Is the Multicolored Asian Ladybeetle, Harmonia axyridis, the Most Abundant Natural Enemy to Aphids in Agroecosystems?

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Is the multicolored Asian ladybeetle, *Harmonia axyridis*, the most abundant natural enemy to aphids in agroecosystems?

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Abstract

The multicolored Asian ladybeetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), was introduced into Western Europe in the late 1990s. Since the late 2000s, this species has been commonly considered one of the most abundant aphid predators in most Western European countries. In spite of the large amount of research on *H. axyridis*, information concerning its relative abundance in agroecosystems is lacking. This study aims to evaluate the abundance of *H. axyridis* within the aphidophage community in four crops situated in southern Belgium: wheat, *Triticum aestivum* L. (Poales: Poaceae), corn, *Zea mays*, potato, *Solanum tuberosum* (Solanales: Solanaceae), and broad bean *Vicia faba* (Fabales: Fabaceae). In order to assess the species diversity, the collected data were analyzed by considering (1) the species richness and (2) the evenness according to the Shannon diversity index. Eleven aphidophages were observed in every inventoried agroecosystem, including five abundant species: three coccinellids, the seven-spotted ladybug, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), the 14-spotted Ladybird, *Propylea quatuordecimpunctata*, and *H. axyridis*; one hoverfly, the marmalade hoverfly, *Episyrphus balteatus* De Geer (Diptera: Syrphidae); and one lacewing, the common green lacewing, *Chrysoperla carnea* Stephens sensu lato (= s.l.) (Neuroptera: Chrysopidae). *Harmonia axyridis* has been observed to thrive, breed, and reproduce on the four studied crops. *Harmonia axyridis* is the most abundant predator of aphids in corn followed by *C. septempunctata*, which is the main aphid predator observed in the three other inventoried crops. In wheat and potato fields, *H. axyridis* occurs in low numbers compared to other aphidophage. These observations suggest that *H. axyridis* could be considered an invasive species of agrosystems, and that potato and wheat may intermittently act as refuges for other aphidophages vulnerable to intraguild predation by this invader. *Harmonia axyridis* is not the most abundant aphid predator in the main Belgian crops.

Keywords: aphidophagous insects, biological control, crop pests, Coccinellidae, invasive species
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Introduction

The multicolored Asian ladybeetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), was introduced from Asia into Western Europe and other parts of the world to control aphid and coccid populations (Adriaens et al. 2008; Brown et al. 2008). In Belgium, *H. axyridis* was used as a biological control agent beginning in 1997 and was first observed in the wild in 2001. Since then *H. axyridis* populations have increased and gradually expanded into Belgium (Adriaens et al. 2008).

This species presents all the characteristics shared by an efficient aphid predator: large body size, high voracity, high predation efficiency (Labrie et al. 2006), high colonization aptitude (With et al. 2002), rapid development, high fecundity, and low susceptibility to pathogens or natural enemies (Marco et al. 2002). *Harmonia axyridis* has become ubiquitous in many parts of the world, including America, Europe, and Africa (Lombaert et al. 2010; Brown et al. 2011b), and has been reported in many different habitats, such as agroecosystems, gardens, and arboreal habitats (Majerus et al. 2006).

Due to its large body and efficient physical and chemical defenses, *H. axyridis* has become an intraguild predator (Sato and Dixon 2004; Ware and Majerus 2008). Intraguild predation has been observed among other ladybeetle species (Pell et al. 2008; Ware and Majerus 2008); other aphid natural enemies, including syrphids, chrysopids, and parasitoids (Phoofolo and Obrycki 1998; Wells et al. 2010; Ingels and De Clercq 2011); and aphid pathogenic fungus (Roy et al. 2008). This intraguild predation behavior is thought to have led to a decrease in native species (Brown and Miller 1998; Harmon et al. 2007; Ware et al. 2009; Brown et al. 2011a; Roy et al. 2012). In Belgian urban areas, Adriaens et al. (2010) found a significant decline in native species, including the two-spot ladybird, *Adalia bipunctata* L. (Coleoptera: Coccinellidae), and the 10 spotted ladybird, *Adalia decempunctata* L., on pine, lime, and maple trees following the arrival of *H. axyridis*. The decline of native species can possibly be explained by the decline in number of their principal prey, resulting in reduced survivorship in local habitats and altered dynamics of habitat use and dispersal (Evans 2004).

According to previous reports, the most dominant aphidophage in Belgian agroecosystems appear to be two coccinellids, the seven-spotted ladybug, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), and *H. axyridis*; one hoverfly, the marmalade hoverfly, *Episyrphus balteatus* De Geer (Diptera: Syrphidae); and one braconid, the parasitic wasp *Aphidius ervi* Haliday (Hymenoptera: Braconidae) (Derume et al. 2007; Adriaens et al. 2008; Alhmedi et al. 2009). In arboreal habitats, four coccinellids were reported as abundant species: *A. bipunctata*.,the 14-spotted ladybird, *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae), the 22-spot ladybird *Psyllobora vigintiduopunctata* (L.), and *H. axyridis* (Adriaens et al. 2008). In 2001, the same results were observed by Francis (2001), with the exception of *H. axyridis*.

