



Long-term changes in communities of native coccinellids: population fluctuations and the effect of competition from an invasive non-native species

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Abstract. 1. We assessed the changes in abundance and community composition of native species of coccinellids (Coleoptera: Coccinellidae) on deciduous trees that occurred between 1970s and 2010s, in the Czech Republic.

2. As the composition of adult communities varies with host plant and season, coccinellids were sampled in May–June from *Acer*, *Betula* and *Tilia* trees using a standardised sweeping method. This was done before (1976–1986) and after (2011–2014) the arrival of *Harmonia axyridis* in 2006, with interim samples from a period immediately before it arrived in the Czech Republic (2002–2006).

3. Twenty-one native species were identified in the total sample of 2674 adults. The abundance of *Adalia bipunctata*, *Coccinella quinquepunctata* and *Propylea quatuordecimpunctata* decreased over the whole period sampled. Declines in abundance of these species were already evident prior to the arrival of *H. axyridis*. Recent declines in *Adalia decempunctata* and *Calvia quatuordecimguttata* followed the arrival *H. axyridis*. Their abundance was increasing prior to the arrival of *H. axyridis*, but decreased following its invasion and the latter species might have affected their decline. The abundance of only one species, *Calvia decemguttata*, increased. Although the abundance of many species decreased and the frequency of some species varied, the diversity of native coccinellid populations (Shannon index) was similar over the 40 years of this study.

4. The changes in species composition can in part be attributed to *H. axyridis*, the role of other factors (e.g. climate change, habitat degradation) in the long-term fluctuations in abundance of coccinellids should be considered in future assessments.

Key words. *Adalia*, *Anatis*, *Calvia*, *Coccinella*, *Halyzia*, *Harmonia*, intraguild predation, invasive alien species, ladybird beetles, *Propylea*.

Spread of non-native organisms in areas outside their native geographic range are an important problem in a globalised World (Hulme, 2009). Invasive non-native species in recently occupied areas frequently cause economic

loss or become a threat to biodiversity (DAISIE, 2009; Vila *et al.*, 2011). An important rapidly spreading invader is the Harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), which is native to eastern Asia and Siberia (Roy & Brown, 2015). After unsuccessful attempts to introduce it into Europe and North America, this aphidophagous species, originally considered a useful biological control agent, started to spread spontaneously

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through tropical and temperate biotas around the world with the exception of Australia (Brown *et al.*, 2008; Roy *et al.*, 2012). In addition to its supposed positive role in regulating pest aphid populations on crops, it has negative effects on native guilds of aphid predators (Pell *et al.*, 2008). In recently occupied areas, *H. axyridis* is a top intraguild predator and potentially negatively affects the diversity of native aphidophagous species (Roy *et al.*, 2012). Under laboratory conditions, larvae of this species win inter-specific contests and eat larvae of native coccinellids and other aphidophagous insects. Consequently, *H. axyridis* is predicted to decrease the diversity of native coccinellid communities (Pell *et al.*, 2008). Therefore, it is relevant to study the long-term changes in the abundance of native species of ladybirds.

The dominance of *H. axyridis* within coccinellid communities since its establishment through western Europe has been extensively documented (Brown *et al.*, 2011; Panigaj *et al.*, 2014). The negative consequences of *H. axyridis*, through competition and predation, have been demonstrated (Brown *et al.*, 2008; Roy *et al.*, 2012; Roy & Brown, 2015). However, as for many other invaded communities, it is difficult to precisely quantify the effect of invasive non-native species on native coccinellid communities. The lack of records of coccinellids for years before the arrival of *H. axyridis* can be limiting; indeed, many studies were initiated after its arrival and so document developments in native coccinellid communities in which *H. axyridis* is already present (Eschen *et al.*, 2007; Adriaens *et al.*, 2008; Roy *et al.*, 2012). Occurrence data compiled over decades by volunteer recorders can be used to assess distribution trends before and after the arrival of an invasive non-native species (Roy *et al.*, 2012). However, these long-term datasets comprise occurrence data that are not collected systematically (Pocock *et al.*, 2015). Therefore, datasets comprising abundance of species sampled in a standard way (standardising part of season and sampled host plant species) can provide valuable additional population-level information.

