

Article (refereed) - postprint

Honek, Alois; Martinkova, Zdenka; Roy, Helen E.; Dixon, Anthony F.G.; Skuhrovec, Jiri; Pekár, Stano; Brabec, Marek. 2019. **Differences in the phenology of *Harmonia axyridis* (Coleoptera: Coccinellidae) and native coccinellids in Central Europe.** *Environmental Entomology*, 48 (1). 80-87.
<https://doi.org/10.1093/ee/nvy173>

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1 **Differences in the phenology of *Harmonia axyridis* and native**
2 **coccinellids in central Europe (Coleoptera: Coccinellidae)**

3

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15

16

17 **Abstract**

18 *Harmonia axyridis* (Pallas), an invasive non-native species in central Europe, can outcompete
19 other aphidophagous species. The distribution and abundance of *H. axyridis* vary depending
20 on different host plants, and its effects on native coccinellid communities may change
21 accordingly. The distribution and abundance of coccinellids in central Europe (50°N, 14°E)
22 were investigated from 2010 to 2016. Coccinellids were counted at regular intervals on
23 cereals (*Avena*, *Hordeum*, and *Triticum*), herbaceous plants (*Matricaria* and *Urtica*) and trees
24 (*Acer*, *Betula*, and *Tilia*). Additionally, the occurrence over time of each species on these
25 plants was assessed and used as an index of persistence. Across all years, the adults and larvae
26 of *H. axyridis* were the dominant species of coccinellid on trees. However, *H. axyridis* was
27 less abundant on herbaceous plants and cereals than on trees. Populations of native
28 coccinellids and *H. axyridis* co-occurred on trees and persisted for the same length of time,
29 while native coccinellids persisted longer than *H. axyridis* on herbaceous plants and cereals.
30 Compared to 1976–1986, in the 2010s, the abundance of native species decreased on all
31 plants by 50–70%. The presence of *H. axyridis* could be considered as a factor driving
32 changes in the assemblages of native coccinellids.

33

34 **Keywords.** invasive alien species, adults, larvae, cereals, herbaceous plants, trees

35

36

37 **Introduction**

38 *Harmonia axyridis* (Pallas), an invasive alien species in many regions of the world (Roy et al.
39 2016), was first recorded in central Europe (Czech Republic) in 2006 (Sprynar 2008). By
40 2009, it had become abundant, principally on trees but also on herbaceous plants and crops
41 (Honek et al. 2014). This species can outcompete other aphidophagous species (Howe et al.
42 2016) and is an intraguild predator, principally consuming the immature stages of other
43 aphidophagous species (Lucas 2005, Ware et al. 2008a, Ingels et al. 2013). *H. axyridis* is
44 considered not only a threat to biodiversity but also a pest to viticulture and a nuisance to
45 humans because it forms large overwintering aggregations in buildings and occasionally bites
46 humans, which can lead to allergic reactions (Nakazawa et al. 2007, Chakir et al. 2016). The
47 general outline of its life cycle is well known (Honek et al. 2018).

48 There are a number of important determinants of coccinellid occurrence, including host
49 plant, prey abundance and microclimate (Ipert 1999). Some species occur on a wide range of
50 plant species (e.g., *Propylea quatuordecimpunctata* (L.)), while others are specialists on trees
51 (e.g., *Adalia decempunctata* (L.)) or herbaceous plants (e.g., *Hippodamia variegata* (Goeze))
52 (Honek and Rejmanek 1982, Honek 1985). Studies in Western Europe have revealed that *H.*
53 *axyridis* has a preference for trees (Adriaens et al. 2008; Brown et al. 2008, 2011; Panigaj et
54 al. 2014; Roy et al. 2016; Brown and Roy 2018), particularly those growing in urban areas
55 (Purse et al. 2015). In contrast, the abundance of *H. axyridis* is comparatively low on
56 herbaceous vegetation and cereals (Adriaens et al. 2008, Jansen and Hautier 2008). The global
57 distribution of *H. axyridis* is well documented (Roy et al. 2016) but detailed observations on
58 particular hostplants (e.g. Gardiner et al. 2009) are still incomplete. Such studies would not
59 only increase our understanding of the population dynamics of *H. axyridis* but also provide
60 empirical data to underpin predictive models specifically assessing the effects of this alien
61 species on coccinellid assemblages.

