E F
F E *Entomologie Faunistique – Faunistic Entomology* 2015 **68**, 3-15

Aphid species and associated natural enemies in field crops: what about the invasive ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae)?

Axel Vandereycken*, Delphine Durieux, Emilie Joie, Fréderic Francis, Eric Haubruge, François J. Verheggen

University of Liege, Gembloux Agro-Bio Tech, Entomologie fonctionnelle et évolutive, Passage des Déportés 2, B-5030 Gembloux (Belgium).

* E-mail: a.vandereycken@ulg.ac.be, +32 81 62 22 81

Article reçu le 6 mars 2014, accepté le 6 juin 2014.

Following the introduction in the 80's of the invasive coccinellid species *Harmonia axyridis* (Pallas) in Europe, several studies have begun to focus on the interactions with other aphid predator species. In this study, aphids and associated predators were sampled to determine their relative abundance in four agricultural crops (broad bean, corn, potato, and wheat) in Belgium during 2010 and 2011. The Moericke trap was used to quantify the mean number of aphids and aphid predators from May to September in both years. A total of 28 aphid species and 21 aphidophagous species were observed. In both years, *H. axyridis* was among the most abundant aphidophagous predators in all four crops, and was the second most abundant coccinellid species after *Coccinella septempunctata* L. The community of aphidophagous species was similar across all four inventoried crops. However, the highest population densities of this alien species were recorded in broad bean and potato crops, which also hosted the highest aphid population densities. In conclusion, this study demonstrates that the communities of aphid predators are highly diversified in the agroecosystems, despite the high occurrence of *H. axyridis*, an introduced predator that has become well established in this environment.
Keywords: *Harmonia axyridis*, Coccinellidae, agrosystems, alien species, aphid predator, culture, invasive.

Depuis l'introduction de la coccinelle asiatique *Harmonia axyridis* (Pallas) en Europe dans les années 80, plusieurs études se sont concentrées sur les interactions qu'elle pouvait avoir avec les autres espèces de prédateurs de pucerons. Dans cette étude, les pucerons et les leurs ennemis naturels ont été inventoriés afin de déterminer leur abondance relative au sein de quatre cultures agricoles (la fève, le maïs, la pomme de terre et le blé) en 2010 et 2011. Des pièges Moericke ont été utilisés pour échantillonner les prédateurs et les pucerons de mai à septembre. 28 espèces de pucerons et 21 espèces d'aphidiphages ont été observées. *H. axyridis* est la deuxième espèce la plus abondante après la coccinelle à sept points *Coccinella septempunctata* L. Les plus fortes densités de population de *H. axyridis* ont été observé dans la fève et la pomme de terre. Les densités de populations de pucerons y étaient également élevées. La communauté d'aphidiphages présente les mêmes espèces au sein des quatre cultures inventoriées. En conclusion, cette étude démontre que les communautés de prédateurs de pucerons sont très diversifiées dans les agroécosystèmes, aussi bien dans les cultures où *H. axyridis* est abondante que dans celles où elle n'est que faiblement présente.
Mots-clés: *Harmonia axyridis,* Coccinellidae, agrosystèmes, espèces exotiques, prédateur de puceron, culture, invasive.

1 INTRODUCTION

Within the aphid predators community, the coccinellid community in Europe, present in agroecosystems is generally undiversified and is composed of three or four dominant species, including *Coccinella septempunctata* L. (Hodek & Honěk, 1996). In cereal crops (Honěk, 1983), corn (Radwan & Lovei, 1983) and potato (Clayhills & Markkula, 1974) three coccinellid species are abundant: *C. septempunctata*, *Propylea quatuordecimpunctata* L. and *C. quinquepunctata* L. The hoverfly *Epysirphus balteatus* De Geer (Gilbert, 2005) and the lacewing *Chrysoperla carnea* Stephens (Bozsik *et al.*, 2002) are two other aphid predators species also abundantly observed in agroecosystems.

An alien species that is deliberately or accidentally introduced to a given site may compete with and potentially displace indigenous species and thereby threaten biodiversity. The introduction of the seven-spotted ladybird *C. septempunctata* in the United States has induced a decrease of native coccinellids populations such as *Adalia bipunctata* (L. 1758) and *C. transversoguttata richardsoni* Brown 1962 in agricultural crops in eastern South Dakota (Elliott *et al.*, 1996). The displacement of an invasive species on native communities is based on the evaluation of both direct (competition for food and intraguild predation) and indirect (apparent competition) interactions; however, this requirement is often difficult to be tested under field conditions (Holt & Lawton, 1994). Because alien species exhibit habitat selectivity, such surveys should be realized in representative habitats. For instance, the habitat selectivity of a specific species may be identified through the use of graphical food webs (Bersier *et al.*, 2002). These illustrations have been widely used to identify links between species from different trophic levels (Cohen, 1978; Rott & Godfray, 2000), such as parasitoids and their hosts (e.g., Gagic *et al.*, 2012) or leafminers and their hosts (Morris *et al.*, 2005). A quantitative food web contains sets of binary links between trophic species, in addition to information about species abundance (Alhmedi *et al.*, 2011).

The multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), has been introduced from 80's to many European countries, including Belgium, to control aphid and coccid populations (Gordon, 1985; Adriaens *et al.*, 2008; Brown *et al.*, 2008; Durieux *et al.*, 2012). Following the introduction in 1997 of this species to Belgium, the occupancy of *H. axyridis* has been reported with an average rate of increase of 189% between 2002 and 2006 (Adriaens *et al.*, 2008).