Here, we evaluate the community composition of coccinellid species and compare their abundance and distribution before and after the arrival of *H. axyridis*. It is possible to evaluate the changes that occurred in the species composition of all the coccinellids in a community including *H. axyridis* after its invasion. In doing this, the mere presence of an added component changes the relative abundance of native species and characteristics of the community. In this case, the invasive non-native species becomes a part of the form taken by the community, and as a consequence, a 'formal cause' of the change. Alternatively, one may compare the community of native coccinellids *per se*, i.e. the assemblage of species in this community before and after the invasion of *H. axyridis*. The introduced species can then be considered an 'efficient cause', an external factor acting upon the native community, which changes its abundance, diversity, equitability, etc. The meaning of the term 'community of native coccinellids' is adopted in this paper when evaluating long-

term changes in communities caused by an invading species.

Our main interest is in the processes determining the structure of native coccinellid communities, which may have been affected by the arrival of *H. axyridis*. The long-term (1976–2014) standardised, systematic surveys of the abundance of coccinellids on different host plants within the Czech Republic provide an invaluable source of data for evaluating the effects of *H. axyridis* on coccinellid communities (Honek *et al.*, 2014). The aim of this paper is to describe the pattern in the long-term changes that have occurred in the structure of communities. We used a part of this data, those collected from trees and at a particular time of the year. This was done to determine whether (i) the species composition of a native coccinellid community varied over time and (ii) the arrival of *H. axyridis* has adversely affected native coccinellid communities.

Material and methods

Coccinellids were sampled in the western part of the Czech Republic. Sampling was performed in a c. 50 km² area at north-west margin of Prague situated in between 50.08 and 50.14 N and 14.21 and 14.33 E (see Honek *et al.*, 2015 for details). At this area, coccinellids were sampled at 24 sites with an area of 0.2–0.5 ha grown by a stand of tree species sampled for coccinellid presence. At each site, there was a group of ≥ 5 trees of a particular species aged ≥ 30 years, and at some sites, there were more than one species of tree (Honek *et al.*, 2015). The sampled tree species were lime (*Tilia cordata* Mill. and *Tilia platyphyllos* Scop.), maple (*Acer platanoides* L. and *Acer pseudoplatanus* L.) and birch (*Betula pendula* Roth.). A sampling of coccinellids at particular site, tree species and date is further called a sampling session. We limited the analysis to data of sampling sessions made in May–July whose list is provided in Appendix S1. The beetles were swept from the lower canopy (below c. 3 m height) using an entomology sweepnet (35 cm diam., 140 cm handle). The survey was standardised by using the same person (AH) to collect the beetles and a standard sweepnet. Sampling was done on sunny and still days, between 08:00 and 18:00 h. Each sampling session lasted 15–30 minute depending on the number of trees. The coccinellid adults were identified to species immediately and released at the site. This was done from 1976 to 1986 (period 1 = P1, 56 sampling sessions), 2002–2006 (period 2 = P2, 28 sessions) and 2011–2014 (period 3 = P3, 245 sampling sessions). In total, there were 329 sampling sessions with a mean of 113 ± 4 (range 50–300) sweeps per session. The coccinellids were thus sampled long before (P1), shortly before (P2) and shortly after (P3) the arrival of *H. axyridis* to central Czech Republic in 2006 (Sprynar, 2008).