62 We studied the variations in the abundance of *H. axyridis* and the community of native
63 species of coccinellids. This is because invasive *H. axyridis* likely affects, by different
64 mechanisms, many species constituting the native community of coccinellids (Bahlai et al.
65 2013, Diepenbrock and Finke 2013, Diepenbrock et al. 2016). The presence of invasive *H.*
66 *axyridis* and native coccinellids was recorded on trees, herbaceous plants and cereals from
67 2010 to 2016. For comparison, we used an existing dataset containing the abundance of
68 coccinellids but spanning 1976 to 1986, before the arrival of *H. axyridis*. The temporal
69 changes in the abundance of coccinellids, including in the later time period, and *H. axyridis*,
70 on particular plants provides the basis for exploring the hypothesis that long-term declines in
71 the abundance of native coccinellids are correlated with the high abundance and wide
72 distribution of *H. axyridis*.

73

74 **Materials and Methods**

75 Field surveys

76 *Harmonia axyridis* and native species of coccinellids were sampled in 2010–2016, in the
77 western part of the Czech Republic in an 11 x 7 km area centred at 50.105°N and 14.264°E.
78 Surveys focused on trees (*Acer platanoides* L., *A. pseudoplatanus* L., *Betula pendula* Roth,
79 *Tilia cordata* Mill., and *Tilia platyphyllos* Scop.), herbaceous plants (*Tripleurospermum*
80 *inodorum* (L.) Schultz-Bip. and *Urtica dioica* L.) and small-grain cereals (*Avena sativa* L.,
81 *Hordeum vulgare* L., and *Triticum aestivum* L.). These host plants were considered as three
82 distinct types: trees, herbaceous plants and cereal crops. The same locations were sampled
83 over the years for the trees and *U. dioica* stands, whereas because of crop rotation, cereal
84 stands and *T. inodorum* were sampled at different sites each year but all within close
85 proximity. Each year surveys on trees started in April and terminated in November. On
86 herbaceous plants and cereals, surveys started when the vegetation was ≥ 30 cm high and

87 terminated when plants became senescent. At particular sites surveys were repeated at 14-day
88 intervals. Sampling was conducted on sunny and calm days, between 08:00–18:00 h. On
89 trees, coccinellids were sampled from the canopy below 3 m in height, on herbaceous plants
90 and cereals, they were sampled from the upper 20–30 cm stratum of vegetation. Coccinellids
91 were sampled by sweeping with a standard entomology net (35 cm diam., 140 cm handle).
92 The same person (AH) carried out all the surveys and ensured similar sampling efficiency in
93 sweeping. Sampling intensity was quantified by the number of sweeps per survey. In each
94 survey, sampling coccinellid adults and larvae on a particular plant at a particular site, lasted
95 15–30 min. Adults and larvae of the 3rd and 4th instars were identified to species, counted, and
96 immediately released at the site. In total, there were 1588 survey visits, with a mean of $129 \pm$
97 1.5 sweeps per survey (range 50–400 sweeps). Localities and dates of sampling are listed in
98 supplementary Table 1 and Table 2. To compensate for the different sampling intensities, in
99 terms of number of sweeps, the numbers of individuals recorded during a particular survey
100 were recalculated to numbers per 100 sweeps (further ‘n/100’) except for the GLM analyses
101 where raw data were used. The duration of persistence of adults and larvae on particular
102 plants was calculated as the difference (days) between the first and the last record in a
103 particular year. The term "persistence" for the native species means persistence at the
104 community level. This term indicates the amount of time for which each taxon, *H. axyridis*
105 and community of native species, was present at a given hostplant in a given year. This metric
106 is useful for understanding differential use of the various plant habitats. To establish long-
107 term changes in the abundance of native coccinellids, the recent data were compared with the
108 data for 1976–1986 when the same surveys were used. In this period, there were 71 surveys
109 on trees, 94 on herbaceous plants and 150 on cereals.

