either during insect samplings or as part of Integrated Pest Management (IPM) programs. Studies have referenced *H. axyridis* on 106 plant taxa (35 arboreal species, 21 crop species, 27 herbaceous species, 11 ornamental species, and 12 orchard species) and have identified 89 plant-prey relationships (34 arboreal species, 16 crop species, 13 herbaceous species, 10 ornamental species, and 16 orchard species) in different countries. *Harmonia axyridis* is more abundant in forest areas, principally on *Acer*, *Salix*, *Tilia* and *Quercus*, than in agroecosystems. Some plant species, such as *Urtica dioica* L., which surround crops, contain large numbers of *H. axyridis* and could constitute important reserves of this alien species in advance of aphid invasions into crops. This review highlights the polyphagy and eurytopic aspect of *H. axyridis*.
Keywords. Coccinellidae, biological control agents, habitats, integrated pest management, predatory insects, introduced species, invasive species, forests, agroecosystems, censuses.

Diversité des habitats de la coccinelle asiatique *Harmonia axyridis* Pallas (Coleoptera : Coccinellidae) au sein des différents écosystèmes agricoles et forestiers (synthèse bibliographique). La coccinelle asiatique, *Harmonia axyridis* (Pallas), originaire d'Asie, est une espèce invasive dans de nombreux pays européens et américains. Introduite comme agent de contrôle biologique afin de lutter contre les pucerons et les cochenilles dans les serres, cette espèce a rapidement envahi différents habitats tels que les forêts, les cultures agricoles, les prairies, les jardins et les vergers. Cet article présente une synthèse des habitats où *H. axyridis* a été observée lors d'inventaires et dans lesquels elle a été utilisée dans la gestion de lutte contre les ravageurs. Cent-six taxons de plantes sur lesquelles *H. axyridis* a été observée (35 espèces arborescentes, 21 espèces de culture, 27 espèces herbacées, 11 espèces ornementales et 12 espèces de verger) et 89 relations plantes-proies (34 espèces arborescentes, 16 espèces de culture, 13 espèces herbacées, 10 espèces ornementales et 16 espèces de verger) ont été dénombrés dans différents pays. *Harmonia axyridis* est plus abondante en milieu forestier et plus précisément sur *Acer*, *Salix*, *Tilia* et *Quercus* qu'en milieu agricole. Certaines espèces végétales, telles que l'ortie *Urtica dioica* L., présentes à proximité des habitats agricoles, contiennent de grandes quantités d'*H. axyridis* et peuvent donc servir de réserve de prédateurs avant les invasions de pucerons en grandes cultures. Cette synthèse bibliographique souligne la polyphagie et le comportement eurytopique de cette coccinelle exotique.
Mots-clés. Coccinellidae, agent de lutte biologique, habitat, agriculture, insecte prédateur, espèce envahissante, espèce introduite, forêt, agroécosystème, recensement.

1. INTRODUCTION

The Multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to south-east Asia, between Siberia and China (Chapin, 1965). This species has long been used as a biological control agent against aphids and coccids on both sides of the Atlantic Ocean. Since 1988, *H. axyridis* has become

established in at least 38 countries around the world: 9 in America, 26 in Europe and 3 in Africa (Brown et al., 2011).

In America, the first introduction of *H. axyridis* was conducted in California in 1916, but the first established populations were referenced 72 years later (Gordon, 1985; Chapin et al., 1991). In this area, *H. axyridis* has been commonly used for biological control in diverse crops such as pecans (Tedders et al., 1994), red pines (McClure, 1987), apple orchards (Brown et al., 1998), soybeans (Fox et al., 2004), sweet corn (Musser et al., 2003), alfalfa (Buntin et al., 1997; Colunga-Garcia et al., 1998), cotton (Wells et al., 2001), tobacco (Wells et al., 1999) and winter wheat (Colunga-Garcia et al., 1998). *Harmonia axyridis* was introduced into Europe in 1964 and has been commercialized as a biological control agent since 1982 (Iperti, 1991; Katsoyannos et al., 1997). Thanks to a rapid reproductive cycle allowing this beetle to achieve two or three generations per year, *H. axyridis* has become the dominant coccinellid in many ecosystems (Brown et al., 2008).