In Belgian urban areas, prior to the invasion of *H. axyridis*, *A. bipunctata* was the dominant ladybird on *Tilia* sp. and *Acer* sp. and was co-dominant with the native congeneric ladybird *H. quadripunctata* (Pontoppidan 1763) (Coleoptera: Coccinellidae) on *Pinus* sp. Only two years after its establishment, *H. axyridis* quickly became the predominant ladybird specie (Ottart, 2005). In agricultural landscape the situation in other countries seems to be similar with this exotic species as a dominant or co-dominant coccinellids (Tedders & Schaefer, 1994; Brown, 2003; Lucas *et al.*, 2007)

This study aimed to compare the communities of aphids and associated insect predator species in four different crops (i.e., wheat, broad bean, corn, and potato) in 2010 and 2011, with a primary focus on *H. axyridis*, an alien coccinellid species. The diversity and abundance of aphids and associated predator species were used to determine if *H. axyridis*, dominates in Walloon agricultural landscape the native aphidophagous species, 10 years after its first observation.

2 MATERIALS AND METHODS

2.1 Study site

The study was conducted during 2010 and 2011 in Hesbaye (50°34' N; 5°15' E), which is an intensive agricultural production area in the southern region of Belgium. The climate in this area is temperate, with an average annual temperature of 10.5 °C (min. 3 °C, max 18 °C) during the two study years. The mean annual rainfall was 850 mm during the two study years, and was uniformly distributed across both years. Four crops were selected for their agronomic importance; namely, wheat, *Triticum aestivum* (L. 1753); corn, *Zea mays* (L. 1753); potato, *Solanum tuberosum* (L. 1753); and broad bean, *Vicia faba* (L. 1753) Three fields (each surface area >1 ha) were selected for each crop, and inventoried. All 12 fields were surrounded by conventional crops (intensive farming area).

2.2 Sampling methods

Wheat and broad bean fields were sampled weekly from mid-May to late August, while the

sampling period for corn and potato extended from mid-May to late September. Three Moericke traps spaced 50 m apart were set per field (yellow water traps, 30 cm diameter) to assess the diversity and abundance of aphids and their predators. Mean species densities are expressed as the numbers of specimens per trap. Hoverfly and ladybird adults were identified using the keys of Verlinden (1994) and Baugnée & Branquart (2000), respectively. Chrysopids were determined with the key of San Martin (2004). Aphid species (all development stages) were identified using two keys developed by Leclant (1999a,b).

2.3 Statistical analysis

The mean number of aphid and aphidophagous species was calculated per crop per year. Insect abundance data was calculated per trap per week. Aphid abundance was compared among crops, and analyzed by Analysis of Variance (ANOVA: General Linear Model), using crop type (q = 4) and month (n = 5) as factors. The factor "month" was used to reduce any natural variability of insect populations across the sampling period. ANOVA was also used to compare abundance between years (q = 2), also with months (n = 5) being used as factors. Within crops, predator abundance was compared by the Least Square Difference (LSD; $\alpha = 0.05$). Data were $\log_{10}(x+1)$ transformed before performing the statistical analyses on Minitab® 15.1.30.0 (State College, Pennsylvania, USA).

2.4 Graphical representation

Graphical results were presented in earlier works on the natural enemy communities of aphids (Muller *et al.*, 1999; Alhmedi *et al.*, 2011). Aphid species (**Figure 1**) and natural enemies (**Figure 2**) were organized as a series of bars in an upper register, with the width of each bar being proportional to the relative abundance of each species. In **Figure 1**, crops were arranged as a series of bars in a lower register, with the width of each bar being equal. In **Figure 2**, aphid species were organized as a series of bars in a lower register with the width of each bar being proportional to the relative abundance of all aphids species caught in each crop. Natural enemies and crops were linked by triangular wedges, the relative widths of which represented the proportion of the natural enemies observed for each crop type.

3 RESULTS

Aphid species diversity

Twenty-eight aphid species were observed during two years on the four studied crops. In 2010, 16, 15, 17 and 15 aphid species were observed in the broad bean crops, potato crops, wheat crop and in the corn crops respectively. Eleven aphid species were common to all four crops. In 2011 the number of aphid species was higher than in 2010 with 20, 19, 17 and 17 species for the same crop respectively. In **Figure 1** the diversity of aphid species is observed by crops with their corresponding identities being provided in **Table 1**. The most abundant aphid species are *Metopolophium dirhodum* Walker, *Aphis fabae* Scopoli, *Acyrthosiphon pisum* Harris, *Cavariella aegopodii* Scopoli and *Macrosiphum euphorbiae* Thomas (**Figure 1**). Total aphid density varied between years ($F_{1,954} = 37.21$; $p < 0.001$) with four times more aphids in 2011 than in 2010. Aphids varied also among crops in 2011 with more aphids in wheat than in other crops (2010: $F_{3,468} = 1.02$; $p = 0.385$; 2011: $F_{3,463} = 11.02$; $p < 0.001$) (**Figure 1**).

Table 1: Predator and aphid species caught in broad bean, corn, wheat and potato crops during 2010 and 2011 (Code numbers represent the species shown in Figures 1-2).

Code	Aphid species	Code	Predator species
1	*Metopolophium dirhodum* Walker 1849	Coccinellidae	
2	*Sitobion avenae* Fabricius 1775	1	*Coccinella quinquepunctata* L. 1758
3	*Sitobion fragariae* Walker 1848	2	*Coccinella septempunctata* L. 1758
4	*Aphis fabae* Scopoli 1763	3	*Coccinella undecimpunctata* L. 1758
5	*Aphis craccivora* Koch 1854	4	*Harmonia axyridis* Pallas 1773
6	*Aphis nasturtii* Kaltenbach 1843	5	*Hippodamia undecimnotata* Schneider 1792
7	*Megoura viciae* Buckton 1876	6	*Hippodamia variegata* Goeze 1777
8	*Acyrthosiphon pisum* Harris 1776	7	*Propylea quatuordecimpunctata* L. 1758
9	*Myzus persicae* Sulzer 1776	Syrphidae	
10	*Rhopalosiphum padi* L. 1899	8	*Episyrphus balteatus* De Geer 1776
11	*Rhopalosiphum maidis* Fitch 1856	9	*Melanostoma mellinum* L. 1758
12	*Nasonovia ribisnigri* Mosley 1841	10	*Metasyrphus corollae* Fabricius 1794
13	*Rhopalosiphum insertum* Walker 1849	11	*Metasyrphus latifasciatus* Macquart 1829
14	*Hyperomyzus lactucae* L. 1758	12	*Metasyrphus luniger* Meigen 1822
15	*Capitophorus horni* Börner 1931	13	*Metasyrphus nitens* Zetterstedt 1843
16	*Cavariella pastinacea* L. 1758	14	*Parasyrphus macularis* Zetterstedt 1843
17	*Cavariella aegopodii* Scopoli 1763	15	*Platycheirus clypeatus* Meigen 1822
18	*Macrosiphum rosae* L. 1758	16	*Scaeva pyrastri* L. 1758
19	*Macrosiphum euphorbiae* Thomas 1878	17	*Sphaerophoria menthastri* L. 1758
20	*Aulacorthum solani* Kaltenbach 1843	18	*Sphaerophoria scripta* L. 1758
21	*Sarucallis kahawaluokalani* Kirkaldy 1907	19	*Syrphus ribesii* L. 1758
22	*Cinara* sp.	20	*Syrphus vitripennis* Meigen 1822
23	*Tetraneura* sp.	Chrysopidae	
24	*Metopolophium festucae* Theobald 1917	21	*Chrysoperla carnea* Stephens 1836
25	*Brevicoryne brassicae* L. 1758		
26	*Schizaphis graminum* Rondani 1852		
27	*Phyllaphis fagi* L. 1767		
28	*Phorodon humuli* Schrank 1801		