110

111 Data analysis

112 Analyses only included surveys where ≥ 1 coccinellid was captured, i.e., one or more adults
113 of any species in the analysis of adult populations, or one or more larvae of any species in the
114 analysis of larval populations. For 2010–2016, the differences in the abundance of *H.*
115 *axyridis*, and all native species among three plant types (trees, herbaceous plants, and cereals)
116 were compared using generalized estimating equations (GEE). This method is an extension of
117 GLM for correlated data (Yan and Fine 2004). As the sampling dates were nested within
118 years, and an exchangeable correlation structure was used (Pekár and Brabec 2018). To
119 correct for the different sampling intensity each year, the natural logarithm of the total number
120 of sweeps per year was set as an offset in the model formula because we expected that the
121 mean value of abundance would be proportional to the sampling intensity. Total abundance
122 per year was used as a response variable. GEE with a Poisson error structure (GEE-p) was
123 used due to the counting process and heteroscedasticity. The differences in the length of
124 coccinellid occurrence (days between the first and the last record in a particular year) on
125 particular plants were compared using GEE with a normal distribution of errors (GEE). Plant
126 type and coccinellid species (*H. axyridis* and natives) were used as factors. Analyses of
127 abundance and occurrence were performed separately for the adults and larvae. Differences in
128 the abundance of native coccinellid communities among plant types and between two periods,
129 1976–1986 and 2010–2016, were also compared using GEE-p, with an offset of sampling
130 effort and exchangeable correlation structure. Post-hoc tests with Tukey adjustment were used
131 on pairwise comparisons of *H. axyridis* vs. native species for all factor combinations. All
132 analyses were performed in the R program (R Core Team 2015).

133

134 **Results**

135 The abundance of all coccinellids varied between host plants (Table 1). There was a
136 significant interaction between plant type and the abundance of adult coccinellid species

137 (GEE-p, $X^2_2 = 361$, $P < 0.0001$). Adults of *H. axyridis* were dominant on trees (Fig. 1).
138 Indeed, the average abundance (17.8 ± 1.62 n/100) on trees was 7.5 times greater than on
139 herbaceous plants (3.6 ± 2.25 n/100) and 89 times greater than on cereals (0.2 ± 0.06 n/100).
140 The abundance of native coccinellids exhibited a markedly different pattern. The average
141 abundance of native coccinellids on trees (5.2 ± 0.90 n/100) and cereals (9.1 ± 1.92 n/100)
142 was lower compared to that on herbaceous plants (16.7 ± 2.38 n/100). The high abundance of
143 native coccinellids on herbaceous plants and cereals was attributed to the occurrence of
144 *Coccinella septempunctata* L., *Propylea quatuordecimpunctata* (L.) and, on herbaceous
145 plants in some years, also *Ceratomegilla undecimnotata* (Schneider) and *Hippodamia*
146 *variegata* (Goeze). There was also a significant interaction between plant type and larval
147 coccinellid species (GEE-p, $X^2_2 = 286.4$, $P < 0.0001$). The larvae of *H. axyridis* were on the
148 same host plants as the adults (Fig. 1). The average abundance of *H. axyridis* on trees ($8.8 \pm$
149 2.38 n/100) was approximately 3 times greater than that on herbaceous plants (3.4 ± 1.26
150 n/100) and 44 times greater than that on cereals (0.2 ± 0.07 n/100). The abundance pattern of
151 the larvae of native species (Fig. 1) also mirrored that of the adults. The mean abundance on
152 herbaceous plants (17.4 ± 3.45 n/100) was nearly two times greater than that on cereals ($9.3 \pm$
153 4.82 n/100) and 12 times greater than that on trees (1.4 ± 0.23 n/100). In summary, *H.*
154 *axyridis* was dominant on trees, and native coccinellids prevailed on herbaceous plants and
155 cereals.

156 The persistence of coccinellid species on particular plants (Table 1) varied. There was a
157 significant interaction between plant type and coccinellid species for adults (GEE, $X^2_2 = 74$, P
158 < 0.0001 , Fig. 2). Native species persisted longer than *H. axyridis*, particularly on herbs and
159 cereals. On trees, the adults of native species were present for nearly the same period of time
160 (182 ± 5.8 d) as those of *H. axyridis* (179 ± 5.7 d). The difference was greater on herbaceous
161 plants where the adults of native species were present for 118 ± 12.5 d and those of *H.*

162 *axyridis* for 149 ± 11.6 d, and on cereals, where adult native species and *H. axyridis* were
163 present for 77 ± 6.2 d and 33 ± 5.8 d, respectively. There was also a significant interaction
164 between the plant type and the larvae of coccinellid species (GEE, $X^2_2 = 63.9$, $P < 0.0001$).
165 The persistence of larvae was significantly shorter than that of adults (GEE, $X^2_2 = 47.5$, $P <$
166 0.0001). On trees, the larvae of *H. axyridis* persisted for 123 ± 21.0 d, which is longer than
167 that for the larvae of native coccinellids at 96 ± 16.8 d. On herbaceous plants, *H. axyridis*
168 larvae were present for 34 ± 8.9 d and native coccinellids for 94 ± 14.6 d, and on cereals, *H.*
169 *axyridis* and native coccinellids were present for 17.5 ± 2.5 and 35 ± 5.5 d, respectively.