Our study was conducted eight years after the first observation of *H. axyridis* in the wild in Belgium (Adriaens et al. 2003). Following aphidophagous decline highlighted by several studies, the current study was conducted in order to assess the relative abundance of *H. axyridis* through the quantification of the abundance of this exotic species and other aphidophages in four important Belgian crops (wheat, *Triticum aestivum* L. (Poales:

Poaceae), corn, *Zea mays*, potato, *Solanum tuberosum* (Solanales: Solanaceae), and broad bean *Vicia faba* (Fabales: Fabaceae)) using a three-year inventory.

Materials and Methods

Study site

Aphidophagous insect populations were sampled from 2009 to 2011 in Hesbaye, an intensive agricultural production area in Wallonia, the southern region of Belgium (individual sites given in Table 1). Four crops were chosen for their agronomic importance: wheat, corn, potato, and broad bean *Vicia faba*. The sampling period ran from mid-May to late September. Every week, nine fields of each crop were sampled.

Sampling methods

The sampling methods used to assess the numbers of aphidophagous predators and aphids consisted of whole-plant visual inspections, using 1 m^2 quadrats distributed randomly throughout the whole field. In order to avoid the influence of surrounding crops, a 20 m buffer zone around the edge of each field was not sampled. Visual sampling was conducted, as it provides an easy and accurate method for the estimation of larval and adult densities of coccinellids in agroecosystems (Michels and Behle 1992). Forty-eight quadrats were examined in each crop every week. Quadrats were located along transect lines across each field and spaced 20 m apart. All leaves and stems within the quadrat were examined, and all aphidophagous stages were recorded. Aphid species were also quantified on all leaves and stems. Larvae and pupae were brought to the laboratory to develop under laboratory conditions (24 ± 1° C, 75 ± 5% RH) for identification at the species level. All aphid predators were identified, with the exception of members of the common green lacewing, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) species complex, which were pooled together. This group comprises three cryptic species, *C. kolthoffi* Navas, *C. lucasina* Lacroix, and *C. carnea* Stephens, which can only be differentiated using molecular techniques (Bozsik et al. 2003; Lourenco et al. 2006).

Statistical analysis

In order to assess the species diversity, the collected data were analyzed by considering (1) species richness and (2) evenness according to the Shannon diversity index (H) (Magurran 1988), which considers both the number of species and the distribution of individuals among species. H is minimal if all individuals belong to only one species or if all species are represented by one individual; H is maximal if all individuals are evenly distributed. Evenness (J) varies from 0, if only one species dominates, to 1, if all species show similar abundance. Evenness (J) and the Shannon diversity index (H) were calculated as follows:

$$\text{Diversity:} \quad H = -\sum(pi \ \ln(pi))$$

$$\text{Maximal diversity:} \quad H_{max} = \ln k$$

$$\text{Evenness:} \quad J = \frac{H}{H_{max}}$$

Because mean densities per m^2 were low, these values are presented per 100 m^2. The mean abundance per species was analyzed with an analysis of variance (ANOVA: general linear models) with crops (q = 4) and years (n = 3) used as factors ($\alpha = 0.05$). Within crops, densities of species were compared using the least square difference (LSD; $\alpha = 0.05$). To account for the variations of predator abundances, the abundance per species was analyzed using an analysis of covariance (ANCOVA: general linear models) with crops (q = 4) and years (n = 3) used as factors ($\alpha = 0.05$) and aphid densities used as the covariable. Prior to analyses, a $\log_{10}(x + 1)$ was used to transform the data distribution (counting) due to its asymmetry (Dagnelie 2011). Although statistical analyses were performed on transformed data, untransformed data are presented in Tables 4 and 5. Statistical analyses were performed using Minitab® release 1.5 (www.minitab.com).

Results

Diversity of aphidophages

During the three years (2009–2011), 11 aphidophagous taxa were observed on the four different cultures: the hoverfly *E. balteatus*, the coccinellids *C. septempunctata, C. quinquepunctata* L. (Coleoptera: Coccinellidae), *C. undecimpunctata* (L.), *H. axyridis*, *P. quatuordecimpunctata*, *A. bipunctata*, *A. decempunctata,* the cream-spot ladybird, *Calvia quatuordecimguttata* (L.), *Hippodamia variegata* Goeze; and the *C. carnea* species group (Table 2).

From 2009 to 2011, species richness increased in broad bean, corn, and wheat, reaching 6, 8, and 7 species respectively (Table 3). Species richness did not evolve in potato crops, remaining at five species during the entire period. Overall, five aphidophages were continually observed during the three-year period in each crop and represented 95% of all the aphidophage observed in 2009 and 99% in both 2010 and 2011: *E. balteatus, C. carnea* s.l., *C. septempunctata*, *P. quatuordecimpunctata*, and *H. axyridis*.