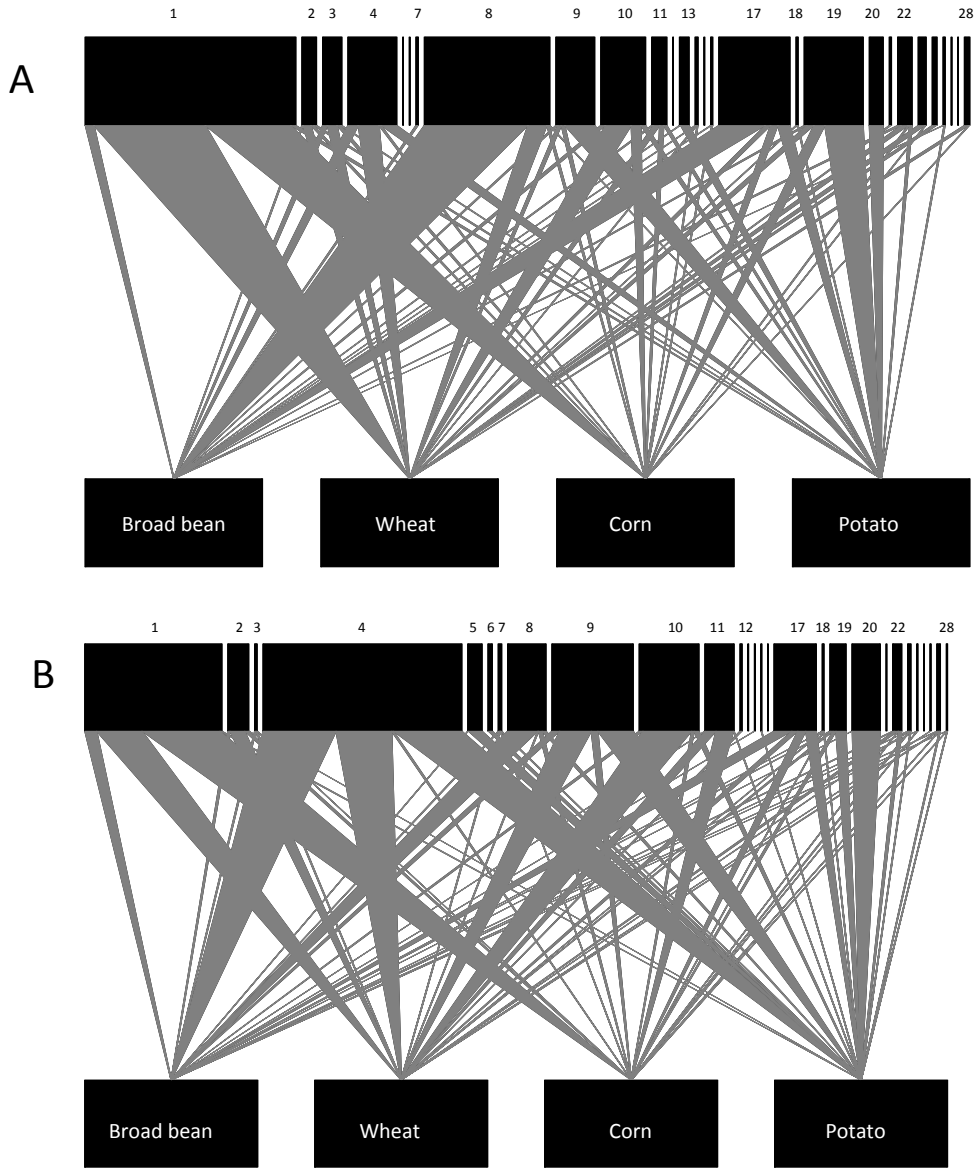

Figure 1: Graphical presentation of aphid abundance on broad bean, wheat, corn, and potato crops during 2010 (A) and 2011 (B). The top bars represent aphid abundance. The numbers refer to the species code in Table 1.

Aphid predator species diversity

We observed 21 aphid predator species in the four studied crops (**Tables 2-3**, **Figure 2**). The community of predator species differed among crops and between years in 2010 and 2011. In 2010, 12 species were observed in broad bean, wheat and corn and 11 species in potato. In 2011, 16, 14, 14 and 12 were observed in broad bean, wheat, corn and potato respectively. Of these 21 observed predators, 7 were coccinellid species, 13 were syrphid species, and one was a chrysopid species (**Tables 2-3**). Out of the 21 observed predators, 10 species were recorded in all four crops; namely, *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, *E. balteatus*, *M. mellinum*, *M. corollae*, *M. latifasciatus*, *S. menthastri, S. scripta*, and *C. carnea* (**Tables 2-3**). Five of these 10 species were abundant (more than 99% of the total observed individuals) on all four crops in both years; namely, *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, *E. balteatus*, and *C. carnea*.