For each sampling session, the number of individuals of each species per 100 sweeps was counted. We compared the coccinellid communities in the three periods by assessing the changes in (i) the abundance of the following ten

dominant species: *Adalia bipunctata* (L.), *A. decempunctata* (L.), *Anatis ocellata* (L.), *Calvia decemguttata* (L.), *C. quatuordecimguttata* (L.), *Coccinella quinquepunctata* L., *C. septempunctata* L., *Oenopia conglobata* (L.), *Propylea quatuordecimpunctata* (L.), and *Halyzia sedecimguttata* (L.); and (ii) indices of community structure. All collected species (regardless of their trophic specialisation) were used to calculate the indices describing community structure: (i) Shannon index of diversity, H' , calculated as $H' = -\sum(p_i * \ln(p_i))$, where p_i is the proportion of the total number of captured individuals of species i and N is the total number of individuals in the sample. Indices were calculated using data for each sampling session in which >1 species were captured.

Data on abundance, Shannon index of diversity and Simpson index of dominance were subjected to linear mixed-effect model (LME) (Pinheiro & Bates, 2000) to assess the change over study periods as the samples were taken repeatedly at the same sites. Abundance of beetles was log-transformed prior to analysis in order to homogenise variance. The linear predictor contained beetle species and period as fixed effects and date of sampling and sites as random effects. Comparisons of mean estimates were done based on 95% confidence intervals. Data on diver-

sity (H') and dominance (c) estimated for each sampling date and site were not transformed prior to analysis by LME. The linear predictor included interaction between month and period as fixed effects and date of sampling and sites as random effects. Comparisons of mean estimates were based on linear contrasts. Analyses were performed in R environment (R Core Team 2015).

Results

There were 21 species in the community of native coccinellids studied (Table 1). Eight species were present in all three periods and the other 13 species only in some of the periods. Differences in abundance over three periods were analysed for 10 abundant species (Fig. 1). The effect of species: site interaction was significant (LME, $F_{9,3247} = 35.5$, $P < 0.0001$) revealing that the temporal change over study periods was species specific. None species was significantly more abundant ($P < 0.05$) in P3 (2011–2014) than in P1 (1976–1986). Three species, *A. bipunctata*, *P. quatuordecimpunctata* and *C. quinquepunctata* were significantly more abundant ($P < 0.05$) in P1 than in P3 (Fig. 1). For five species, *C. septempunctata*, *O. conglobata*, *C. decemguttata*, *Anatis ocellata* and *Halyzia sedecimguttata*, their abundances did not differ

Table 1. Numbers of individuals of native and invasive coccinellid species recorded on *Acer* spp., *Betula* spp. and *Tilia* spp. in May–July, in 1976–1986 (period P1, total 6042 sweeps), 2002–2006 (P2, 3269 sweeps) and 2011–2014 (P3, 27941 sweeps).

	Species	Year			Total
		1976–1986	2002–2006	2011–2014	
	Native				
1	<i>Adalia bipunctata</i> (L.)	331	72	117	520
2	<i>Adalia conglomerata</i> (L.)	0	0	1	1
3	<i>Adalia decempunctata</i> (L.)	96	194	572	862
4	<i>Anatis ocellata</i> (L.)	5	3	0	8
5	<i>Aphidecta oblitterata</i> (L.)	4	0	24	28
6	<i>Calvia decemguttata</i> (L.)	9	13	107	129
7	<i>Calvia quatuordecimguttata</i> (L.)	13	48	153	214
8	<i>Chilocorus bipustulatus</i> (L.)	0	0	16	16
9	<i>Coccinella quinquepunctata</i> L.	50	0	3	53
10	<i>Coccinella septempunctata</i> L.	69	13	180	262
11	<i>Coccinella undecimpunctata</i> L.	1	0	0	1
12	<i>Exochomus quadripustulatus</i> (L.)	0	0	15	15
13	<i>Halyzia sedecimguttata</i> (L.)	0	0	34	34
14	<i>Harmonia quadripunctata</i> (Pontoppidan)	0	0	5	5
15	<i>Hippodamia variegata</i> (Goeze)	3	0	0	3
16	<i>Oenopia conglobata</i> (L.)	26	18	118	162
17	<i>Propylea quatuordecimpunctata</i> (L.)	197	8	133	338
18	<i>Psyllobora vigintiduopunctata</i> (L.)	2	2	11	15
19	<i>Rhyzobius litura</i> (F.)	0	0	3	3
20	<i>Scymnus</i> sp.	0	0	3	3
21	<i>Subcoccinella vigintiquatuoropunctata</i> (L.)	0	0	2	2
	Total	806	371	1497	2674
	Invasive				
24	<i>Harmonia axyridis</i> (Pallas)	0	0	2373	2373