Harmonia axyridis has been released as a biocontrol agent into numerous crops, arboreal habitats, and orchards (**Tables 1** to **5**). These releases partly explain the rapid expansion of this alien ladybeetle, favored by its notable dispersal abilities (Koch et al., 2006).

This review will focus on the natural and semi-natural habitats of the multicolored Asian ladybeetle *H. axyridis* both inside and outside of its native range, and will highlight its associated plant species and prey species.

2. HABITATS OF *HARMONIA AXYRIDIS*

2.1. Arboreal habitats

In both native and invaded areas, arboreal habitats are commonly colonized by *H. axyridis* for growth and reproduction. The most common trees on which *H. axyridis* is observed are *Acer*, *Salix*, *Tilia*, *Quercus* and *Pinus* (LaMana et al., 1996; Osawa, 2000; Adriaens et al., 2008; Brown et al., 2008) (**Table 1**). In Oregon, this species represents 70% of the coccinellid community in forest stands, where it is often considered as a dominant generalist aphidophagous predator (LaMana et al., 1996). In western Europe, Adriaens et al. (2008) inventoried several habitats and found that *H. axyridis* was present on more than 100 plant species. In that study, 52% of *H. axyridis* observations were made on trees and 14% on shrubs. The plants on which *H. axyridis* was most frequently observed were *Acer*, *Salix*, *Tilia*, *Quercus*, *Betula*, *Pinus*, and *Crataegus*. In eastern Europe, the first detection of *H. axyridis* was recorded on the same arboreal species, including *Tilia*, *Quercus* and *Acer*, respectively infested by the following aphid species: *Eucallipterus tiliae* L. (Hemiptera: Aphididae), *Myzocallis walshii* Monell (Hemiptera: Aphididae) and *Drepanosiphum* sp. (Hemiptera: Aphididae) (Tomov et al., 2009) (**Table 1**).

The presence of forest ecosystems increases the occurrence of *H. axyridis* in the surrounding habitats such as agroecosystems (Gardiner et al., 2009). A consequence of a higher density of the species in landscapes in close proximity to forests is that predation on native species is higher than that observed in fields surrounded by other croplands (Gardiner et al., 2011).

Trees are not the only arboreal areas where *H. axyridis* are able to find food. In addition, *H. axyridis* has been observed on shrubs, feeding on *Tinocallis kahawaluokalani* Kirkaldy (Hemiptera: Aphididae) and has also been observed on crape myrtle, *Lagerstroemia indica* L. (de Almeida et al., 2002).

Most of these studies have reported observations of *H. axyridis* mainly in arboreal habitats and in high density. Two reasons may explain the occurrence of this alien coccinellid in arboreal habitats: first, the arboreal taxa cited are affected by high aphid populations in spring and are thus attractive to the coccinellid; second, these arboreal taxa are the most popular taxa in Europe. Further information on studies concerning

Table 1. List of arboreal species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis — Liste des espèces arborées sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis.

Plant species	Prey species	References
Abies procera Rehder	*Cinara* sp.	LaMana et al., 1996
Acacia sp.	Cicadellidae	Saini, 2004
Acer negundo L.	*Periphyllus negundinis* (Thomas)	Koch et al., 2003
Acer pseudoplatanus L.	*Drepanosiphum* sp.	Tomov et al., 2009
Acer saccharum Marsh	*Drepanaphis idahoensis* Smith & Dilley *Drepanosiphum platanoides* Schrank *Periphyllus testudinaceae* Fernie	LaMana et al., 1996

Table 1 (continued). List of arboreal species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis* — *Liste des espèces arborées sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis.