Table 2: Mean number and standard error (SE) of aphidophagous species per trap per week during 2010. Species are sorted by family (Coccinellidae, Syrphidae, Chrysopidae).

	Mean number (SE) of aphidophagous species per trap per week during 2010							
	Broad bean		Wheat		Corn		Potato	
Coccinellidae								
Coccinella quinquepunctata	0.020	(0.014)	0		0		0	
Coccinella septempunctata	1.267	(0.248)	0.318	(0.062)	0.365	(0.089)	0.563	(0.099)
Coccinella undecimpunctata	0		0		0.007	(0.007)	0	
Harmonia axyridis	0.396	(0.087)	0.027	(0.016)	0.034	(0.015)	0.270	(0.054)
Hippodamia variegata	0.040	(0.024)	0		0		0.008	(0.008)
Propylea quatuordecimpunctata	0.178	(0.055)	0.109	(0.035)	0.081	(0.026)	0.063	(0.025)
Syrphidae								
Episyrphus balteatus	0.099	(0.033)	0.755	(0.359)	0.338	(0.087)	0.373	(0.177)
Melanostoma mellinum	0.020	(0.014)	0		0.007	(0.007)	0	
Metasyrphus corollae	0.010	(0.009)	0.055	(0.028)	0		0.016	(0.011)
Metasyrphus latifasciatus	0.030	(0.022)	0.064	(0.030)	0.007	(0.007)	0.008	(0.008)
Metasyrphus luniger	0		0		0		0.008	(0.008)
Metasyrphus nitens	0		0.009	(0.009)	0		0	
Parasyrphus macularis	0		0		0.007	(0.007)	0	
Scaeva pyrastri	0		0.073	(0.046)	0.007	(0.007)	0.024	(0.014)
Spaerophoria scripta	0.040	(0.019)	0.182	(0.058)	0.007	(0.007)	0.063	(0.025)
Sphaerophoria menthastri	0.020	(0.014)	0.073	(0.042)	0.014	(0.009)	0	
Syprhus ribesii	0		0.009	(0.009)	0		0	
Chrysopidae								
Chrysoperla carnea	0.188	(0.053)	0.127	(0.039)	0.047	(0.024)	0.167	(0.057)

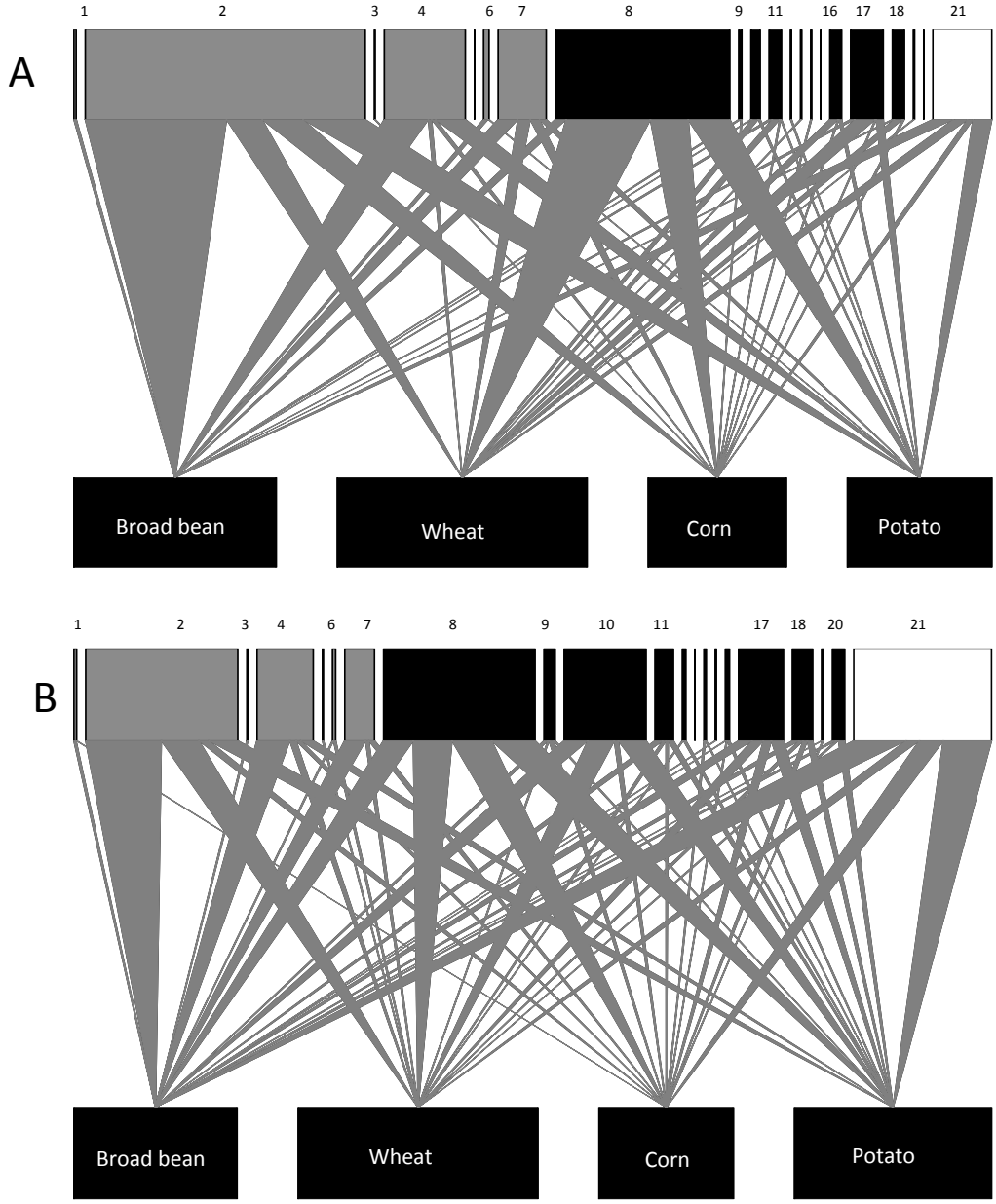

Figure 2: Graphical presentation of aphid predator abundance on broad bean, wheat, corn, and potato crops during 2010 (A) and 2011 (B). The top bars represent predator abundance. The numbers refer to the species code in Table 1. (Upper bars: grey = coccinellids; black = syrphids; white = chrysopids).