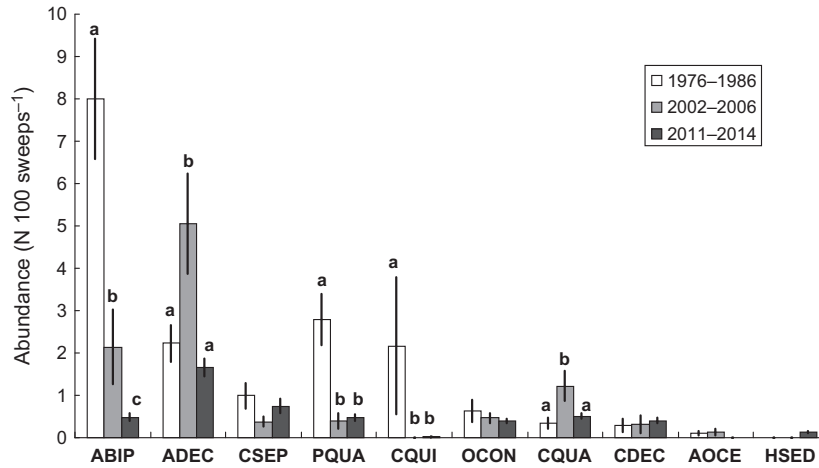


Fig. 1. Comparison of average abundance (\pm SE) of coccinellid species in period 1 (1976–1986), 2 (2002–2006) and 3 (2011–2014). Acronyms: ABIP – *Adalia bipunctata*, ADEC – *Adalia decempunctata*, CSEP – *Coccinella septempunctata*, PQUA – *Propylea quatuordecimpunctata*, CQUI – *Coccinella quinquepunctata*, OCON – *Oenopia conglobata*, CQUA – *Calvia quatuordecimguttata*, CDEC – *Calvia decemguttata*, AOCE – *Anatis ocellata*, HSED – *Halyzia sedecimguttata*. Statistically significant differences ($P < 0.05$) are indicated by different letters.

significantly among periods ($P > 0.05$). In two species, *A. decempunctata* and *C. quatuordecimguttata*, their abundances in P2 were significantly higher than in both P1 and P3 ($P < 0.05$).

Despite the changes in abundance of particular species, the community structure was similar in the periods 1976–1986 (P1) and 2011–2014 (P3). The community characteristics were calculated for native species not including *H. axyridis*, which in P3 was present at all the sites investigated and caught on 220 out of 245 (90%) sampling sessions. The average Shannon diversities in P1 ($H' = 0.456 \pm 0.033$) and P3 ($H' = 0.436 \pm 0.013$) were not significantly different (LME, $F_{1,316} = 1.2$, $P = 0.25$).

With the exception of the dominant species (P1: *A. bipunctata* - 41.1% of the total sample; P3 *A. decempunctata* 38.2%) and two subdominant species, all minority species with rankings of 4–18 in their order of abundance in particular samples, were more abundant in P3 than P1 (Fig. 2). An important difference between the communities recorded in P1 and P3 was the seasonal variation in H' . In P1, there was no seasonal trend in H' (LME, $F_{2,28} < 0.1$, $P = 0.93$), whereas in P3 the values of H' significantly increased (LME, $F_{1,355} = 5.4$, $P = 0.005$) from May to July (Fig. 3a). This was due to an opposite trend in species dominance indicated by the Simpson index. While in P1, there was no significant change between