170 We found a significant effect of plant type (GEE-p, $X^2_2 = 40$, $P < 0.0001$) and time
171 period (1976–1986 (early) or 2010–2016 (late)) on the abundance of adults (GEE-p, $X^2_1 =$
172 56.8 , $P < 0.0001$). In the early time period, the average abundance of native coccinellid adults
173 (31.9 ± 1.48 n/100) was 3.1 times greater than in 2010–2016 (9.9 ± 0.71 n/100) (Fig. 3). In
174 both periods, coccinellids were most abundant on wild herbaceous plants. The native
175 coccinellids decreased in abundance mostly on trees between the two time periods; the
176 abundance in the early period was 4.4 times greater than that in the late period, and the
177 abundance was less (3.4 times) on herbaceous plants and least (2.1 times) on cereals. The
178 difference was mainly due to a decline in the abundance of the previously dominant species
179 (Table 2) *A. bipunctata* (abundance decreased 22 times on trees and 84 times on herbaceous
180 plants), *C. septempunctata* (abundance decreased 2–13 times) and *P. quatuordecimpunctata*
181 (abundance decreased 2–7 times). The order of dominance of the species in the communities
182 on particular plants changed over time. Among the most abundant species on trees were
183 *Adalia bipunctata* (L.) and *Adalia decempunctata* (L.), followed by *P. quatuordecimpunctata*
184 in the early period and *C. septempunctata* in the late period. On herbaceous plants, *C.*
185 *septempunctata* and *H. variegata* were dominant, followed by *A. bipunctata* in the early
186 period and *P. quatuordecimpunctata* in the late period. On cereals, *C. septempunctata* and *P.*

187 *quatuordecimpunctata* were dominant, followed by *Coccinella quinquepunctata* L. in the
188 early period and *H. variegata* in the late period.

189

190 **Discussion**

191 *Harmonia axyridis* was the most abundant coccinellid on trees, but it only occurred at low
192 abundance (only a few individuals) on herbaceous and cereals. Other studies across Europe
193 that considered the abundance patterns of coccinellids on different host plants are consistent
194 with the findings from our study in the Czech Republic, with a high frequency of *H. axyridis*
195 on trees (Vandereycken et al. 2012) and *Urtica* (Alhmedi et al. 2007) and a low abundance on
196 most herbaceous plants and field crops except maize (Vandereycken et al. 2013a, b).
197 However, this scenario is not the case further afield. In North America, *H. axyridis* is
198 abundant on cotton (Conway and Kring 2010), maize (Musser and Shelton 2003, Hesler and
199 Kieckhefer 2008), potato (Alyokhin and Sewell 2004), soybean (Hesler 2014) and wheat
200 (Nault and Kennedy 2003) while in Chile it occurs nearly exclusively on alfalfa (Grez et al.
201 2014, 2016). The variation in host plant preference globally may be a consequence of the
202 global genetic diversification of the populations (Lombaert et al. 2010), variations in flight
203 capacity (Lombaert et al. 2014), and opportunistic preferences for anthropogenic habitats
204 (Sloggett 2017). Within the native range of *H. axyridis*, there is also a considerable variability
205 in host plant associations, with a low relative abundance on field crops in eastern Siberia
206 (Kuznetsov and Pinsker 1973, Arefin and Ivliev 1988) but a high abundance on crops in Japan
207 (Komai and Hosino 1951) and China (Liu et al. 2012). In contrast, the occurrence of *H.*
208 *axyridis* on trees is consistently high across its native range (Osawa 2011, Dong et al. 2015,
209 Kuznetsov 1972) and in areas it has recently colonized (Brown 2002, Michaud 2002,
210 Frechette et al. 2008, Milleo et al. 2008, Johnson and Giliomee 2012, Torres-Acosta and
211 Sanchez-Pena 2015).

212 In North and South America, recently invaded *H. axyridis* apparently outcompetes
213 native species on crops (Diepenbrock and Finke 2013, Grez et al. 2016, Diepenbrock et al.
214 2016). One reason for this scenario could be the larger body size of *H. axyridis* compared to
215 that of the native species. A larger body size is advantageous in both competitive interactions
216 and intraguild predation. Crop habitats were populated by small native species (e.g.,
217 *Hippodamia convergens* Guerin, *H. quinquesignata* (Kirby), and *H. sinuata* Mulsant in North
218 America). The large non-native species, *C. septempunctata* and *H. axyridis*, largely replaced
219 the small native species, which may survive and coexist only if they are temporally (Kajita et
220 al. 2000, Kajita and Evans 2010) or spatially segregated (Evans, 2004). In contrast, European
221 coccinellid communities on cereals are dominated by the large *C. septempunctata* (Honek and
222 Rejmanek 1982, Nedved 1999), which endured the competition from *H. axyridis* and
223 remained the dominant species in crops and most herbaceous stands even after the arrival of
224 *H. axyridis*. Similarly in the Eastern Palaearctic, these two species can coexist because of
225 spatial niche segregation: *H. axyridis* occupies trees and *C. septempunctata* herbaceous plant
226 stands (Takahashi 1987).

