



Effect of aphid abundance and urbanization on the abundance of *Harmonia axyridis* (Coleoptera: Coccinellidae)

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Abstract. The factors that affect the local distribution of the invasive *Harmonia axyridis* are not yet completely resolved. Hypotheses predicting positive and independent effects of prey abundance and degree of urbanization on the adult abundance of this species in Central Europe were tested. Populations of *H. axyridis* were sampled in a period when it was most abundant, by sweeping lime trees (*Tilia* spp.) at 28 sites along a 20 km transect across urban (western Prague) and surrounding rural areas. The sites differed in aphid abundance (number of *Eucallipterus tiliae* per 100 sweeps) and degree of urbanization (percentage of the surrounding area within a 500 m radius covered by impervious human constructions). Multiple linear regression analysis of log-transformed data revealed that abundance of *H. axyridis* (number of adults per 100 sweeps) increased significantly with both aphid abundance ($P = 0.015$) and urbanization ($P = 0.045$). The positive relationship between degree of urbanization and abundance of *H. axyridis* was thus not a side effect of variation in aphid abundance, which was also greater in urban than rural areas. The effect of urbanization might constrict the habitat available to *H. axyridis* and force this species to aggregate in urban green “refugia”. These results point to a plurality of factors that determine coccinellid abundance at natural sites.

INTRODUCTION

Harmonia axyridis (Pallas), an aphidophagous lady beetle species native to the eastern Palearctic, Japan, China, Mongolia and Russian Siberia east of the Urals (Kovar, 2007; Bidinger et al., 2012), is worthy of attention because of its recent spread across the rest of world except Australia and New Zealand (Brown et al., 2011). The history, causes and consequences of this invasion are well investigated and authoritatively reviewed by Roy et al. (2016).

Great attention is paid to the factors affecting the distribution of *H. axyridis* in invaded areas (Bidinger et al., 2012). In Europe, this species gradually spread east and west from France, Belgium and Great Britain, where it first became established in the early 2000s (Adriaens et al., 2008). The spread was rapid in a longitudinal direction resulting in *H. axyridis* arriving in central and southern Russia in the 2010s (Korotayev, 2013; Ukrainsky & Orlova-Bienkowskaja, 2014; Zakharov, 2015) but less rapid in a latitudinal direction (Brown et al., 2008; Honek et al., 2017; Soares et al., 2017) resulting in this species arriving later in Greece (Ceryngier & Romanowski, 2017) and Bulgaria (Tomov et al., 2009). It seems that *H. axyridis*, despite optimistic predictions (Poutsma et al., 2008), is possibly kept from colonizing dry subtropical Mediterranean

areas because in these areas its life cycle is not synchronized with that of its potential prey (Honek et al., 2017).

The pattern of the local distribution of *H. axyridis* in invaded areas is also interesting. It is determined by several factors, the most important of which is its preference for particular plants. In contrast to in its native and some of the areas it has invaded, where *H. axyridis* is abundant in low-growing vegetation (Grez et al., 2014; Lu et al., 2015), in the western Palearctic it prefers trees and rarely occurs in stands of wild herbaceous plants and crops unless they are heavily infested with aphids (Adriaens et al., 2008). *Harmonia axyridis* aggregates at sites where aphids are abundant (Jovicic et al., 2016; Soares et al., 2017; Viglasova et al., 2017) as an abundance of food is a prerequisite for reproduction (Ovchinnikova et al., 2016) and the adults are capable of locating and populating such sites (Osawa, 2000; With et al., 2002).

Another factor affecting the distribution of *H. axyridis* is its affinity for urban areas, in Europe (Adriaens et al., 2008), North America (Colares et al., 2015), South America (Wagner et al., 2017) and South Africa (Mukwevho et al., 2017). In this tendency, *H. axyridis* is not exceptional as urban habitats are also preferred by other species of coccinellids (Gardiner et al., 2014; Latibari et al., 2016). However, the abundance of aphids (Philpott & Bichier, 2017)