Plant species	Prey species	References
Acer sp.		San Martin, 2003; Adriaens et al., 2008; Brown et al., 2008
Alnus spp.		Adriaens et al., 2008
Betula pendula L.	*Callipterinella calipterus* Hartig *Euceraphis betulae* Kalterbach	LaMana et al., 1996
Betula sp.		Adriaens et al., 2008
Corylus spp.		Adriaens et al., 2008
Crataegus sp.		Adriaens et al., 2008
Fagus sylvatica L.	*Phyllaphis fagi* L.	LaMana et al., 1996
Juniperus sp.	*Cinara juniperi* De Geer	Saini, 2004
Lafoensia pacari L.	Psyllidae	Martins et al., 2009
Liriodendron tulipifera L.	*Illinoia liriodendri* Monell	LaMana et al., 1996
Magnolia macrophylla Michaux		Tedders et al., 1994
Myrciaria cauliflora Mart. O. Berg	Curculionidae	Martins et al., 2009
Nicotiana tabacum L.	*Myzus nicotianae* Blackman	Wells et al., 1999
Nicotiana tabacum L.	*Helicoverpa armigera* Hübner *Spodoptera exigua* Hübner	Knutson et al., 1996
Picea spp.		Adriaens et al., 2008
Pinus resinosa Aiton	*Matsucoccus resinosae* Bean & Goodwin	McClure, 1987
Pinus sp.		San Martin, 2003; Adriaens et al., 2008
Pinus sp.	*Cinara atlantica* Wilson *Cinara pinovora* Wilson	de Almeida et al., 2002; Martins et al., 2009
Pinus sp.	*Essigella californica* Essig	Martins et al., 2009
Pinus sylvestris L.		Brown et al., 2008
Pinus taeda L.	*Eulachnus agilis* (Kaltenbach)	Tedders et al., 1994
Podocarpus sp.	*Neophyllaphis podocarpi* Takahashi	Tedders et al., 1994
Podocarpus sp.	*Neophyllaphis podocarpini* Carrilo	Martins et al., 2009
Populus sp.		Colunga-Garcia et al., 1998
Quercus rubra L.	*Myzocallis occultus* Richards	LaMana et al., 1996
Quercus rubra L.	*Myzocallis walshii* Monell	Tomov et al., 2009
Quercus sp.		Adriaens et al., 2008
Salix koriyanagi Kimura	*Chaitophorus horii horii* Takahashi	Osawa, 2000
Salix sieboldiana Bi.	*Aphis farinosa yanagicola* Matsumura *Tuberolachnus salignus* Gmellin	Osawa, 2000
Salix sp.	*Tuberolachnus salignus* Gmellin	LaMana et al., 1996
Salix sp.		Adriaens et al., 2008
Sambucus sieboldiana (Miq.)	*Aulacorthum magnoliae* Essig & Kuwana	Osawa, 2000
Tilia americana L.	*Eucallipterus tiliae* L.	LaMana et al., 1996
Tilia cordata Mill.	*Eucallipterus tiliae* L.	Tomov et al., 2009
Tilia sp.		San Martin, 2003; Adriaens et al., 2008; Brown et al., 2008
Tipuana tipu (Benth.) Kuntze	Psyllidae	Martins et al., 2009

H. axyridis in arboreal ecosystems can be seen in **table 1**. Thirty-five plant species and 34 plant-prey-predator relationships have been observed on diverse continents.

2.2. Agroecosystems

Agroecosystems may be infested by large quantities of prey and so can constitute habitats where ladybeetles are able to thrive and reach their adult stage. Nevertheless, in these particular ecosystems, the numbers of the most abundant coccinellid species are generally low (three or four dominant species) (Hodek et al., 1996). The composition of the aphidophagous community differs from one crop to another and is influenced by several abiotic factors, such as insolation and humidity (Honěk, 1985) and by biotic factors including the quantity and quality of host plants (Alhmedi et al., 2009), aphid density and diversity (Wright et al., 1980; Honěk, 1982; Thalji, 2006) and adjacent habitats (Colignon et al., 2000; Alhmedi et al., 2009).