227 In contrast to the large differences in abundance, there was little difference in the
228 duration of persistence of *H. axyridis* and native coccinellids. Adults were present when the
229 plant foliage was lush and infested with prey. On trees, coccinellids persisted from leaf
230 appearance in late April–early May until leaf fall in late October–early November. Over the
231 course of a growing season, stands of herbaceous plants may be regenerated by cutting
232 (*Urtica*), or the development of plants may occur at different times during the vegetative
233 season (*Tripleurospermum*), and coccinellids can persist on such vegetation for long periods.
234 Native coccinellids, particularly *C. septempunctata*, move readily from patch to patch
235 throughout the vegetative season (Honek 1989), while *H. axyridis* only occupies low-growing
236 patches of vegetation when aphids are abundant on these plants, i.e., in late May to early July

237 (Honek et al. 2015). Consequently, native coccinellids remain longer in patches of wild
238 herbaceous plants than *H. axyridis*. On cereals, the abundance of prey depends to a large
239 extent on the stage of development of the crop. Coccinellids arrive following aphid
240 immigration (May) and leave when the crop matures (July).

241 Evaluating the effect of invasive alien species on native species is critical for
242 biodiversity conservation. Several mechanisms can explain the common persistence of native
243 species and *H. axyridis*: temporal and spatial segregation of native coccinellid and *H. axyridis*
244 populations and physical resistance of native species to intraguild predation or competitive
245 exploitation. On trees *Adalia decempunctata* (L.) and *Calvia quatuordecimguttata* (L.) were
246 able to persist following the arrival of *H. axyridis* but their abundance was reduced (Honek et
247 al. 2016). The survival of *A. decempunctata* populations may be an example of temporal
248 segregation. It appears to be facilitated by alternating temporal presence both species on trees
249 where *A. decempunctata* dominates coccinellid communities until early June and is then
250 replaced by *H. axyridis* (Honek et al. 2015). An example of physical resistance may be *C.*
251 *quatuordecimguttata*. This species may have thrived because the large and mobile larvae may
252 resist intraguild predation by *H. axyridis* (Ware and Majerus 2008); this endurance is further
253 supported by the chemical protection of its eggs (Ware et al. 2008b). An example of spatial
254 segregation was already addressed: *C. septempunctata* and *P. quatuordecimpunctata*
255 successfully resist competition of *H. axyridis* because their breeding takes place mostly on
256 crops and herbs (Honek and Rejmanek 1982, Honek 1985) where the latter species is not
257 abundant.

258 Native coccinellid communities were 2–4 times more abundant in the 1980s than in the
259 2010s (Fig. 2). The large decrease in the abundance of the native species communities was
260 apparent on all plants, regardless of the abundance of *H. axyridis*. However, the change in
261 abundance was most pronounced on trees where *H. axyridis* was abundant and least on

262 cereals where its presence was sporadic. These differences again show importance of overall
263 negative effect of *H. axyridis* on the abundance of native coccinellids.

264 In summary, the data from 2010–2016 provide quantitative evidence of the abundance
265 and persistence of adult and larval coccinellids on different plants. While *H. axyridis* occurs
266 mainly on trees, native coccinellids were most abundant (in terms of individuals) on
267 herbaceous plants, followed by cereals and trees. A comparison with data from 1976–1986
268 revealed a general decrease in the abundance of native coccinellids but with variation in the
269 extent of the decrease in particular plants, which is inversely correlated with the abundance of
270 *H. axyridis*. It is clear that coccinellids and other insects are undergoing rapid large-scale
271 changes in distribution and abundance (Hickling et al. 2006) as well as small-scale changes
272 within habitats and on particular plants. Such changes are likely to be due to a number of
273 interacting factors. The spread of invasive alien species is one such threat. However, the
274 decrease in the overall abundance of native coccinellids, as outlined here, is unlikely to be due
275 solely to the presence of *H. axyridis*. The decline in the abundance of *A. bipunctata* on
276 planted (Honek et al. 2016) and forest trees (Nedved 2014) and of *C. septempunctata* on
277 herbaceous plants and cereals (Honek and Martinkova 2005, Bianchi et al. 2007, Honek et al.
278 2016) was apparent before the arrival of *H. axyridis*. Other changes in native coccinellid
279 communities are also not explained by the arrival of *H. axyridis*, e.g., the extinction of
280 *Coccinella undecimpunctata* L. in the area of this study, the general decline in the abundance
281 of *Coccinella quinquepunctata* L. or, in contrast, the increased abundance of the
282 thermophilous *Ceratomegilla undecimnotata* (Schneider) and *H. variegata*. (Honek et al.
283 2014). The changes indicated that climate and habitat change (for example, through
284 agricultural intensification) may also influence the dynamics of coccinellids (Honek et al.
285 2017). Therefore, the importance of considering multiple, interacting factors when assessing
286 the potential effects of an alien species on biodiversity cannot be overstated.