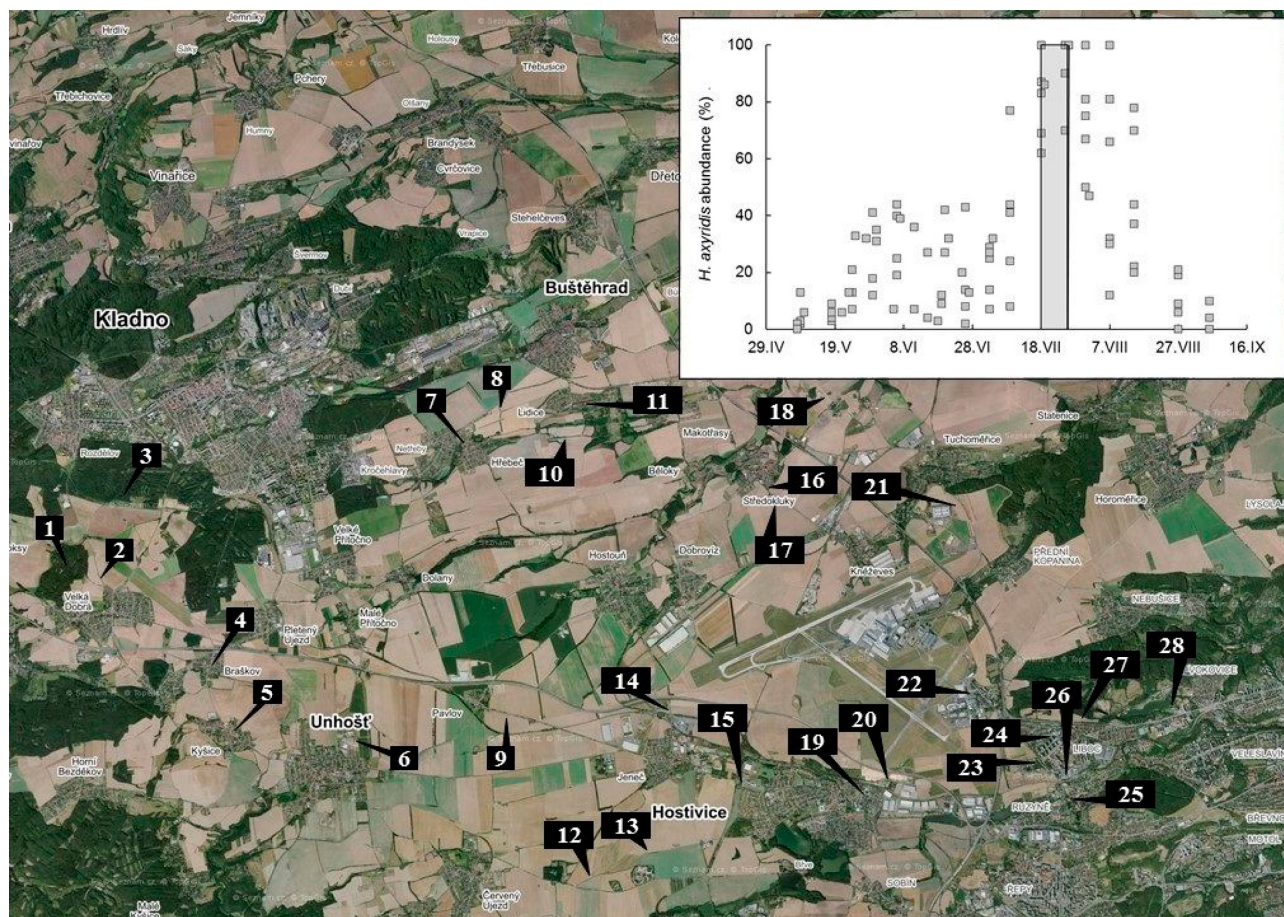


Fig. 1. Map showing the sites where the populations of *H. axyridis* were sampled. The size of the pictured area is 23 × 16 km and centred at 50.134°N, 14. 207°E. Insert: Standardized abundances (percentage of maximum at each site) of *H. axyridis* recorded at sites 19, 20, 22, 23, 24 and 28 in the vegetative season in 2018. Shaded area – period when the sampling occurred.

and other sucking Hemiptera (Hanks & Denno, 1993) is also higher in urban areas. The positive correlation between the above two factors, prey abundance and urbanization, complicates and confounds an analysis of the factors determining the abundance of *H. axyridis*.

In order to resolve this problem, the relationships between the abundance of *H. axyridis*, abundance of aphids and degree of urbanization, was studied using a standardized protocol that minimizes the confounding effects of temporal (Honek et al., 2015) and regional (Viglasova et al., 2017) differences in the abundance of *H. axyridis*. This study focused on adults that were sampled over a short period and on a single host-plant/aphid system. We tested three hypotheses: The abundance of *H. axyridis* increases (i) with aphid abundance and (ii) with the degree of urbanization (iii), and that these increases are independent of one another. The aim was to elucidate the relationship between both of the factors that are associated with the abundance of this coccinellid.

MATERIAL AND METHODS

Sites sampled

Abundance of *H. axyridis* was recorded at 28 sites scattered along an ~20 km long longitudinal transect that extended from the west Prague into the surrounding area (Fig. 1). The tree stands

at particular sites consisted of ≥ 5 lime trees (*Tilia cordata* Mill., *Tilia platyphyllos* Scop.) infested with the aphid *Eucallipterus tiliiae* (L.) (Sternorrhyncha: Aphididae). Continuous monitoring of coccinellid abundance on trees (Honek et al., 2018) revealed that *Tilia* spp. were the most infested trees at that time. There were very few ladybirds on the other species of trees growing in the urban and rural areas (*Acer* spp., *Betula* spp., *Quercus* spp.).