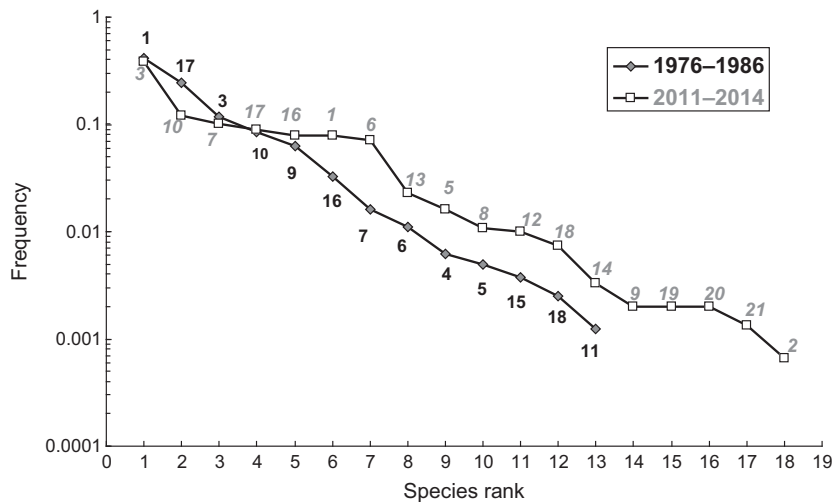


Fig. 2. Frequency (proportion in the total sample of all native species) of particular species of coccinellids ranked in order of their abundance, in period 1 (1976–1986) and period 3 (2011–2014). The species are identified by figures shown in Table 1 (P3 in italics).

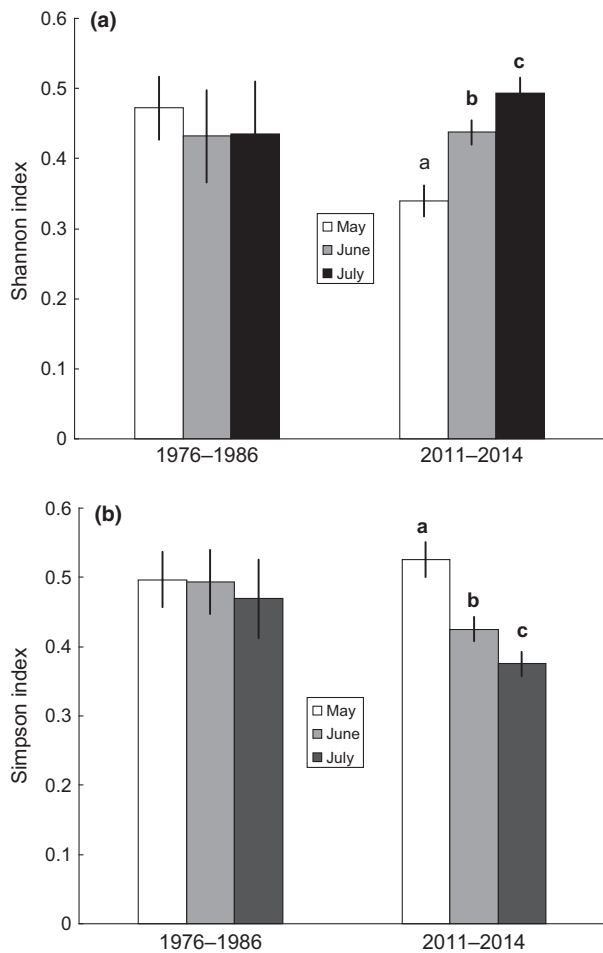


Fig. 3. Composition of the native coccinellid community in period 1 (1976–1986) and period 3 (2011–2014). (a) Shannon index of diversity (H') and (b) Simpson index of species dominance (c). The results of May–July are presented separately; statistically significant differences ($P < 0.05$) are indicated by different letters.

periods (LME, $F_{1,315} = 0.7$, $P = 0.38$), the Simpson index revealed a significant decrease (LME, $F_{1,358} = 6.7$, $P = 0.01$) in P3 from May to July (Fig. 3b).