287

288 **Acknowledgements**

289 AH was supported by grant QJ 1530373 of The Ministry of Agriculture of the Czech
290 Republic, ZM and JS by grant 17-06763S of GACR and RO0418 of The Ministry of
291 Agriculture of the Czech Republic, AFGD by grant no. CZ.1.05/1.1.00/02.0073 of The
292 Ministry of Education of the Czech republic, MB was supported by the long-term strategic
293 development financing of the Institute of Computer Science (Czech Republic RVO
294 67985807) and HER received support from NERC National Capability Funding.

295

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501

502 **Legends to Figures and Tables**

503

504 **Fig. 1.** Comparison of the abundance of adults and larvae of *H. axyridis* and native
505 coccinellids on trees, low growing herbaceous plants (Herbs) and cereals. Statistically
506 significant differences (Tukey post-hoc tests, $P < 0.05$) between *H. axyridis* and Native
507 species within each plant type evaluated separately for adults and larvae are indicated by
508 different letters. Bars are means (\pm SE).

509

510 **Fig. 2.** Duration of persistence of coccinellid populations (the number of days elapsed from
511 the date of capture of the first individual to the day of capture of the last individual) of adults
512 and larvae of *H. axyridis* and native coccinellids on particular plants, trees, low-growing
513 herbaceous plants (Herbs) and cereals. Statistically significant differences (Tukey post-hoc
514 tests, $P < 0.05$) between *H. axyridis* and Native species within each plant type evaluated
515 separately for adults and larvae are indicated by different letters. Bars are means (\pm SE).

516

517 **Fig. 3.** Abundance of adults of native coccinellids on trees, low-growing herbaceous plants
518 (Herbs) and cereals in two periods, 1976–1986 and 2010–2016. Statistically significant
519 differences between plants within periods (Tukey post-hoc tests, $P < 0.05$) are indicated by
520 different letters. Differences between the periods for particular plants are all significant. Bars
521 are means (\pm SE).

522

523 **Table 1.** The occurrence of adults and larvae of *H. axyridis* and native coccinellids on trees,
524 low-growing herbaceous plants (Herbs) and small grain cereals in 2010–2016. For each plant
525 and year, the table indicates number of samples and species collected; for *H. axyridis* and the
526 community of native coccinellids, the number (n) of individuals, mean abundance (number of

527 individuals * 100 sweeps⁻¹ [n/100]) and the characteristics of temporal persistence, date of the
528 first catch (Start), date of the last catch (End) and number of days (d) from the first to the last
529 catch (Length) are indicated. Mean values of Abundance (Fig. 1) and Length (Fig. 2) are
530 presented in graphs. Each sample represents a set of individuals collected on a particular date
531 on a group of trees, a herb stand or in a field.

532

533 **Table 2.** Composition of native coccinellid communities sampled in the early (1976–1986)
534 and late (2010–2016) periods on trees, low-growing herbaceous plants (Herbs) and cereals
535 (for a list of species see Methods). Total number of adults (n) and average abundance (n
536 individuals * 100 sweeps⁻¹, n/100) is in brackets, and bold figures indicate dominant species
537 in terms of abundance.

538

539

1 **Table 1.** The occurrence of adults and larvae of *H. axyridis* and native coccinellids on trees, low-growing herbaceous plants (Herbs) and small
2 grain cereals in 2010–2016. For each plant and year, the table indicates number of samples and species collected; for *H. axyridis* and the
3 community of native coccinellids, the number (n) of individuals, mean abundance (number of individuals * 100 sweeps⁻¹ [n/100]) and the
4 characteristics of temporal persistence, date of the first catch (Start), date of the last catch (End) and number of days (d) from the first to the last
5 catch (Length) are indicated. Mean values of Abundance (Fig. 1) and Length (Fig. 2) are presented in graphs. Each sample represents a set of
6 individuals collected on a particular date on a group of trees, a herb stand or in a field.