The evenness value was low in wheat with J = 0.35, 0.25, and 0.38 in 2009, 2010, and 2011, respectively, with the numerical dominance of two species: *C. septempunctata* and *E. balteatus* (Tables 3, 4, and 5). In broad bean and potato, evenness varied from year to year. In broad bean, *C. septempunctata* was the most abundant in 2010 (J = 0.45) and 2011 (J = 0.59). In potato, *C. carnea* s.l. and *C. septempunctata* numerically dominated the aphidophagous guild in all three years (J = 0.65, 0.79, 0.74) (Table 3). In corn, the evenness during the three years decreased from 0.82 (2009) to 0.61 (2010).

Relative abundance of aphidophage in four crops

The relative abundance of both adult and larval stages of the five aphidophage within each crop showed significant differences (Tables 4 and 5), with the exception of potato in 2010, in which densities of larvae populations of different predators were not significantly different ($F_{4,3570} = 1.4$; $p = 0.25$) (Table 5).

Corn

The most abundant adult species in 2009 and 2010 was *C. carnea* s.l. and *C. septempunctata* (2009: $F_{4,1065} = 10.7$, $p < 0.001$; 2010: $F_{4,3425} = 14.3$, $p < 0.001$) ($p < 0.05$; LSD) (Table 4). In 2011, *H. axyridis* and *C. septempunctata* densities were both significantly higher than those of other species ($p < 0.05$; LSD) ($F_{4,4055} = 24.2$, $p < 0.001$) (Table 4). *H. axyridis* larvae densities were significantly higher in 2009 and 2011 (2009: $F_{4,1065} = 5.4$, $p < 0.001$; 2010: $F_{4,3425} = 25.5$, $p < 0.001$; 2011: $F_{4,4055} = 57.0$, $p < 0.001$) than those observed for the other species (Table 5).

Wheat

Adult populations of *H. axyridis* remained lower than other species during the three-year sampling (2009: $F_{4,1765} = 5.4$, $p < 0.001$; 2010: $F_{4,2925} = 24.1$, $p < 0.001$; 2011: $F_{4,2625} = 38.0$, $p < 0.001$) ($p < 0.05$; LSD) and did not exceed 1.1 ± 0.6 adults per 100 m² (Table 4). *Episyrphus balteatus* was the most frequently encountered adult species in 2009, whereas in 2010 and 2011 *C. septempunctata* was the most abundant species ($p < 0.05$; LSD) (Table 4). Larvae of *E. balteatus* were the most abundant ($p < 0.05$; LSD) of the aphidophage during the three years (2009: $F_{4,1765}$ =11.7, $p < 0.001$; 2010: $F_{4,2925} = 91.1$, $p < 0.001$; 2011: $F_{4,2625} = 273.6$, $p < 0.001$) (Table 5).

Potato

Trends for *H. axyridis* were the same in potato as in wheat: *H. axyridis* was not the most abundant species, and its density did not exceed 2.5 ± 0.7 adults per 100 m² (Table 4). Two species were more abundant than others: *C. carnea* s.l. in 2009 and 2011 (2009: $F_{4,500} = 7.7$, $p < 0.001$; 2011: $F_{4,3250} = 10.8$, $p < 0.001$), and *C. septempunctata* in 2010 ($F_{4,3570} = 12.8$, $p < 0.001$) and 2011 ($p > 0.05$; LSD). In 2009, larvae of *C. carnea* s.l., *P. quatuordecimpunctata*, and *H. axyridis* were the most abundant species but densities remained low (Table 5). In 2010, larvae densities of the five above-mentioned species were not significantly different from each other ($F_{4,3570} = 1.4$, $p = 0.25$) (Table 5). In 2011, only *C. carnea* s.l. numerically dominated the aphidophages community ($F_{4,3250} = 5.5$, $p < 0.001$) ($p > 0.05$; LSD) (Table 5).

Broad bean

In 2009, *H. axyridis* and *C. septempunctata* adults were the only adult species observed in broad bean ($F_{4,160} = 0.7$, $p > 0.05$). *Coccinella septempunctata* was the most abundant species in 2010 ($F_{4,2415} = 22.1$, $p < 0.001$), while in 2011 both *C. septempunctata* and *C. carnea* s.l. were profusely observed ($F_{4,2480} = 37.5$, $p < 0.001$) ($p < 0.05$; LSD) (Table 4). In 2009, three species were present at the larval stage: *P. quatuordecimpunctata, C. carnea* s.l., and *E. balteatus* ($F_{4,160} = 1.0$, $p = 0.43$) ($p < 0.05$; LSD). In 2010 ($F_{4,2415} = 8.35$, $p < 0.001$) and 2011 ($F_{4,2480} = 27.2$, $p < 0.001$), all species were observed, and *C. septempunctata* was the most abundant (Table 5).