Discussion

The abundance and species composition of native coccinellids in the community studied differed in the periods long before (P1: 1976–1986) and shortly after (P3: 2011–2014) the arrival of *H. axyridis*. Abundance of the most dominant species decreased and that of a single species increased, however, with little effect on diversity and dominance indices of the community. One unique difference between the two time periods was the presence of *H. axyridis*, which spread dramatically after 2007 (Brown *et al.*, 2008). *H. axyridis* has indirect and direct effects on other species in aphidophagous coccinellid communities,

particularly those species with a high niche overlap (Comont *et al.* 2014). It is considered to be an intraguild predator (Pell *et al.*, 2008) not only of other coccinellids (Burgio *et al.*, 2005) but also of other taxa belonging to this guild (Ingels & De Clercq, 2010; Wells *et al.*, 2010). Consequently, it may be responsible for some of the changes that have occurred in the abundance of other species and hence the composition of the native coccinellid community. However, it is widely acknowledged that the interactions between drivers of change, such as habitat modification and the arrival of non-native species, rather than a single factor is likely to be responsible for changes in community assemblages (Didham *et al.*, 2007; Bahlai *et al.*, 2015). We examined population trends shortly before the arrival of *H. axyridis* (P2: 2002–2006) to distinguish the effect of long-term trends in population density of particular species from that of any detrimental effect of predation and competition from an invasive non-native species. The data for P2 have, therefore, an important auxiliary function in that they provide an insight into whether the populations of the different species were increasing, stable or decreasing just before the arrival of *H. axyridis*.

The first hypothesis tested was whether the recent species composition of a native coccinellid community is different from that recorded 30–40 years ago. This prediction is supported because one species, *C. quinquepunctata*, virtually disappeared. Eight abundant species remained dominant components of this community, but their abundances changed over time. The abundance of two species (*A. bipunctata*, *P. quatuordecimpunctata*) significantly decreased, whereas abundance of six species (*A. decempunctata*, *C. septempunctata*, *O. conglobata*, *C. quatuordecimguttata*, *C. decemguttata*, and *Halyzia sedecimguttata*) remained similar. Species of coccinellids vary in a number of life history traits, including phenology (Hodek *et al.*, 2012). Therefore, changes in the composition of coccinellid communities will have consequences for the functioning of ecosystems. However, it is difficult to determine the extent and magnitude of changes to community structure on ecosystem function.

The second hypothesis tested was whether the arrival of *H. axyridis* adversely affected the native coccinellid community studied. In order to achieve this aim, it was necessary to make a distinction between temporal co-occurrence and causal determination. The two species that significantly decreased in abundance (*A. bipunctata*, *P. quatuordecimpunctata*) were already significantly less abundant before (P2) the arrival of *H. axyridis* (in P1), and thus the decrease cannot be attributed solely to *H. axyridis*. This is well documented for the formerly dominant *A. bipunctata*, whose abundance decreased shortly before (P2) the arrival of *H. axyridis* to about one-quarter and subsequently shortly after (P3) the arrival of *H. axyridis* to less than one-tenth of its original value long before (P1) the arrival of *H. axyridis*. A long-term study of *A. bipunctata* abundance at a locality in the north-west of the Czech Republic from 1986 to 2010 (Nedved, 2014)