The density of the five most abundant species varied across the four crops (2010: $F_{3,2421} = 9.68$; $p < 0.001$; 2011: $F_{3,2391} = 14.06$; $p < 0.001$) (**Figure 3**) and between the two years ($F_{1,4810} = 7.45$; $p = 0.006$). In 2010, *C. septempunctata* was the most abundant species in broad bean, corn, and potato crops. In contrast, three species dominated the predator guild in wheat crops; namely, *E. balteatus, C. septempunctata*, and *C. carnea* (**Figure 3A**). In 2011, *C. septempunctata* and *C. carnea* were the most abundant species in broad bean crops, whereas *E. balteatus* dominated the wheat crops (**Figure 3B**). In corn, no difference in predator density was observed among the species of the predator guild (**Figure 3B**). *H. axyridis*, had higher densities in broad bean and in potato than the other crop during year (**Figure 3**). *Coccinella septempunctata* was in the main crop the most abundant ladybird (**Figure 3**).

Table 3: Mean number and standard error (SE) of aphidophagous species caught per trap per week during 2011. Species are ordered by family (Coccinellidae, Syrphidae, Chrysopidae).

	Mean number (SE) of aphidophagous species per trap per week during 2011							
	Broad bean		Wheat		Corn		Potato	
Coccinellidae								
Coccinella quinquepunctata	0.020	(0.015)	0		0.007	(0.007)	0	
Coccinella septempunctata	0.768	(0.198)	0.381	(0.078)	0.099	(0.033)	0.298	(0.080)
Coccinella undecimpunctata	0.010	(0.010)	0		0		0	
Harmonia axyridis	0.333	(0.121)	0.062	(0.025)	0.046	(0.019)	0.130	(0.031)
Hippodamia undecimnotata	0		0.010	(0.010)	0		0	
Hippodamia variegata	0.010	(0.010)	0.021	(0.015)	0		0	
Propylea quatuordecimpunctata	0.212	(0.054)	0.031	(0.018)	0.059	(0.019)	0	
Syrphidae								
Episyrphus balteatus	0.303	(0.087)	0.392	(0.080)	0.401	(0.146)	0.443	(0.088)
Melanostoma mellinum	0.040	(0.025)	0.010	(0.010)	0.046	(0.025)	0.015	(0.011)
Metasyrphus corollae	0.242	(0.064)	0.268	(0.075)	0.039	(0.018)	0.282	(0.069)
Metasyrphus latifasciatus	0.081	(0.042)	0.031	(0.018)	0.020	(0.015)	0.053	(0.029)
Metasyrphus luniger	0		0.010	(0.010)	0		0.023	(0.017)
Parasyrphus macularis	0		0		0.013	(0.009)	0.008	(0.007)
Platycheirus clypeatus	0.010	(0.010)	0		0		0	
Scaeva pyrastri	0.010	(0.010)	0		0.007	(0.007)	0.023	(0.013)
Spaerophoria scripta	0.141	(0.047)	0.113	(0.036)	0.079	(0.024)	0.122	(0.039)
Sphaerophoria menthastri	0.071	(0.030)	0.041	(0.025)	0.039	(0.021)	0.053	(0.020)
Syprhus ribesii	0.010	(0.010)	0		0.007	(0.007)	0	
Syrphus vitripennis	0.040	(0.025)	0.021	(0.015)	0		0.061	(0.034)
Chrysopidae								
Chrysoperla carnea	0.535	(0.127)	0.134	(0.035)	0.243	(0.086)	0.489	(0.121)