Many studies highlight the dominance of *H. axyridis* in crop areas, *e.g.*: in Minnesota, 10 years after its initial detection in 1994 (Koch et al., 2003), *H. axyridis* rapidly became the most abundant generalist predator in corn, reaching 77.4% of Coccinellidae on the crop (Koch et al., 2006). In other cases, *H. axyridis* can quickly become the dominant species, as was observed in Michigan crops (alfalfa, soybean, corn and winter wheat), where four years after its arrival, this ladybeetle became dominant, with its proportions varying from 2.8% to 32.3% between 1994 and 1998 on all inventoried crops (Colunga-Garcia et al., 1998). However, some reports claim contrary conclusions. Nault et al. (2003) showed that three years after the arrival of *H. axyridis* in North Carolina agroecosystems, the most abundant species were not *H. axyridis* but *Coccinella septempunctata* L., *Coleomegilla maculata* De Geer and *Hippodamia convergens* Guérin-Méneville. In this area, *H. axyridis* colonized wheat, corn, and potato but reproduced only in wheat and potato (Kidd et al., 1995; Nault et al., 2003). In tobacco plants in Georgia, during 1997 and 1998 (15 years after initial release), *H. axyridis* was dominated by *H. convergens* and *C. septempunctata* (Wells et al., 1999). Finally, in alfalfa in Japan, adult and larval proportions of *H. axyridis* were found to respectively form 24.6% and 15.5% of coccinellids, figures lower than those of *C. septempunctata* and *Propylea japonica* (Thunberg) (Takahashi et al., 1984).

Variations in coccinellid dominance from year to year or between crops are dependent on multiple factors, but these variations are complex and misunderstood. For example, in agricultural habitats, population densities can be influenced by margin strips of herb species situated in close proximity. Nettle, *Urtica dioica* L., is known to be a plant species hosting many *H. axyridis* (Adriaens et al., 2008); the presence of nettle among margin field crops (wheat, green pea) therefore significantly increases the density of *H. axyridis* (Alhmedi et al., 2007) in these crops. These surrounding areas (nettle, forest) may provide a population of *H. axyridis* before aphid invasion in the adjacent field crops. The prey species is also an important factor determining the abundance and reproduction rate of *H. axyridis*. Evans et al. (2005) highlighted that in alfalfa, *H. axyridis* is an efficient predator, consuming both pea aphids *Acyrthosiphon pisum* Scop. (Hemiptera: Aphididae) and larvae of alfalfa weevils *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae), but that the consumption rates of aphids were greater than those for the weevil. Moreover, when alfalfa weevil is the available food source, *H. axyridis* does not reproduce, and both larval survival and development of *H. axyridis* are low (Evans et al., 2005). A second example highlights the problem of prey quality: *Uroleucon nigrotuberculatum* (Olive) (Hemiptera: Aphididae) on *Solidago canadensis* L. represent unsuitable prey for *H. axyridis* during its life cycle (Kamo et al., 2011). These prey species are considered by Hodek et al. (1996) to be "acceptable but inadequate prey" for *H. axyridis*.

At the beginning of the 1990s, LaMana et al. (1996) highlighted that *H. axyridis* was more abundant in arboreal habitats than in agricultural areas. Their results showed that only 4% of *H. axyridis* were observed in agroecosystems such as alfalfa *Medicago sativa* L., clover *Trifolium* sp. L. and peppermint *Mentha piperita* L. In these ecosystems, *H. axyridis* was observed in association with 17 aphid species on 17 host plants. While *H. axyridis* has been more observed in arboreal habitats, it can still thrive and dominate the aphidophagous guild in agroecosystems. In agricultural systems of eastern Canada (pome fruit, grape, field corn, sweet corn, sweet pepper, lettuce, and soybean), *H. axyridis* was clearly one of the dominant coccinellid species from 1999 to 2003 (Lucas et al., 2007). Unlike in American and Asian studies, *H. axyridis* presented in Belgium high population levels only one year after its original detection in potato fields (2004-2005) and was able to complete its larval development even with low aphid population, or with no aphids at all (Jansen et al., 2008). In this invaded area, *H. axyridis* was found to be one of the most abundant coccinellids along with *C. septempunctata* and *Propylea quatuordecimpunctata* L. (Jansen et al., 2008).