indicates that the decline in abundance started in the late 1980s. In 2005–2010, the species was rare and in terms of abundance was less than one-tenth of those recorded in 1986–1991. Similar decline in the abundance of *A. bipunctata* was recorded in western (Roy *et al.*, 2012) and eastern Europe (I. A. Zaslavskii, pers. comm.). While in the UK, the decline in the abundance of *A. bipunctata* coincided with arrival of *H. axyridis* (Roy *et al.*, 2012), in Central and Eastern Europe, it preceded the arrival of this species. Therefore, a direct effect of *H. axyridis* on populations of *A. bipunctata* in the Czech Republic is difficult to evaluate. Similarly in Belgium, *A. bipunctata* was declining prior to the arrival of *H. axyridis*, but the rate of decline increased after the arrival of *H. axyridis* (Roy *et al.*, 2012), which might indicate an interaction between drivers of biodiversity decline. For example, intensification of agricultural practices coupled with the arrival of *H. axyridis* are likely to be important factors in determining the community dynamics of coccinellids.

The abundance of *C. quinquepunctata* and *P. quatuordecimpunctata* also dramatically decreased just before (P2) the arrival of *H. axyridis*. Both species occur in trees prior to moving to crops in spring and after harvest in late summer, and in early autumn, they again occupy trees (Honek, 1982, 1985a). They mainly breed in crops (Honek, 1982, 1985a) where they are unlikely to be subject to intensive competition from *H. axyridis* (Vander eycken *et al.*, 2013a,b; Honek *et al.*, 2014). Very few *C. quinquepunctata* were recorded on trees during P2 and P3. This species breeds mainly in stressed sparse stands of cereals (Honek, 1985a), which are infested by few aphids (Honek, 1985b). Consequently, the decrease in cereal aphid abundance may negatively affect the abundance of *C. quinquepunctata* in the same way as was demonstrated in *C. septempunctata* (Honek & Martinkova, 2005). Causes of local extinction of *A. ocellata* are possibly linked to the abandonment of hop gardens, but this requires further investigation. In 1970–1980, *A. ocellata* dominated coccinellid communities in hop gardens (A. Honek, unpubl. data). The recent dramatic decline in hop growing in the Czech Republic might have contributed to the decline in this species. Thus, changes in abundance of some coccinellids are probably a consequence of long-term oscillations in species abundance driven by changes to habitats rather than the direct effects of *H. axyridis*. Therefore, the second hypothesis, whether the arrival of *H. axyridis* adversely affected the native coccinellid community studied, is not fully supported by our long-term studies.

Some changes in species abundance could be attributed to competition from *H. axyridis*. The abundance of *A. decempunctata* increased from P1 to P2 and decreased in P3. An increase in *A. decempunctata* numbers in P2 compared to P1 might be due to decline in competition from *A. bipunctata*, which has a high niche overlap with *A. decempunctata* (Honek & Rejmanek, 1982). The decline in abundance of *A. decempunctata*, which occurred between P2 and P3 is concurrent with the arrival of *H. axyridis*

and might result from competition with this species, which also favours deciduous trees. Similar increases in abundance from P1 to P2 followed by declines between P2 and P3 were recorded for *C. quatuordecimguttata*. Although eggs of *C. quatuordecimguttata* are chemically protected from predation (Ware *et al.*, 2008), competition from *H. axyridis* could be a possible cause of decline. Much of the research on interactions between *H. axyridis* and other aphidophagous species has focused on predation (Burgio *et al.*, 2005; Pell *et al.*, 2008; Ingels & De Clercq, 2010), however, there is considerable scope to explore competitive interactions. Such research could provide important insights into the complex dynamics of species within the aphidophagous guild.