	Total			<i>Harmonia axyridis</i>				Native species				
	Samples n	Species N	Individuals n	Abundance n/100±SE	Persistence			Individuals n	Abundance n/100±SE	Persistence		
					Start	End	Length d			Start	End	Length d
Adults												
Trees												
2010	56	15	839	15.5±2.70		08-Oct		465	8.5±1.02		08-Oct	
2011	120	15	2643	17.0±3.57	20-Apr	18-Oct	181	1049	7.3±1.06	20-Apr	18-Oct	181
2012	96	19	2412	18.0±2.84	09-May	19-Oct	163	994	7.2±1.26	09-May	19-Oct	163
2013	109	16	1707	12.3±2.34	04-May	16-Oct	165	478	3.7±0.85	04-May	16-Oct	165
2014	160	20	3716	14.6±3.12	19-Apr	04-Nov	199	756	3.1±0.55	19-Apr	05-Nov	200
2015	165	17	4807	24.0±3.07	22-Apr	03-Nov	195	654	3.2±0.41	22-Apr	03-Nov	195
2016	198	17	4070	23.0±1.96	06-May	08-Nov	186	678	3.3±0.43	06-May	09-Nov	187
Herbs												
2010	25	11	23	1.5±0.29		11-Aug		611	26.2±7.05		11-Aug	
2011	79	15	1271	17.1±3.54	19-May	23-Aug	96	1539	20.4±2.82	19-May	23-Aug	96
2012	67	12	90	1.5±0.57	24-May	15-Oct	144	1416	16.9±3.62	09-May	19-Oct	163
2013	62	14	32	0.4±0.13	20-May	04-Oct	137	683	7.1±1.69	15-May	04-Oct	142
2014	64	17	101	0.9±0.39	08-May	17-Sep	132	1043	10.2±2.81	08-May	04-Nov	180
2015	75	16	199	2.3±0.78	18-May	26-Oct	161	1076	11.2±3.38	05-May	26-Oct	174

2016	47	11	91	1.7±0.36	08-Jun	19-Aug	72	1173	25.0±7.07	09-May	26-Sep	140
Cereals												
2010	19	8	3	0.1±0.09	09-Jul	16-Jul	7	221	9.0±1.02		22-Jul	
2011	57	10	31	0.3±0.16	29-Jun	03-Aug	35	1857	17.3±1.06	10-May	03-Aug	85
2012	37	8	7	0.1±0.09	02-Jul	26-Jul	24	688	11.6±1.26	09-May	26-Jul	78
2013	55	6	3	0.0±0.03	20-Jun	17-Jul	27	342	3.1±0.85	13-May	16-Aug	95
2014	46	9	8	0.1±0.08	17-Jun	01-Aug	45	802	10.9±0.55	06-May	06-Aug	92
2015	19	7	2	0.1±0.07	26-Jun	01-Aug	36	236	8.6±0.41	02-Jun	01-Aug	60
2016	32	11	28	0.5±0.28	30-May	23-Jul	54	138	2.7±0.43	30-May	23-Jul	54
Larvae												
Trees												
2012	31	5	114	3.3±0.77	21-May	09-Oct	141	69	1.8±0.80	09-May	27-Jul	79
2013	34	7	207	4.9±1.64	19-Jun	08-Sep	81	38	1.0±0.33	17-Jun	15-Sep	90
2014	64	7	953	8.6±3.72	19-May	05-Nov	170	80	0.8±0.29	21-May	19-Oct	151
2015	44	6	519	10.0±3.01	18-May	23-Jul	66	113	2.3±0.74	18-May	07-Jul	50
2016	89	7	1303	17.0±3.43	27-May	02-Nov	159	106	1.1±0.32	06-Jun	23-Sep	109
Herbs												
2012	15	7	26	1.8±0.81	23-May	06-Jul	44	200	14.7±4.85	23-May	15-Oct	145
2013	18	7	8	0.3±0.22	08-Jul	27-Jul	19	305	8.6±4.70	28-Jun	24-Aug	57
2014	17	7	204	8.4±8.81	18-Jun	18-Aug	61	297	11.2±9.02	15-May	06-Aug	83
2015	23	7	122	4.9±2.08	11-Jun	16-Jul	35	697	21.0±5.18	04-Jun	26-Aug	83
2016	23	7	33	1.3±0.50	16-Jun	27-Jun	11	860	31.5±15.47	16-Jun	26-Sep	102
Cereals												
2012	15	3	6	0.3±0.34	05-Jul	05-Jul		808	32.0±15.27	29-May	11-Jul	43
2013	16	4	1	0.0±0.06	17-Jul	17-Jul		100	3.1±1.71	28-Jun	02-Aug	35
2014	22	4	11	0.3±0.21	02-Jul	17-Jul	15	78	1.9±0.77	17-Jun	27-Jul	40
2015	9	3	0	0.0±0.00				66	4.9±1.55	03-Jul	17-Jul	14
2016	18	3	12	0.4±0.31	23-Jun	13-Jul	20	188	4.8±5.97	10-Jun	23-Jul	43