Effect of aphid densities and sampling year on relative abundance of aphidophage

Abundances of *H. axyridis* in wheat and potatoes were not analyzed, due to very low numbers of individuals observed during the three-year inventory. Over the three-year sampling, adult populations of *H. axyridis* in corn significantly increased ($F_{2,1709} = 14.5$, $p < 0.001$) (Table 6) from 7.8 ± 2.0 in 2009 to 19.9 ± 1.8 individuals per 100 m² in 2011 (Table 4). Larval populations in the same crop also increased statistically ($F_{2,1709} = 39.9$, $p < 0.001$) (Table 6), rising from 11.9 ± 4.2 to 70.8 ± 6.6 larvae per 100 m² (Table 5). In broad bean, relative abundance of *H. axyridis* was not significantly different among the three years, neither at the adult (Table 6) nor larval (Table 7) stages.

Coccinella septempunctata larvae declined in broad bean ($F_{2,1011} = 4.7$, $p = 0.009$), wheat ($F_{2,1463} = 14.4$, $p < 0.001$), and corn ($F_{2,1709} = 31.9$, $p < 0.001$) (Table 7); densities decreased by 10 and 29.6 times in corn and broad bean respectively. In wehat, no larvae were observed in 2011, while 13.4 ± 3.9 larvae per 100 m² were observed in 2009.

The abundances of three other aphidophage showed variable changes (Tables 6 and 7).

Aphid populations and correlation with aphidophage densities

In 2009, 2010, and 2011, seven, nine, and 10 species of aphids were identified, respectively: the pea aphid, *Acyrthosiphon pisum* Scopoli (Hemiptera: Aphididae); the cowpea aphid, *Aphis craccivora* Koch; the black bean aphid, *Aphis fabae* Scopoli; *Aphis frangulae* Walker; the buckthorn aphid, *Aphis nasturtii* Kaltenbach; the potato aphid, *Macrosiphon* *euphorbiae* Thomas; the vetch aphid, *Megoura viciae* Buckton; the rose grain aphid, *Metopolophium dirhodum* Walker; the green peach aphid, *Mizus persicae* Sulzer; *Rhopalosiphum* sp.; and *Sitobion* sp. (Table 8). The mean number of observed aphids increased in corn ($F_{2,2589} = 39.$, $p < 0.001$) and potato ($F_{2,1410} = 17.11$, $p < 0.001$) from 2009 to 2011. Aphid densities also statistically varied in broad bean ($F_{2,974} = 8.7$, $p < 0.001$) and wheat ($F_{2,1392} = 102.7$, $p < 0.001$) from 2009 to 2011, but without any general evolution (Table 8).

The ANCOVA analyses showed a linear relationship between aphid and predator populations in 55% of adult populations (Table 6) and 35% of larvae populations (Table 7) ($p_{\text{aphids}} < 0.05$, ANCOVA). In these cases, aphid densities influenced the predator abundance. Results (p_{years}) comparison between ANOVA and ANCOVA showed that the influence of aphid populations on predator abundance variations between years was not statistically significant.; p_{years} of the two statistic analyses showed the same results.

Discussion

Since the invasive coccinellid *H. axyridis* spread over Europe (Brown et al. 2008), imposing negative impacts on native aphidophage and affecting composition of several guilds (Soares et al. 2008; Roy et al. 2012), studies have evaluated the population spread of this coccinellid. The current study's sampling of aphid predators in Belgian agroecosystems from 2009 to 2011 showed that *H. axyridis* lives and reproduces more efficiently in corn and broad bean than in wheat and potato. In corn, the evenness during the three years decreased when *H. axyridis* population increased strongly and was higher than the population of other species.

During the three-year sampling, 11 aphidophage were observed in these agroecosystems, but five of them predominated: *E. balteatus*, *C. septempunctata, P. quatuordecimpunctata*, *H. axyridis*, and *C. carnea* s.l. Five dominant species in agroecosystems is a common observation (Hodek and Honěk 1996). Observations on predator densities highlight that *H. axyridis* was not the numerically dominant species in every crop: in wheat and potato, *C. septempunctata* was more abundant than *H. axyridis*. In many European agricultural crops, both *C. septempunctata* and *P. quatuordecimpunctata* were dominant prior to the arrival of *H. axyridis* (Honěk 1979; Bode 1980; Chambers et al. 1982), and it appears that these two species have maintained their dominance in spite of being prone to intraguild predation by *H. axyridis* in the field (Hautier et al. 2008).

In our study, larvae of *E. balteatus* were the most abundant observed predators in wheat, which has already been reported by Tenhumberg and Poehling (1995) prior to the arrival of *H. axyridis*. *Episyrphus balteatus* has also been previously reported as one of the most abundant aphidophage in vegetable crops, such as broad beans (Colignon et al. 2001; Colignon et al. 2002). This could be explained by abiotic conditions (high density cereal crop, with high humidity and low temperature) that are more favorable to the larvae of *E. balteatus* (Honěk 1983).