One of the most important pests of American soybean is the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae). In 2000, *H. axyridis* was found to constitute more than 25% of the aphidophagous species in this crop; other such species present included *Orius insidiosus* (Says)

(Hemiptera: Anthocoridae) and *Leucopis* spp. (Diptera: Chamaemyiidae), which are able to control *A. glycines* (Fox et al., 2004). *Harmonia axyridis* was found to cause a reduction in aphid populations by 21-56% in the early season and by 54-95% in midseason (Landis et al., 2004). Five years later, *H. axyridis* was found to occur at levels of 45 to 62% of the total coccinellid community (Gardiner et al., 2009).

Despite the fact that *H. axyridis* is an arboreal species, a high diversity of crops (21) is subject to invasion by this coccinellid (**Table 2**). *Harmonia axyridis* invades selected crops according to the aphid species present and to the microclimate inside the field. The high density and high voracity of *H. axyridis* make it a highly efficient beneficial species. It would be interesting to use *H. axyridis* as part of a pest control approach (*e.g.* through a push-pull strategy) in organic crops to control aphid populations.

2.3. Herbs, domestic and ornamental gardens

Harmonia axyridis also occurs in herbaceous habitats such as heathland, meadows, and wetlands (Adriaens et al., 2008). Among these habitats, *H. axyridis* has been most frequently observed on *U. dioica* (Adriaens et al., 2008), but also on *Bidens pilosa* L. (Martins et al., 2009), *Phragmites* spp. (Adriaens et al., 2008), *Artemisia vulgaris* L. (Agarwala et al., 2003), and *Typha angustifolia* L. (Osawa, 2000). The alien species has also been observed in urban habitats, such as in domestic gardens, on *Hibiscus rosa sinensis* L. (Martins et al., 2009), *Lagerstroemia indica* L. (Chapin et al., 1991), and *Rosa* sp. (de Almeida et al., 2002).

Harmonia axyridis can be used as a biocontrol agent in gardens, but it is not common *e.g.*: *H. axyridis* can be used to control *Chaetosiphon fragaefolii* (Cockerell) (Hemiptera: Aphididae) on strawberry (Sun et al., 1996) and *Macrosiphum rosae* L. (Hemiptera: Aphididae) on roses (Finlayson et al., 2010). *Harmonia axyridis* can also be used to control pests on ornamental plant species *e.g.*: on greenhouse roses (*Rosa hybrida* L.), the aphid, *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae), can be controlled by *H. axyridis* and a wasp, *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae). *Harmonia axyridis* can be used to complement aphid biocontrol, without disrupting control through intraguild predation (Snyder et al., 2004).

The presence of *H. axyridis* in gardens is more anecdotal. The use of ladybeetles as beneficial species needs to be focused on native species such as *A. bipunctata*. Further examples of *H. axyridis* habitats, including herbs and ornamental species, are presented in **tables 3** and **4**. *Harmonia axyridis* individuals have been observed on herbs and ornamental habitats containing respectively 27 and 11 plant taxa.