Sampling period

The lime trees were sampled in one week 18 to 24 July 2018, which was when *H. axyridis* was most abundant on the lime trees. This is confirmed by the results of a season-long monitoring of *H. axyridis* abundance at sites 19, 20, 22, 23, 24 and 28 (Fig. 1), during which the abundance of *H. axyridis* was monitored at weekly intervals. This revealed that sampling occurred when the abundance of adult *H. axyridis* was at a maximum. One-way ANOVA using abundance of *H. axyridis* at particular sites from 15–31 July (abundance at the date included in this study and one week before and one week after, i.e., 3 records for each site, total $n = 18$) as the response variable and site as factor revealed that in this period, differences between sites accounted for 95.1% of the variance in *H. axyridis* abundance.

Sampling method

Beetles were swept from the canopy up to a height of cca 3 m. Sampling was standardised by using a standard sweep net (35 cm diameter, 140 cm handle) operated by the same person (A.H.). All the days on which samples were collected were sunny and calm,

and maximum temperatures (experienced in the afternoon) were between 27.7 and 32.1°C. Sampling occurred between 08.00 and 18.00 h and consisted of 100 sweeps at each site. In each sampling session, we recorded (i) abundance of *H. axyridis* (number of adults caught per 100 sweeps), (ii) abundance of aphids (approximate number of aphids caught per 100 sweeps, pilot observations revealed that aphid numbers were determined with ~10% precision), and urbanization quantified as (iii) the percentage of the surrounding area (a circle of 500 m radius centred at the sampling site) covered by impervious surfaces (buildings, streets, parking places, etc.). The latter value was called “degree of urbanization”. It was determined using maps available at (<https://en.mapy.cz>).

Data analysis

The relationships between the abundance of *H. axyridis*, abundance of aphids and degree of urbanization were obtained using raw data and linear regression, $y = a + bx$, in which y is the abundance of *H. axyridis* and x either aphid abundance or degree of urbanization. The relationship between the abundance of aphids and degree of urbanization was tested using the same formula where y is the abundance of aphids and x the degree of urbanization. To linearize the relationship between data variables (abundance of aphids, degree of urbanization and abundance of *H. axyridis*), the data were log transformed. Using log-transformed data, we used multiple linear regression, $\log(y + 1) = a + b_1 \log(x_1 + 1) + b_2 \log(x_2 + 1)$, in which y is the abundance of *H. axyridis*, x_1 abundance of aphids and x_2 degree of urbanization. We then tested the significance of the regression coefficients b_1 and b_2 in order to determine the effect of abundance of aphids and degree of urbanization on *H. axyridis* abundance. Calculations were performed using SigmaStat 3.5 (Systat Software Inc., 2006).

RESULTS

Abundance of *E. tiliae* (0 to 820 individuals per 100 sweeps) and degree of urbanization (2 to 59 percent of surrounding area impervious) varied greatly among sites. Variability in the abundance of *H. axyridis*, which made up 86% of all the coccinellids sampled, was related to both factors (Fig. 2). The abundance of *H. axyridis* significantly ($F_{1,27} = 27.022$, $P < 0.001$) increased with increase in the abundance aphids ($a = 14.706$, $b = 0.0848$, $R^2 = 0.510$) and ($F_{1,27} = 18.968$, $P < 0.001$) with increase in the degree of urbanization ($a = 11.176$, $b = 0.986$, $R^2 = 0.422$). However, the abundance of aphids also significantly ($F_{1,27} = 28.996$, $P < 0.001$) increased with the degree of urbanization ($a = 11.339$, $b = 9.276$, $R^2 = 0.527$).

Multiple regression using log transformed data ($a = -0.194$, $b_1 = 0.445$, $b_2 = 0.484$, $R^2 = 0.599$) revealed a highly significant effect of both factors ($F_{2,27} = 18.706$, $P < 0.001$). Partial regressions revealed a significant effect of both the abundance of aphids ($P = 0.015$) and urbanization ($P = 0.047$) on *H. axyridis* abundance.