The fact that *H. axyridis* is not the most abundant aphidophage in agrosystems is probably due to its generalist behavior and arboreal habitat selection (Hodek 1973; Chapin and Brou 1991; LaMana and Miller 1996; Brown and Miller 1998; Labrie 2007). However, it has been reported that *H. axyridis* can also thrive in agrosystems such as wheat, corn, and potato (LaMana and Miller 1996; Buntin and

Bouton 1997; Colunga-Garcia and Gage 1998; Michaud 2002; Brown 2003; Nault and Kennedy 2003; Snyder et al. 2004; Jansen and Hautier 2008), as well as in herbaceous habitats (LaMana and Miller 1996; Koch et al. 2006; Alhmedi et al. 2007).

There were evident changes in the abundance of aphidophages in crops through the years, but this study does not propose to identify a global evolution (increase or decline) in any of the species that were observed in this study. The causes of such fluctuations are diverse and may include factors such as the diversity and abundance of aphid species (Wright and Laing 1980; Honěk 1982; Thalji 2006). The results of the ANCOVA showed that there was a linear relationship between prey and predator populations, but additional biotic and abiotic factors contribute to the annual variability of predator abundance. Climate could be one such factor, due to its influence on natural enemies, overwintering mortality, and aphid populations (Hodek and Honěk 1996; Szentkirályi 2001; Rotheray and Gilbert 2011). Several other factors could also explain the variation between crops: insolation, humidity (Honěk 1985), quantity and quality of host plants (Alhmedi et al. 2009), and adjacent habitats (Colignon et al. 2001; Alhmedi et al. 2009).

A particularly interesting finding is that although *H. axyridis* breeding occurred in all four inventoried crops to some extent, adults of this species are not ubiquitous; few immature individuals were recovered from potato and wheat. Assuming that declines in native species are caused by *H. axyridis* (Roy et al. 2012), this suggests that certain crops, such as wheat and potato, could act as refuges from *H. axyridis* at certain times, while native species, such as *E. balteatus* and *C. septempunctata*, are able to breed with a lower risk of intraguild predation or other forms of competition from the invaders. Such habitats could become even more important as native species adapt to the invader by evolving to avoid habitats where *H. axyridis* occurs in high numbers, as has been seen in co-occurring aphidophages in their native habitats (Sloggett 2012).

In conclusion, our study indicates that *H. axyridis* was not the most frequently observed aphidophage in the four most important Belgian agronomical crops. In future studies, longer samplings would be preferable in order to eventually identify quantitative changes in the native fauna suggested from other studies. Agroecosystems may even constitute an ecological reservoir for certain native aphidophage.

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Table 1. Sites surveyed for aphidophage from 2009 to 2011 in Belgium.

Year	Site	Latitude	Longitude	Crops
2009	Bassenge	5.652	50.768	wheat (2.5 ha), corn (1.9 ha)
	Bousval	4.505	50.63	wheat (9.3 ha), corn (6.9 ha), potato (15.2 ha)
	Geer	5.19	50.67	wheat (11.6 ha), corn (6.4 ha)
	Godardville	4.284	50.482	wheat (9.2 ha), potato (4.4; 13.9 ha)
	Loyers	4.934	50.454	wheat (5.8 ha)
	Perwez	4.813	50.645	broad bean (13.8; 2.4; 1.3; 1.8 ha), wheat (13.7 ha), corn (0.7; 1.3 ha), potato (9.9 ha)
	Ramillies	4.866	50.624	wheat (3.5 ha), corn (3.8 ha)
	Redu	5.158	50.004	corn(5.7; 6.2 ha)
	Rhisnes	4.83	50.5	broad bean (8.7; 4.2; 4.5; 1.3; 6.2 ha) , wheat (9.6 ha), corn (2.7 ha), potato (5.6; 6.7 ha)
	Walhain	4.735	50.616	wheat (7.5 ha), corn(0.5 ha)
2010	Eben-Emael	5.676	50.789	potato (2.9; 6.7 ha), corn (3.5 ha)
	Gembloux	4.695	50.563	broad bean (3.2 ha)
	Isnes	4.732	50.515	broad bean (1.6 ha)
	Nil-St-Vincent	4.689	50.646	broad bean (3.4 ha)
	Perwez	4.813	50.645	potato (12.0; 9.4 ha), corn(7.5; 3.6 ha), broad bean (22.7 ha), wheat (10.2; 13.3; 10.7; 25.4; 22.1 ha)
	Plancenoit	4.398	50.664	corn (0.6 ha), broad bean (3.4 ha)
	Ramillies	4.866	50.624	potato(10.0 ha), corn (3.6 ha), wheat (4.8 ha)
	Rhisnes	4.83	50.5	wheat (8.7ha; 6.7; 5.6 ha), broad bean (9.7 ha)
	Richelle	5.703	50.713	potato (1.5; 1.1 ha), corn (4.5; 11.1 ha), broad bean (1.3; 6.3 ha)
	Walhain	4.735	50.616	potato (7.7; 9.6 ha), corn (5.8; 8.7 ha), broad bean (2.7 ha)
2011	Gembloux	4.695	50.563	potato(4.5;7.8; 3.7 ha), corn (6.9 ha), broad bean (1.5 ha)
	Grez-Doiceau	4.696	50.741	corn (5.2; 6.2 ha), broad bean (2.1 ha), wheat (4.9 ha)
	Ligny	4.581	50.508	broad bean (0.8 ha)
	Perwez	4.813	50.645	potato (19.3; 9.2; 10.4; 8.0 ha), corn (17.0 ha), broad bean (13.4; 7.6 ha), wheat (19; 21.5; 11.8; 9.8 ha)
	Plancenoit	4.398	50.664	corn (4.9 ha), broad bean (3.4 ha)
	Ramillies	4.866	50.624	potato (4.2 ha), corn (3.7 ha), wheat (6.3 ha)
	Rhisnes	4.83	50.5	wheat (9.1 ha)
	Richelle	5.703	50.713	corn (3.0; 7.8; 2.8 ha), broad bean(4.0; 2.8; 2.7 ha)
	Walhain	4.735	50.616	potato (7.8 ha), wheat (7.6; 9.5 ha)