2.4. Orchards

Before winter, coccinellids also thrive in orchards, for example, on apples (*Malus* spp.) and citrus (*Citrus* spp.). In these habitats, they accumulate fat content and glycogen reserves (polyol myo-inositol) in response to a decline in food resources (Hodek, 1986; Watanabe, 2002; Hodek, 2011). A consequence of insects feeding on apples and pears is that it causes blemishing of the fruits and reduces the value of the crop (Majerus et al., 2006). In Virginian orchards, *H. axyridis* has become the most abundant coccinellid species (representing between 40.9% and 90.7% of those species) and it sometimes replaces the dominant native species (Brown, 2003). In citrus orchards (Florida), *H. axyridis* was also found to be the most abundant coccinellid species between 1997 and 2001. During this period, *H. axyridis* replaced *Cycloneda sanguine* (L.), which had been the numerically dominant species before 1997 (Michaud, 2002). In citrus, *H. axyridis* has also been tested successfully for the control of the root weevil *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae), a major pest in citrus orchards (Stuart et al., 2002). Similar results have been obtained with the citrus aphid, *Aphis spiraecola* Patch (Hemiptera: Aphididae) and with *Toxoptera citricida* (Kirkaldy) (Hemiptera: Aphididae) in Florida (Michaud, 2000). In apple orchards in West Virginia, *H. axyridis* has also provided good biological control of *A. spiraecola*. However, the use of this alien species as a biocontrol agent has displaced *C. septempunctata* (Brown et al., 1998). *Harmonia axyridis* has been used effectively many times in pecan orchards, *Carya illinoinensis* Wangenh., to control the pecan aphid complex comprising *Melanocallis caryaefolia* (Davis) (Hemiptera: Aphididae), *Monellia caryella* Fitch (Hemiptera: Aphididae) and *Monelliopsis pecanis* Bissell (Hemiptera: Aphididae) (Tedders et al., 1994; LaRock et al., 1996). In Georgia, *H. axyridis* was released in pecan with legume cover between 1978 and 1981. Nine years after its release, the species had spread and was recorded at a distance of 174 km from the release point. In 1994, *H. axyridis* was found to be the dominant species at the release site, comprising 54% of coccinellids (Tedders et al., 1994). In Argentina, *H. axyridis* was also found to be the most abundant coccinellid in *Carya* sp., with its proportion among coccinellids increasing from 51% in 2001 to 74% in 2003 (Saini, 2004).

The presence of *H. axyridis* in orchard crops is more controversial than in other crops. While *H. axyridis* acts as efficient biocontrol agent, in the fall season, the species causes damage to fruits. The solution might be to catch *H. axyridis* adults once the presence of aphids has reached its peak, in order to avoid yield loss through fruit damage. For more examples, see **table 5** for a list

Table 2. List of crop species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis — Liste des cultures agricoles sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis.

Plant species	Prey species	References
Allium schoenoprasum L.	*Neotoxoptera formosana* Takahashi	Martins et al., 2009
Apium graveolens L.		Lucas et al., 2007
Brassica napus L.		Lucas et al., 2007
Brassica oleracea L.		de Almeida et al., 2002
Brassica oleracea L. var. *italica*	*Myzus persicae* Sulzer	Martins et al., 2009
Brassica oleracea L. var. *italica*	*Lipaphis erysimi* Kaltenbach	Martins et al., 2009
Brassica oleraceae L. var. *capitata*	*Brevicoryne brassicae* L.	Martins et al., 2009
Brassica oleraceae L. var. *leucocephala*	*Brevicoryne brassicae* L.	Martins et al., 2009
Cucurbita sp.		Koch et al., 2004
Fragaria sp.	*Chaetosiphon fragaefolii* Cockerell	Sun et al., 1996
Glycine max L.		Colunga-Garcia et al., 1998; Koch et al., 2004; Saini, 2004
Glycine max L.	*Pseudoplusia includens* Walker	Knutson et al., 1996
Glycine max L.	*Aphis glycines* Matsumura	Fox et al., 2004; Landis et al., 2004; Gardiner et al., 2007; Gardiner et al., 2009; Xue et al., 2012; Rutledge CE, personal communication
Gossypium hirsutum L.	*Aphis gossypii* Glover *Helicoverpa zea* Boddie	Knutson et al., 1996
Gossypium hirsutum L.		Wells et al., 2001
Hordeum vulgare L.		Colunga-Garcia et al., 1998
Humulus lupulus L.		LaMana et al., 1996
Lactuca sativa L.	*Uroleucon ambrosiae* Thomas *Uroleucom sonchi* L.	Martins et al., 2009
Lolium perenne L.		Agarwala et al., 2003
Medicago sativa L.		Takahashi et al., 1984; Buntin et al., 1997
Medicago sativa L.	*Acyrtosiphum pisum* Scop.	Saini, 2004; Evans et al., 2005
Medicago sativa L.	*Hypera postica* Gyllenhal	Evans et al., 2005
Medicago sativa L.		LaMana et al., 1996; Colunga-Garcia et al., 1998
Mentha piperita L.		LaMana et al., 1996
Pisum sativum L.		Alhmedi et al., 2007
Solanum tuberosum L.		Nault et al., 2003; Alyokhin et al., 2004; Jansen et al., 2008
Solanum tuberosum L.	*Macrosiphum euphorbiae* Thomas *Myzus persicae* Sulzer	Finlayson et al., 2010
Triticum aestivum L.		Nault et al., 2003; Alhmedi et al., 2007
Zea mays L.		Lucas et al., 2007
Zea mays L.		Colunga-Garcia et al., 1998; Musser et al., 2003; Nault et al., 2003