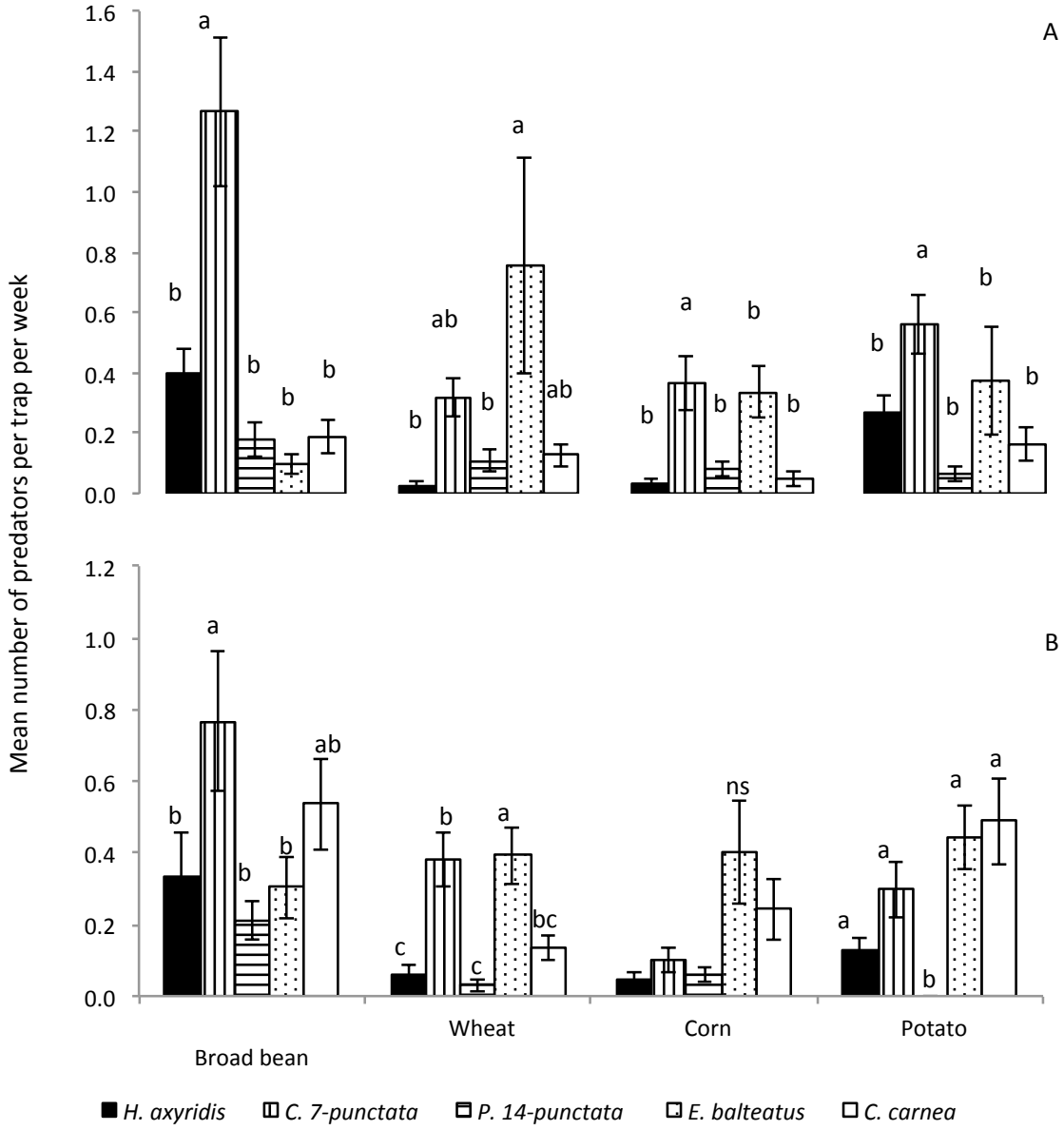

Figure 3: Abundance (mean and SE) of aphidophagous species trapped in the four agrosystems during 2010 (A) and 2011 (B). Means within a crop followed by the same letter are not significantly different (P > 0.05; LSD test), (*C. 7-punctata* represents *C. septempunctata; P. 14-punctata represents P. quatuordecimpunctata*).

4 DISCUSSION

This study identified 28 aphid species and 21 associated predators in communities sampled from four of the most important crops in Belgium. In 2011, aphid abundance significantly differed across the four crops. This variation might be explained by the intrinsic proprieties of crop species, including architecture, blends of volatile organic components, and sap composition (Webster *et al.*, 2008). Alternatively, this variation might be explained by different plot management practices used for the four crops, including differences in mechanical field preparation. Plant density was also lower in the corn crops (12 m^{-2}) compared to the other crops (wheat and broad bean: 100–150 m^{-2}). Moreover, many factors that regulate the size of insect populations might influence aphid abundance, including abiotic environmental conditions (micro-climate), plant volatiles (Park & Hardie, 2004), plant structure (Goffreda *et al.*, 1988; Powell *et al.*, 1999), and host plant diversity around the crops (Alhmedi *et al.*, 2007).

Although 10 predator species were observed in the four inventoried crops, five species were

consistently dominant; namely, *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, *E. balteatus*, and *C. carnea*. Species from these five taxa are frequently considered as major aphid predators in agrosystems worldwide (Honěk, 1979; Bode, 1980; Chambers *et al.*, 1982; Evans, 2000; Thalji, 2006). For instance, *C. septempunctata*, *H. axyridis*, and *E. balteatus* have been documented as dominant predator species in previous works conducted in Belgium (Derume *et al.*, 2007; Adriaens *et al.*, 2008; Alhmedi *et al.*, 2009).

The invasive coccinellid, *H. axyridis,* is known to be uniformly distributed and invasive among various crops (Lombaert *et al.*, 2010; Brown *et al.*, 2011b), and was one of the five most abundant predatory species recorded in the current study. It might affect native aphidophagous communities by decreasing the diversity and density of indigenous species. *P. quatuordecimpunctata* is one of these species that could be negatively impacted (Ware *et al.*, 2009; Brown *et al.*, 2011a; Roy *et al.*, 2012). Furthermore, *H. axyridis* has already been demonstrated to be an efficient intraguild predator (Phoofolo & Obrycki, 1998; Wells *et al.*, 2010; Ingels & De Clercq, 2011). Despite the intraguild predator behavior of this species and its relatively high occurrence (second most abundant species), the diversity of native aphidophagous species remained high (>10 species) in potato and broad bean crops. In both study years, *C. septempunctata* was more abundant compared to *H. axyridis* in broad bean, wheat, potato, and corn crops. This observation was expected, as *H. axyridis* is considered to be an arboreal species, whereas *C. septempunctata* preferentially breed in herbaceous stratum (Hodek, 1973).

Results obtained during this study show that *H. axyridis* was more abundant in potato and in broad bean than in wheat and corn. The results of a previous study showed that *H. axyridis* was more abundant in corn and broad bean (Vandereycken *et al.*, 2013). The difference between theses two studies could be explained by the sampling method used for the estimation of the aphid predator abundance. The water trap seems to underestimate in corn and overestimate in potato the contribution of adult predators. It could be due to the structure of the corn field. The corn plants being higher than the other cultures the water is trapped between two rows of corn plants. Each sampling method only provides a differently biased estimate of relative and absolute abundance (Hodek *et al.*, 2012). Moreover, the difference abundance between our results and those of Vandereycken *et al.* (2013) is also observed in other studies (Michels *et al.*, 1997; Stephens & Losey, 2004).

In addition, the density of *H. axyridis* individuals depends on the type of adjacent habitats (such as hibernation sites, feeding areas represented by nettles, specific species with attracted volatile compounds) (Hodek, 1973; Colignon *et al.*, 2001; Alhmedi *et al.*, 2009; Durieux *et al.*, 2010), with arboreal habitats, which are the preferred habitat type by this species, being scarce in agroecosystems.