DISCUSSION

The results revealed a positive effect of the abundance of aphids on the abundance of adults of *H. axyridis*, which is consistent with the prediction of hypothesis (i). This result is expected and consistent with earlier evidence (Hodek & Evans, 2012; Honek, 2012). While there is no doubt that the abundance of aphids has an important role in determin-

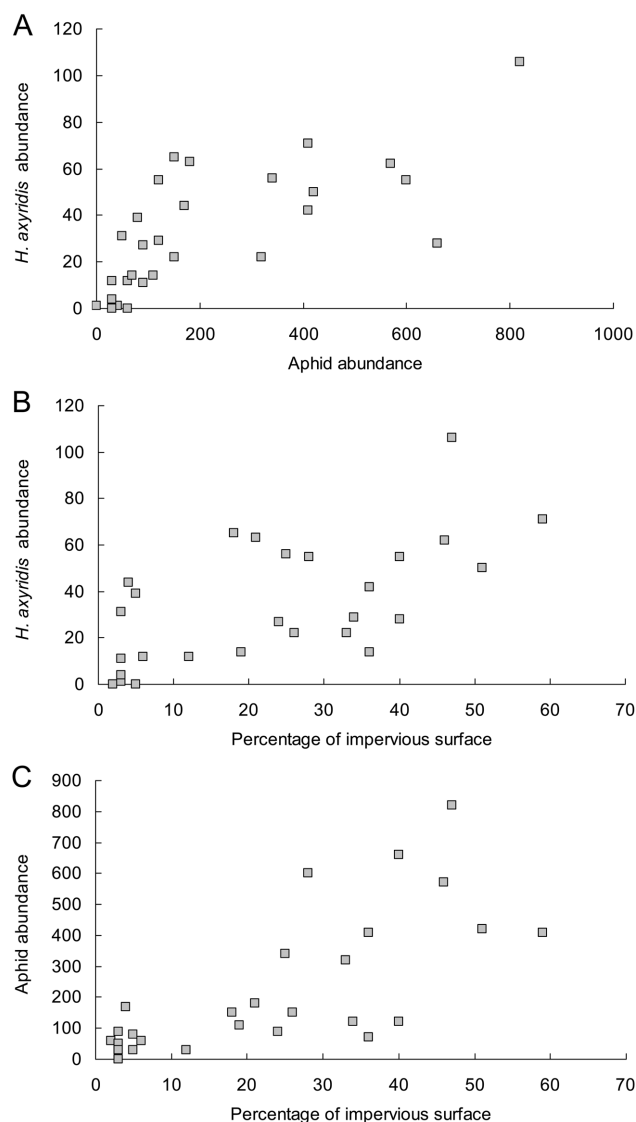


Fig. 2. The relationship between the abundance of *Harmonia axyridis* (n individuals per 100 sweeps) and A – the abundance of aphids (n *Eucallipterus tiliae* individuals per 100 sweeps), B – the degree of urbanization, and C the interrelationship between abundance of aphids and degree of urbanization.

ing the abundance of many coccinellids, identification of the relative importance of the population processes that determine the maximum abundance of *H. axyridis* at a particular site needs further study. Adult populations consist of individuals arriving from the surrounding area as well as individuals that developed at the site. Population size is thus determined by a combined effect of the settling of adult immigrants at a site (Osawa, 2000; With et al., 2002), intensity of oviposition (Osawa, 2005; Seagraves, 2009) and success of pre-imaginal development (Hironori & Katsuhiko, 1997), which are all positively affected by aphid abundance.

The results further reveal a weaker but significant positive effect of urbanization, consistent with hypothesis (ii). The positive effect of the urban environment on the abundance of *H. axyridis* (Adriaens et al., 2008; Mukwevho et al., 2017; Wagner et al., 2017) and its role in facilitating

the rapid spread of this species (Veran et al., 2016) are well documented, but contrary effects are also reported (Rocha & Fellowes, 2018; Rocha et al., 2018). The mechanism behind the effect of urbanization is not yet resolved (Honek et al., 2017; Sloggett, 2017). We hypothesize that in rural areas, coccinellids may be distributed evenly, while in cities, where the suitable habitat is reduced to small patches of green (parks, green courtyards, tree lines bordering streets), coccinellids are forced to aggregate at these sites. Urban greens thus serve as small refugia in an otherwise hostile urban environment.

The positive effect of urbanization on *H. axyridis* abundance may be confounded by its parallel effect on aphid abundance. A positive relation between aphid abundance and urban environment has been established several times (Fluckiger & Braun, 1999; Mackos-Iwaszko et al., 2015), although contrary cases describing lower aphid abundance in urban areas compared to rural area are also reported (Sienkiewicz-Paderewska et al., 2017). In this study, a significant positive relationship was found between degree of urbanization and abundance of *E. tiliae*. Mechanisms underlying the effect of urbanization on aphid abundance include biotic (natural enemies) and abiotic (salinity and drought) factors (Sienkiewicz-Paderewska et al., 2017; Andrade et al., 2017; Rocha & Fellowes, 2018). These effects, while outside the scope of this study, deserve more investigation.

Our study thus established and quantified the separate action of two factors on the abundance of *H. axyridis*, abundance of aphids and urbanization, both of which affected the abundance of *H. axyridis* independently of one another. This result is consistent with the prediction of hypothesis (iii). Both factors contribute to the local diversification of the abundance of *H. axyridis* and point to a plurality of factors that determine coccinellid abundance at natural sites.

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