Table 2. Aphidophage diversity in four crops (broad bean, wheat, corn, and potato) from 2009 to 2011.

Species		Broad bean			Wheat			Corn			Potato		
		2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011
Coccinellidae	*A. decempunctata*		+										
	A. bipunctata							+		+			
	C. septempunctata	+	+	+	+	+	+	+	+	+	+	+	+
	C. quatuordecimguttata						+						
	C. undecimpunctata									+			
	C. quinquepunctata			+				+	+	+			
	H. axyridis	+	+	+	+		+	+	+	+	+	+	+
	H. variegata						+						
	P. quatuordecimpunctata	+	+	+	+	+	+	+	+	+	+	+	+
Syrphidae	***E. balteatus***	+	+	+	+	+	+	+	+	+	+	+	+
Chrysopidae	***C. carnea s.l.***	+	+	+	+	+	+	+	+	+	+	+	+

+: presence of aphidophages; bold is used to call attention to specific species

Table 3. Species richness and diversity index (H= Shannon-Weiner diversity index, where absolute diversity = 1.00; J = evenness or relative diversity (H/Hmax), where absolute evenness = 1.00).

Index	Broad bean			Wheat			Corn			Potato		
	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011
Species Richness	5	6	6	5	4	7	7	6	8	5	5	5
Diversity (H)	1.42	0.8	1.05	0.56	0.35	0.74	1.6	1.47	1.27	1.05	1.27	1.19
Max. Diversity (Hmax)	1.61	1.79	1.79	1.61	1.39	1.95	1.95	1.79	2.08	1.61	1.61	1.61
Evenness (J)	0.88	0.45	0.59	0.35	0.25	0.38	0.82	0.82	0.61	0.65	0.79	0.74

Table 4. Abundance (means and SE) of aphidophage (adults) per 100 m² in four agroecosystems from 2009 to 2011. Means within a crop followed by the same letter were not significantly different for the same field (*p* > 0.05; LSD test).

Crops	Aphidophages	2009	2010	2011
Corn	***H. axyridis***	7.8 ± 2.04 a	3.91 ± 0.96 ab	19.98 ± 1.8 c
	C. septempunctata	10.09 ± 2.42 a	12.03 ± 1.49 c	22.3 ± 2 c
	P. quatuordecimpunctata	0.46 ± 0.46 a	5.65 ± 0.93 b	3.68 ± 0.9 ab
	E. balteatus	8.26 ± 1.87 a	1.16 ± 0.54 a	0.74 ± 0.3 a
	C. carnea s.l.	29.82 ± 5.66 b	4.06 ± 0.86 ab	12.25 ± 1.9 b
Wheat	***H. axyridis***	1.12 ± 0.56 b	0 a	0.19 ± 0.2 a
	C. septempunctata	7.28 ± 1.95 bc	5.01 ± 1.14 c	36.93 ± 4.3 c
	P. quatuordecimpunctata	0 a	0.17 ± 0.17 b	0.95 ± 0.4 a
	E. balteatus	15.97 ± 3.1 c	0.33 ± 0.24 b	14.02 ± 2.4 b
	C. carnea s.l.	2.52 ± 0.92 bc	1 ± 0.41 b	11.17 ± 1.8 b
Potato	***H. axyridis***	1.9 ± 1.34 b	2.5 ± 0.73 a	1.98 ± 0.7 a
	C. septempunctata	1.9 ± 1.34 b	14.19 ± 1.8 b	8.7 ± 1.3 b
	P. quatuordecimpunctata	0 a	0.7 ± 0.31 a	0.31 ± 0.2 a
	E. balteatus	0.95 ± 0.95 b	0.28 ± 0.2 a	3.21 ± 1 a
	C. carnea s.l.	10.48 ± 4.04 c	1.53 ± 0.46 a	14.05 ± 1.9 b
Broad bean	***H. axyridis***	5.71 ± 3.98 b	2.02 ± 0.63 b	5.81 ± 1.5 a
	C. septempunctata	5.71 ± 5.71 b	29.96 ± 4.79 d	35.27 ± 6.1 b
	P. quatuordecimpunctata	0 a	2.23 ± 0.78 b	3.41 ± 0.9 a
	E. balteatus	0 a	0 a	5.01 ± 1.2 a
	C. carnea s.l.	0 a	4.66 ± 0.99 c	50.7 ± 5.7 b