The current study demonstrated that the community of aphids and aphid predator species is highly diverse on four major crops in Belgium. Among the aphid predator species, the invasive ladybird, *H. axyridis*, was the second most abundant coccinellid after *C. septempunctata*. Because this invasive species exhibits intraguild predatory behavior, it might threaten the persistence of other native aphidophagous species, by reducing their population densities. Yet, at present, the community of aphidophagous species around *H. axyridis* was similar in all four crops, and contained a large number of species. The graphical representation (based on foodwebs) provides a useful approach towards determining the diversity of aphidophagous species, based on the identification of habitat diversity ranges of species.

5 ACKNOWLEDGMENTS

We thank Ammar Alhmedi and Charles Godfray for their advice about food web analysis. This research was funded by the Service Public de Wallonie (SPW – DGO3, project n°D31-1247).

REFERENCES

Adriaens T., Gomez G.M.Y. & Maes D. (2008). Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. *BioControl* **53**(1), p. 69-88.

Alhmedi A., Haubruge E., Bodson B. & Francis F. (2007). Aphidophagous guilds on nettle (*Urtica dioica*) strips close to fields of green pea, rape and wheat. *Insect Science* **14**, p. 419-424.

Alhmedi A., Haubruge E. & Francis F. (2009). Effect of stinging nettle habitats on aphidophagous predators and parasitoids in wheat and green pea fields with special attention to the invader

Harmonia axyridis Pallas (Coleoptera: Coccinellidae). *Entomological Science* **12**(4), p. 349-358.

Alhmedi A., Haubruge E., D'Hoedt S. & Francis F. (2011). Quantitative food webs of herbivore and related beneficial community in non-crop and crop habitats. *Biological Control* **58**(2), p. 103-112.

Baugnée J.Y. & Branquart E. (2000). *Clef de terrain pour la reconnaissance des principales coccinelles de Wallonie (Chilocorinae, Coccinellidae & Epilachninae)*. Wavre, Jeunes & Nature asbl et Faculté Universitaire des Sciences Agronomiques de Gembloux. 56 p.

Bersier L.F., Banasek-Richter C. & Cattin M.F. (2002). Quantitative descriptors of food-web matrices. *Ecology* **83**(9), p. 2394-2407.

Bode E. (1980). Aphids in winter wheat: abundance and limiting factors from 1976 to 1979. *Bulletin SROP* **3**(4), p. 49-57.

Bozsik A., Mignon J. & Gaspar C. (2002). The green lacewings in Belgium (Neuroptera : Chrysopidae). *Acta Zoologica Academiae Scientiarum Hungaricae* **48**, p. 53-59.

Brown M.W. (2003). Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl* **48**(2), p. 141-153.

Brown P.M.J., Adriaens T., Bathon H., Cuppen J., Goldarazena A., Hagg T., Kenis M., Klausnitzer B.E.M., Kovar I., Loomans A.J.M., Majerus M.E.N., Nedved O., Pedersen J., Rabitsch W., Roy H.E., Ternois V., Zakharov I.A. & Roy D.B. (2008). *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *BioControl* **53**(1), p. 5-21.

Brown P.M.J., Frost R., Doberski J., Sparks T., Harrington R. & Roy H.E. (2011a). Decline in native ladybirds in response to the arrival of *Harmonia axyridis*: early evidence from England. *Ecological Entomology* **36**(2), p. 231-240.

Brown P.M.J., Thomas C.E., Lombaert E., Jeffries D.L., Estoup A. & Handley L.-J.L. (2011b). The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. *BioControl* **56**(4), p. 623-641.

Chambers R.J., Sunderland K.D., Stacey D.L. & Wyatt I.J. (1982). A survey of cereal aphids and their natural enemies in winter-wheat in 1980. *Annals of Applied Biology* **101**(1), p. 175-178.

Clayhills T. & Markkula M. (1974). The abundance of coccinellids on cultivated plants. *Annales Entomologicae Fennicae* **40**, p. 49-55.

Cohen J.E. (1978). *Food Webs and Niche Space*. Princeton, Princeton University Press. p.

Colignon P., Hastir P., Gaspar C. & Francis F. (2001). Effets de l'environnement proche sur la biodiversité entomologique en cultures maraichères de plein champ. *Parasitica* **56**, p. 59-70.

Derume M., Hauteclair P. & Bauffe C. (2007). Inventaire et comparaison de la faune des coccinelles (Coleoptera: Coccinellidae) des terrils des bassins miniers wallons liégeois et hennuyer (Belgique). *Natura Mosana* **60**(2), p. 33-56.

Durieux D., Verheggen F.J., Vandereycken A., Joie E. & Haubruge E. (2010). Review: chemical ecology of ladybird beetles. *Biotechnologie Agronomie Société et Environnement* **14**(2), p. 351-367.

Durieux D., Vandereycken A., Joie E., Haubruge E. & Verheggen F.J. (2012). Evolution des populations de coccinelles indigènes et de l'espèce exotique, *Harmonia axyridis* (Pallas 1773), en Wallonie et en Région de Bruxelles- Capitale. *Entomologie Faunistique - Faunistic Entomology* **65**, p. 81-92.

Elliott N., Kieckhefer R. & Kauffman W. (1996). Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* **105**(4), p. 537-544.

Evans E.W. (2000). Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera : Coccinellidae) in western North America, Czech Acad Sci, Inst Entomology.

Gagic V., Hänke S., Thies C., Scherber C., Tomanović Z. & Tscharntke T. (2012). Agricultural intensification and cereal aphid-parasitoid-hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. *Oecologia*, p. 1-11.

Gilbert F. (2005). Syrphid aphidophagous predators in a food-web context. *European Journal of Entomology* **102**(3), p. 325-333.

Goffreda J.C., Mutschler M.A. & Tingey W.M. (1988). Feeding behavior of potato aphid affected by glandular trichomes of wild tomato. *Entomologia Experimentalis et Applicata* **48**(2), p. 101-107.

Gordon R.D. (1985). The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* **93**(1), p. 1-912.

Hodek I. (1973). *Biology of Coccinellidae*. The Hague, Netherlands, Dr W. Junk. 260 p.