The frequency of some species and the overall community assemblage of native coccinellids changed from P1 to P3. Formerly dominant *A. bipunctata* was replaced in order of dominance with *A. decempunctata*. The order of the other species ranked according to their abundance varied. Abundant species ranking 2–4 were different in P1 (*P. quatuordecimpunctata*, *A. decempunctata*, *C. septempunctata*) and P3 (*C. septempunctata*, *C. quatuordecimguttata*, *P. quatuordecimpunctata*). A highly significant difference between P1 and P3 is the seasonal variation in community diversity. Unlike in P1, diversity (Shannon index H') in P3 significantly increased during the course of the season. The trend recorded in 2011–2014 was due to a decrease in abundance of the dominant *A. decempunctata* within each year (Honek *et al.*, 2015) while in 1976–1986, there was no seasonal trend in the abundance of the dominant species, in this case *A. bipunctata*. The variation in abundance of the dominant species across seasons may be a consequence of life history characteristics of these species. Thus, catches from a light-trap at Prague-Ruzyně in 1973–1989 (i.e. before the arrival of *H. axyridis*) revealed a narrower period of flight activity of *A. decempunctata* (late May – late August) and an extended period of flight activity in *A. bipunctata* (March – November) (A. Honek and Z. Martinkova, unpubl. data). Arrival of *H. axyridis* might further contribute to seasonal variation in *A. decempunctata* activity through competition for food. This competition increases progressively through the season, in parallel with increasing abundance of *H. axyridis* in tree habitats (Honek *et al.*, 2015).

In conclusion, the composition of native coccinellid communities changed during the course of this long-term (nearly 40 years) study. Although there is some evidence to suggest that *H. axyridis* is responsible for declines in some coccinellid species, it is likely that there are many other interacting factors contributing to the change in community composition, particularly habitat modifications over the study period. We demonstrate the importance of long-term datasets for documenting changes in communities over time, but also highlight the need to consider the complexities of ecological systems when unravelling the mechanisms behind such change. Changes in the composition of native coccinellid communities will be affected not only by the arrival of new species but also

long-term changes in environmental factors. The effects of climate change, which are hard to forecast in terms of pace and pattern, will undoubtedly affect coccinellid communities (Roy & Majerus, 2010). Native coccinellid species (Dobzhansky, 1933) as well as *H. axyridis* (Komai, 1956), are capable of genetic adaptation to local climatic conditions, but the reaction norms of particular species under natural conditions are not known. Also, changes in landscape characteristics may substantially influence abundance of coccinellid species (Bianchi *et al.*, 2007). Urbanisation and degradation of agricultural habitats may favour *H. axyridis* (Adriaens *et al.*, 2008; Comont *et al.*, 2014; Purse *et al.*, 2015), but not all native coccinellids.

It is clear that *H. axyridis* is now numerically dominant in many habitats across Europe (and beyond), but the effects of this species on ecosystem function and resilience are unclear. However, each species of coccinellid is likely to play a specific role within ecosystems and although there may be some redundancy within the communities, it is highly likely that the resilience of coccinellid communities will be undermined by species declines. There is an urgent need for further detailed field studies that quantitatively document the interactions between invaders, other species and wider environmental factors. Approaches such as ecological network analysis provide exciting opportunities for assessing changes across trophic levels and so enhancing understanding of changes in important ecosystem functions such as, in the case of aphidophagous communities, pest control (Roy & Lawson Handley, 2012). The importance of changes to the ecological functioning will contribute to our assessment of the extent of changes to populations and communities which are occurring within the context of environments that are also rapidly changing. Furthermore, such detailed understanding will provide baseline information against which the response to conservation measures can be assessed.

Acknowledging the established niche differences between species in respect of specific preferences for prey and abundance, host plant and microclimate (Honek, 1985a) could be exploited within conservation measures. Conservation managers could be encouraged to preserve specific combinations of habitat characteristics to create refugia for native species throughout the year. Heterogeneity of landscapes has been shown to promote stability of butterfly populations by providing a range of resources and microclimates, which buffer populations against climatic variation (Oliver *et al.*, 2010). Determining the landscape factors that benefit coccinellids under differing environmental regimes would be fruitful. Studies of long-term changes in coccinellid communities such as the one described here will be critical for testing the effectiveness of conservation measures.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12158:

Appendix S1. List of sampling sessions. Each sampling session is indicated by sampling period (1 – 1976–1986; 2 – 2002–2006; 3 – 2011–2014), site (24 sites are determined by geographic coordinates and municipality of sampling), host tree and date of sampling.

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