Bold is used to call attention to specific species

Table 5. Abundance (means and SE) of aphidophage (larvae) per 100 m² in four agroecosystems from 2009 to 2011. Means within a crop followed by the same letter were not significantly different for the same field (*p* > 0.05; LSD test).

Crops	Aphidophages	2009	2010	2011
Corn	***H. axyridis***	11.93 ± 4.19 ab	13.33 ± 2.89 b	70.83 ± 6.6 c
	C. septempunctata	7.34 ± 2.47 a	6.38 ± 1.57 ab	25 ± 3.9 b
	P. quatuordecimpunctata	25.23 ± 5.61 b	2.46 ± 0.72 a	2.57 ± 0.7 a
	E. balteatus	4.59 ± 1.93 a	36.67 ± 5.35 c	19.24 ± 2.1 b
	C. carnea s.l.	3.21 ± 1.2 a	5.51 ± 0.96 ab	0.61 ± 0.3 a
Wheat	***H. axyridis***	2.24 ± 1.48 a	0 a	0.19 ± 0.2 b
	C. septempunctata	3.08 ± 1.39 a	1.5 ± 0.8 b	8.71 ± 1.8 b
	P. quatuordecimpunctata	13.45 ± 3.92 a	0 a	0 a
	E. balteatus	194.4 ± 16.21 b	79.3 ± 10.42 c	160.98 ± 10.2 c
	C. carnea s.l.	2.52 ± 1 a	0.17 ± 0.17 b	1.33 ± 0.5 b
Potato	***H. axyridis***	0.95 ± 0.95 b	0.7 ± 0.37 a	0.46 ± 0.3 a
	C. septempunctata	0 a	2.5 ± 1.26 a	0.31 ± 0.2 a
	P. quatuordecimpunctata	1.9 ± 1.34 b	0.14 ± 0.14 a	0.31 ± 0.2 a
	E. balteatus	12:00 AM	5.42 ± 1.85 a	0.61 ± 0.4 a
	C. carnea s.l.	5.71 ± 2.65 b	3.34 ± 0.75 a	4.43 ± 1 b
Broad bean	***H. axyridis***	0 a	6.68 ± 2.09 a	21.84 ± 6.3 a
	C. septempunctata	0 a	42.92 ± 9.33 b	114.23 ± 35.7 b
	P. quatuordecimpunctata	5.71 ± 5.71 b	0.2 ± 0.2 a	0.2 ± 0.2 a
	E. balteatus	17.14 ± 11.94 b	5.06 ± 1.64 a	2.2 ± 0.8 a
	C. carnea s.l.	2.86 ± 2.86 b	0.61 ± 0.35 a	2 ± 0.6 a

Bold is used to call attention to specific species

Table 6. ANOVA and ANCOVA summary of the effects of aphid abundance and year sampling (2009, 2010, 2011) on the abundane of five predators at the adult stage in four crops (corn, wheat, potato, and broad bean).

Aphidophages		Years		Years/Aphids		Aphids	
Crop	Species	*F*	*p*	*F*	*p*	*F*	*p*
Corn	***H. axyridis***	14.53	***	15.36	***	6.62	*
	C. septempunctata	5.21	**	6.4	**	12.35	***
	P. quatuordecimpunctata	4.04	*	4.18	*	0.61	ns
	E. balteatus	19.71	***	16.93	***	15.74	***
	C. carnea s.l.	20.96	***	17.87	***	38.98	***
Wheat	***H. axyridis***	5.78	**	5.62	**	0.23	ns
	C. septempunctata	32.52	***	36.18	***	5.4	*
	P. quatuordecimpunctata	1.63	ns	1.54	ns	0.04	ns
	E. balteatus	10.47	***	13.3	***	5.39	*
	C. carnea s.l.	13.59	***	16.51	***	4.58	*
Potato	***H. axyridis***	2.02	ns	2.54	ns	6.81	**
	C. septempunctata	1.72	ns	2.22	ns	9.49	**
	P. quatuordecimpunctata	0.18	ns	0.19	ns	0.01	ns
	E. balteatus	0.86	ns	0.71	ns	0.65	ns
	C. carnea s.l.	10.62	***	9.63	***	23.04	***
Broad bean	***H. axyridis***	0.41	ns	0.2	ns	0.96	ns
	C. septempunctata	2.34	ns	2.78	ns	0.65	ns
	P. quatuordecimpunctata	0.98	ns	0.82	ns	1.25	ns
	E. balteatus	3.94	*	5.14	**	7.98	**
	C. carnea s.l.	17.97	***	22.38	***	0.06	ns