8

9

1 **Table 2.** Composition of native coccinellid communities sampled in the early (1976–1986) and late (2010–2016) periods on trees, low growing
 2 herbaceous plants (Herbs) and cereals (for list of species see methods). Total number of adults (n) and average abundance (n individuals * 100
 3 sweeps⁻¹, n/100) in bracketts, bold figures indicate dominant species in terms of abundance.

4

	1976–1986						2010–2016					
	Trees		Herbs		Cereals		Trees		Herbs		Cereals	
	n	n/100	n	n/100	n	n/100	n	n/100	n	n/100	n	n/100
<i>Adalia bipunctata</i>	585	(9.81)	1290	(26.77)	10	(0.04)	416	(0.45)	130	(0.32)		
<i>Adalia conglomerata</i>							1	(0.00)				
<i>Adalia decempunctata</i>	209	(3.33)	11	(0.15)	2	(0.01)	1150	(0.98)	16	(0.04)	1	(0.00)
<i>Anatis ocellata</i>	7	(0.09)			1	(0.00)	8	(0.01)	1	(0.00)		
<i>Aphidecta oblitterata</i>	4	(0.04)					83	(0.07)			1	(0.00)
<i>Calvia decemguttata</i>	9	(0.22)					443	(0.44)	2	(0.01)	1	(0.00)
<i>Calvia quatuordecimguttata</i>	19	(0.35)	11	(0.24)			287	(0.28)	38	(0.09)	5	(0.01)
<i>Ceratomegilla undecimnotata</i>									251	(0.72)	2	(0.00)
<i>Chilocorus bipustulatus</i>							38	(0.03)	1	(0.00)		
<i>Coccidula rufa</i>			6	(0.13)								
<i>Coccinella quinquepunctata</i>	54	(1.76)	58	(1.00)	295	(1.39)	29	(0.02)	425	(0.69)	57	(0.13)
<i>Coccinella septempunctata</i>	105	(1.32)	593	(12.27)	3603	(13.46)	1151	(0.99)	3617	(7.30)	2715	(5.87)
<i>Coccinella undecimpunctata</i>	1	(0.02)	164	(3.49)	19	(0.08)						
<i>Coccinulla quatuordecimpustulata</i>									3	(0.01)		
<i>Exochomus quadripustulatus</i>	2	(0.03)	1	(0.02)			269	(0.26)	2	(0.00)		
<i>Halyzia sedecimguttata</i>							138	(0.15)	5	(0.01)		
<i>Harmonia quadripunctata</i>							24	(0.02)				
<i>Hippodamia septemmaculata</i>									2	(0.01)	1	(0.00)
<i>Hippodamia variegata</i>	3	(0.02)	207	(4.34)	8	(0.03)	4	(0.00)	1657	(3.20)	105	(0.26)
<i>Oenopia conglobata</i>	34	(0.56)	16	(0.34)			358	(0.32)	3	(0.01)		
<i>Propylea quatuordecimpunctata</i>	259	(2.93)	192	(3.67)	1398	(5.09)	462	(0.42)	549	(1.14)	1264	(2.92)
<i>Psyllobora vigintiduopunctata</i>	2	(0.01)					117	(0.11)	391	(0.90)	10	(0.02)
<i>Rhyzobius litura</i>							5	(0.01)			2	(0.00)
<i>Scymnus sp.</i>			1	(0.02)			18	(0.02)	10	(0.02)	2	(0.00)
<i>Subcoccinella vigintiquatuor punctata</i>							48	(0.03)	47	(0.11)	15	(0.04)

Tytthaspis sedecimpunctata

2 (0.00)

383 (0.97)

103 (0.22)

5
6