of studies of *H. axyridis* in orchard ecosystems. Twelve plant species and 16 plant-prey relationships have been observed on diverse continents.

3. CONCLUSION

This review focused on the diversity of natural and semi-natural habitats where *H. axyridis* has been observed or introduced as a biocontrol agent. The following topics were considered: evaluation of the efficiency of *H. axyridis* for biological control, the impact of *H. axyridis* on native species, its occurrence among aphidophagous species, and the evolution of its invasion. Sixty-six studies have referenced *H. axyridis* on 106 plant taxa (35 arboreal species, 21 crop species, 27 herbaceous species, 11 ornamental species, and 12 orchard species) and have identified 89 plant-prey relationships (34 arboreal species, 16 crop species, 13 herbaceous species, 10 ornamental species, and 16 orchard species) in different countries. This diversity of plants and habitats where *H. axyridis* has

Table 3. List of herbaceous species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis — Liste des espèces herbacées sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis.

Plant species	Prey species	References
Achillea millefolium L.		Lucas et al., 2007
Artemisia vulgaris L.		Agarwala et al., 2003
Baccharis sp.	*Aphis spiraecola* Patch; Coccidae; *Aphis coreopsidis* Thomas	Martins et al., 2009
Bidens pilosa L.	*Uroleucom sonchi* L.	Martins et al., 2009
Bidens pilosa L.	*Hyperomyzus lactucae* L.	Martins et al., 2009
Bidens sulphurea Cav. Sch. Bip.	*Macrosiphoniella yomogifoliae* Shinji	Martins et al., 2009
Capsicum annuum var. *angulosum*	*Aphis gossypii* Glover *Myzus persicae* (Sulzer)	Iguchi et al., 2012
Capsicum sp.		Lucas et al., 2007
Chrysanthemum leucanthemum L.	*Brachycaudus helichrysi* Kaltenbach	Martins et al., 2009
Cirsium arvense L.		LaMana et al., 1996
Cirsium spp.		Adriaens et al., 2008
Dipsacus sylvestris Huds		LaMana et al., 1996
Duranta repens L.	Coccidae	Martins et al., 2009
Echinacea purpurea (L.) Moench		Lucas et al., 2007
Foeniculum vulgare Miller	*Aphis fabae* Scopoli	Martins et al., 2009
Helianthus annuus L.	*Aphis fabae* Scopoli	Martins et al., 2009
Hipochoeris radicata L.	*Uroleucon ambrosiae* Thomas	Martins et al., 2009
Hypericum perforatum L.		Lucas et al., 2007
Nasturtium sp.		LaMana et al., 1996
Phragmites spp.		Adriaens et al., 2008
Rubus sp.		Koch et al., 2004; Lucas et al., 2007
Schefflera arboricola (Hayata) Merr.	*Aphis* sp.	Martins et al., 2009
Sonchus oleraceus L.	*Uroleucom sonchi* L.	Martins et al., 2009
Spartium junceum L.	*Aphis craccivora* Koch	Martins et al., 2009
Tanacetum spp.		Adriaens et al., 2008
Typha angustifolia L.	*Schizaphis acori* Theobald	Osawa, 2000
Urtica dioca L.		Adriaens et al., 2008
Valeriana officinalis L.		Lucas et al., 2007

Table 4. List of ornamental species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis — Liste des espèces ornementales sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis

Plant species	Prey species	References
Hibiscus rosa sinensis L.	*Toxoptera* sp.; *Aphis* sp.	Martins et al., 2009
Hibiscus sp.		Agarwala et al., 2003
Lagerstroemia indica L.	*Tinocallis kahawaluokalani* Kirkaldy	de Almeida et al., 2002
Lagerstroemia indica L.	*Toxoptera aurantii* Boyer de Fonscolombe	Martins et al., 2009
Lagerstroemia sp.	*Tinocallis kahawaluokalani* Kirkaldy	Chapin et al., 1991
Leucaena leucocephala (Lam.) de Wit	*Heteropsylla cubana* Crawford	de Almeida et al., 2002
Rosa multiflora Thumb.	*Macrosiphum pseudorosae* Patch	Finlayson et al., 2010
Rosa sp.		LaMana et al., 1996; de Almeida et al., 2002
Rosa sp.	*Macrosiphum rosae* L.	Saini, 2004; Martins et al., 2009
Spirea blumei L.	*Aphis spiraecola* Patch	Osawa, 2000
Spirea douglasii Hook		LaMana et al., 1996
Spirea thunbergii Sieb.	*Aphis spiraecola* Patch	Osawa, 2000
Tabebuia sp.	Psyllidae	Martins et al., 2009

Table 5. List of orchard species where *Harmonia axyridis* was observed. The column "prey species" contains phytophagous species observed with *H. axyridis — Liste des espèces de verger sur lesquelles* Harmonia axyridis *a été observée. La colonne «* Prey species *» contient les espèces phytophages observées en même temps qu'*H. axyridis.

Plant species	Prey species	References
Carya illinoinensis (Wangenh.) K.Koch	*Melanocallis caryaefolia* Davis	Tedders et al., 1994; LaRock et al., 1996
Carya illinoinensis (Wangenh.) K.Koch	*Monellia caryella* Fitch	Tedders et al, 1994; LaRock et al., 1996; Saini, 2004
Carya illinoinensis (Wangenh.) K.Koch	*Monelliopsis pecanis* Bissell	Tedders et al., 1994; LaRock et al., 1996
Citrus aurantiifolia (Christm.) Swingle		de Almeida et al., 2002
Citrus limon L.	*Toxoptera citricida* Kirkaldy	Martins et al., 2009
Citrus reticulata L.	Aphididae	Martins et al., 2009
Citrus sinensis L.	Aphididae	Martins et al., 2009
Citrus spp.	*Diaprepes abbreviatus* L.	Stuart et al., 2002
Citrus spp.	*Toxoptera aurantii* Boyer de Fonscolombe	Katsoyannos et al., 1997
Citrus spp.	*Aphis spiraecola* Patch	Katsoyannos et al., 1997; Michaud, 2000
Citrus spp.	*Aphis gossypii* Glover	Katsoyannos et al., 1997
Malus domesticas Borkh.		Brown, 2003
Malus sp.	*Aphis spiraecola* Patch	Chapin et al., 1991; Brown et al., 1998; Brown, 2011
Malus sp.		Koch et al., 2004; Kovach, 2004; Lucas et al., 2007
Malus sp.	*Aphis pomi* DeGeer	Coderre et al., 1995
Prunus persica (L.) Batsch	*Hyalopterus pruni* Geoffroy *Myzus varians* Davidson Passerini	Osawa, 2000
Prunus sp.	*Hyalopterus pruni* Geoffroy	LaMana et al., 1996
Prunus sp.		Adriaens et al., 2008; Burgio et al., 2008
Psidium guajava L.	*Triozoida* sp.	Martins et al., 2009
Vitis sp.		Koch et al., 2004; Lucas et al., 2007

been observed has been used to justify the classification of this alien species as an eurytopic species. The high abundance of *H. axyridis* within the aphidophagous guild in the majority of the habitats where it is found has had an impact on native species. This highlights the ecological problems provoked by *H. axyridis*: its presence causes a decline in biodiversity and the displacement of native species. *Harmonia axyridis* is one of the most abundant species in all natural and semi-natural ecosystems. Its ability to spread across ecosystems raises the interesting proposition of using individuals of the species in nature to control aphid populations. A push-pull strategy could be implemented to control alien species populations in order to decrease their impact on native aphidophagous species.

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