p values come from GLM, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant, $p > 0.05$; bold is used to call attention to specific species

Table 7. ANOVA and ANCOVA summary of the effects of aphid abundance and year sampling (2009, 2010, 2011) on the abundance of five predators at the larval stage in four crops (corn, wheat, potato, and broad bean).

Aphidophages		Years		Years/Aphids		Aphids	
Crop	Species	*F*	*p*	*F*	*p*	*F*	*p*
Corn	***H. axyridis***	39.99	***	41.24	***	2.65	ns
	C. septempunctata	4.69	**	5.02	**	1.06	ns
	P. quatuordecimpunctata	31.86	***	33.62	***	5.06	*
	E. balteatus	9.82	***	8.28	***	7.11	**
	C. carnea s.l.	9.72	***	9.67	***	0.14	ns
Wheat	***H. axyridis***	1.3	ns	1.19	ns	0.88	ns
	C. septempunctata	2.54	**	5.3	**	0.18	ns
	P. quatuordecimpunctata	14.42	***	15.13	***	1.91	ns
	E. balteatus	38.69	***	48.75	***	10.74	**
	C. carnea s.l.	1.87	ns	2.99	ns	2.3	ns
Potato	***H. axyridis***	0.05	ns	0.08	ns	0.77	ns
	C. septempunctata	0.61	ns	0.54	ns	3.85	*
	P. quatuordecimpunctata	1.11	ns	1.11	ns	0.03	ns
	E. balteatus	1.29	ns	2.41	ns	29.79	***
	C. carnea s.l.	0.28	ns	0.21	ns	0.25	ns
Broad bean	***H. axyridis***	1.72	ns	1.59	ns	0.65	ns
	C. septempunctata	4.14	*	3.01	*	102.38	***
	P. quatuordecimpunctata	4.69	**	4.33	*	9.77	**
	E. balteatus	2.59	ns	2.55	ns	0.01	ns
	C. carnea s.l.	2.11	ns	1.43	ns	2.69	ns

p values come from GLM, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant; bold is used to call attention to specific species

Table 8. Mean numbers and SE of aphids/100 m² observed in four fields (wheat, broad bean, corn, and potato) from 2009 to 2011.

Crop	Year	*A. pisum*	*A. craccivora*	*A. fabae*	*A. frangulae*	*A. nasturtii*	*M. euphorbiae*	*M. viciae*	*M. dirhodum*	*M. persicae*	*Rhopalosiphum sp.*	*Sitobion sp.*	TOTAL
Wheat	2009			3.4 + 1.9					2892.2 + 272.0			18.8 + 12.4	2914.3 + 272.1 a
	2010								244.1 ± 38.8			11.3 ± 5.2	255.4 ± 0.4 b
	2011								3491.5 ± 284.9			43.6 ± 14.1	3535.0 ± 287.2 a
Broad bean	2009	42.9 ± 22.2		845.7 ± 337.7				305.7 ± 217.6					1194.3 ± 381.2 a
	2010	454.6 ± 77.2		39.2 ± 31.8					6.8 ± 6.2				500.6 ± 0.8 b
	2011	303.6 ± 43.4		4325.7 ± 1859.5				8.4 ± 4.6					4637.7 ± 1859.2 a
Corn	2009			56.0 ± 16.4					698.6 ± 188.7		45.9 ± 45.8	2.3 ± 2.3	802.8 ± 192.9 b
	2010								2045.2 ± 230.4		300.9 ± 119.2	118.0 ± 14.3	2464.1 ± 2.6 b
	2011								12366.8 ± 1073.4		49.0 ± 16.1	278.9 ± 51.2	12694.7 ± 1098.1 a
Potato	2009			5.7 ± 2.6			1.0 ± 0.9	2.9 ± 1.6					9.5 ± 3.2 c
	2010			10.8 ± 2.9	0.1 ± 0.1	1.9 ± 1.1	14.6 ± 7.7			228.1 ± 62.4			255.6 ± 0.7 b
	2011	0.6 ± 0.4	259.1 ± 33.9	3.1 ± 0.8		458.0 ± 78.3	3.7 ± 1.4			15.4 ± 4.2			739.8 ± 92.1 a