Hodek I. & Honěk A. (1996). *Ecology of Coccinellidae*. Dordrecht, Netherlands, Kluwer Academic Publishers. 480 p.

Hodek I., Van Emden H.F. & Honěk A. (2012). *Ecology and behaviour of the ladybird beetles (Coccinellidae)*, Wiley-Blackwell. 561 p.

Holt R.D. & Lawton J.H. (1994). The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* **25**, p. 495-520.

Honěk A. (1979). Plant -density and occurrence of *Coccinella septempunctata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in cereals. *Acta Entomologica Bohemoslovaca* **76**(5), p. 308-312.

Honěk A. (1983). Factors affecting the distribution of larvae of aphid predators (Col., Coccinellidae and Dipt., Syrphidae) in cereal stands. *Journal of Applied Entomology* **95**(4), p. 336-345.

Ingels B. & De Clercq P. (2011). Effect of size, extraguild prey and habitat complexity on intraguild interactions: a case study with the invasive ladybird *Harmonia axyridis* and the hoverfly *Episyrphus balteatus*. *BioControl*, p. 1-12.

Lombaert E., Guillemaud T., Cornuet J.M., Malausa T., Facon B. & Estoup A. (2010). Bridgehead Effect in the Worldwide Invasion of the Biocontrol Harlequin Ladybird. *PLoS ONE* **5**(3).

Lucas E., Vincent C., Labrie G., Chouinard G., Fournier F., Pelletier F., Bostanian N.J., Coderre D., Mignault M.P. & Lafontaine P. (2007). The multicolored Asian ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae) in Quebec agroecosystems ten years after its arrival. *European Journal of Entomology* **104**(4), p. 737-743.

Michels G.J., Elliott N.C., Romero R.L. & French W.B. (1997). Estimating Populations of Aphidophagous Coccinellidae (Coleoptera) in Winter Wheat. *Environmental Entomology* **26**(1), p. 4-11.

Morris R.J., Lewis O.T. & Godfray H.C.J. (2005). Apparent competition and insect community structure: towards a spatial perspective. *Annales Zoologici Fennici* **42**(4), p. 449-462.

Muller C.B., Adriaanse I.C.T., Belshaw R. & Godfray H.C.J. (1999). The structure of an aphid-parasitoid community. *Journal of Animal Ecology* **68**(2), p. 346-370.

Ottart N. (2005). *L'impact de la coccinelle invasive Harmonia axyridis sur les populations de coccinelles indigènes à Bruxelles*. Master Travail de fin d'études, Université Libre de Bruxelles, 84 p.

Park K.C. & Hardie J. (2004). Electrophysiological characterisation of olfactory sensilla in the black bean aphid, *Aphis fabae*. *Journal of Insect Physiology* **50**(7), p. 647-655.

Phoofolo M.W. & Obrycki J.J. (1998). Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomologia Experimentalis et Applicata* **89**(1), p. 47-55.

Powell G., Maniar S.P., Pickett J.A. & Hardie J. (1999). Aphid responses to non-host epicuticular lipids. *Entomologia Experimentalis et Applicata* **91**(1), p. 115-123.

Radwan Z. & Lovei G.L. (1983). Strucure and seasonal dynamics of larval, pupal, and adult coccinellid (Col, Coccinellidae) assemblages in 2 types of maize fields in Hungary. *Zeitschrift Fur Angewandte Entomologie-Journal of Applied Entomology* **96**(4), p. 396-408.

Rott A.S. & Godfray H.C.J. (2000). The structure of a leafminer-parasitoid community. *Journal of Animal Ecology* **69**(2), p. 274-289.

Roy H.E., Adriaens T., Isaac N.J.B., Kenis M., Onkelinx T., Martin G.S., Brown P.M.J., Hautier L., Poland R., Roy D.B., Comont R., Eschen R., Frost R., Zindel R., Van Vlaenderen J., Nedvěd O., Ravn H.P., Grégoire J.-C., de Biseau J.-C. & Maes D. (2012). Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions*, p. 717-725.

San Martin G. (2004). *Clé de détermination des Chrysopidae de Belgique*. Wavre, Jeunes & Nature. 42 p.

Stephens E.J. & Losey J.E. (2004). Comparison of sticky cards, visual and sweep sampling of Coccinellid populations in Alfalfa. *Environmental Entomology* **33**(3), p. 535-539.

Tedders W.L. & Schaefer P.W. (1994). Release and establishment of *Harmonia axyridis* (Coleoptera, Coccinellidae) in the Southeastern United-States. *Entomological News* **105**(4), p. 228-243.

Thalji R. (2006). Composition of coccinellid communities in sugar beet fields in Vojvodina. *Zbornik Matice Srpske za Prirodne Nauke* **110**, p. 267-273.

Vandereycken A., Brostaux Y., Joie E., Haubruge E. & Verheggen F.J. (2013). Occurrence of *Harmonia axyridis* (Coleoptera: Coccinellidae) in field crops. *European Journal of Entomology* **110**(2), p. 285-292.

Verlinden L. (1994). *Faune de Belgique. Syrphides (Syrphidae)*. Bruxelles, Institut Royal des Sciences Naturelles de Belgique. 289 p.

Ware R., Yguel B. & Majerus M. (2009). Effects of competition, cannibalism and intra-guild predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species

Harmonia axyridis. *Ecological Entomology* **34**(1), p. 12-19.

Webster B., Bruce T., Dufour S., Birkemeyer C., Birkett M., Hardie J. & Pickett J. (2008). Identification of volatile compounds used in host location by the black bean aphid, *Aphis fabae*. *Journal of Chemical Ecology* **34**(9), p. 1153-1161.

Wells P.M., Baverstock J., Majerus M.E.N., Jiggins F.M., Roy H. & Pell J.K. (2010). Intraguild predation of non-coccinellid aphid natural enemies by *Harmonia axyridis*: prey range and factors influencing intraguild predation. *IOBC/WPRS Bulletin* **58**, p. 185-192.

(53 réf.)