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**Changes in arthropod communities of maple trees (*Acer* spp.)  
along stress gradients in urban environment**

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**Dávid Korányi (PhD candidate)**

Supervisors:

PROF. DR. VIKTOR MARKÓ

Department of Entomology

Institute of Plant Protection

Hungarian University of Agriculture and Life Sciences

PROF. DR. ELŐD KONDOROSY

Department of Conservation Biology

Institute for Wildlife Management and Nature Conservation

Hungarian University of Agriculture and Life Sciences

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Írta: Korányi Dávid

Témavezetők:

Dr. Markó Viktor

Elfogadásra javaslom (igen / nem)

.....

Dr. Markó Viktor

Dr. Kondorosy Előd

Elfogadásra javaslom (igen / nem)

.....

Dr. Kondorosy Előd

A jelölt a doktori szigorlaton .....%-ot ért el,

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# 1. Abstracts

## 1.1. Abstract

Maples (*Acer* spp.) are among the most commonly planted urban tree species in North America and Europe. In Central Europe, sycamore (*Acer pseudoplatanus*), Norway (*A. platanoides*), and field maple (*A. campestre*) are common native tree species and are often selected for urban forestry. The aim of this thesis is to assess the arthropod fauna of these maple species, and to examine how bottom-up (host plant identity and condition) and top-down (abundance and composition of predator communities) forces influence phytophagous insect communities in the canopy of maple trees in urban environment.

In the first study, we performed a comprehensive faunal survey. As a result, five new arthropod species for the Hungarian fauna are reported and characterized with detailed descriptions.

In the second study, we compared the phytophagous insect community of the canopy of field, sycamore, and Norway maple in urban conditions. The physiological condition of the trees (expressed as peroxidase [POD] enzyme activity, degree of leaf necrosis and leaf fall) and its relationship to abundance of phytophagous insects was also examined. Field maple trees were in the best while Norway maple trees in the worst condition. Most herbivorous species were associated with field maple, sycamore had the highest aphid densities, and Norway maple had the least abundant and least characteristic phytophagous insect community. The super-abundant planthopper species, *Metcalfa pruinosa* positively affected the POD activity of trees, but reached higher abundances on healthier trees. Based on tree condition, in this study, field maple had high while Norway maple had low tolerance to urban stress.

In the third study we examined the effect of urbanization on aphids, predatory arthropods, and ants on field maple trees. We used the percentage of impervious surfaces within a 500 m radius of each site as an index of the degree of urbanization. The abundance of aphids positively, while the abundance of predatory arthropods and occurrence of poorly dispersing species within the predator community were negatively related to urbanization. The abundance and dispersal ability of predators were significant predictors of aphid abundances. The numbers of ants decreased with urbanization and did not affect the abundance pattern of aphids. These results show that

urbanization can disrupt biological control of aphid populations and thus may contribute to aphid outbreaks on urban trees.

## 1.2. Kivonat

A juharfajok (*Acer* spp.) mind Észak-Amerikában, mind Európában a városok leggyakoribb fafajai közé tartoznak. A hegyi (*Acer pseudoplatanus*), a korai (*A. platanoides*), és a mezei juhar (*A. campestre*) Közép-Európában őshonos fafajok, melyeket gyakran ültetnek városi környezetben.

Értekezésem célkitűzése a városi juharfákon kialakuló ízeltlábú együttesek faunisztikai feltárása volt, valamint annak meghatározása, hogy milyen szerepet játszanak a tápnövény (faj és kondíció) és a természetes ellenségek (ragadozó egyedszám és közösség-összetétel) irányából megnyilvánuló hatások ezen fitofág rovaregyüttesek szabályozásában.

Az első vizsgálatban juharfák lombotlakó ízeltlábú faunájának átfogó felmérését végeztem el. Ennek eredményeként munkatársaimmal öt, a magyar faunára új fajról számoltam be azok részletes ismertetésével.

A második vizsgálatban három juharfaj (mezei, korai és hegyi juhar) fitofág rovaregyütteseit hasonlítottam össze városi környezetben. Felmértem továbbá a fák fiziológiai kondícióját (peroxidáz [POD] enzimaktivitás, lomhullás és levélnekroízis intenzitása) és meghatároztam annak kapcsolatát a fitofág rovarcsoportok egyedszámával. A legtöbb fitofág rovarfaj a mezei juharhoz kötődött, a hegyi juharon volt a legnagyobb a levéltetvek egyedsűrűsége, míg a korai juharfákon alakult ki a legkisebb egyedsűrűségű és legkevésbé sajátos fitofág rovaregyüttes. A szuperdomináns kabócafaj, a *Metcalfa pruinosa* növelte a fák POD aktivitását, ugyanakkor egyedsűrűsége a fák javuló kondíciójával (csökkenő levélnekroízis és levélhullás) együtt nőtt. A fák kondíciójának (levélnekroízis) felmérése alapján megállapítottam, hogy a mezei juhar rendelkezett a legjobb, míg a korai juhar a legrosszabb várostűrő képességgel.

A harmadik vizsgálatban az urbanizáció levéltetvekre, ragadozó ízeltlábúakra és hangyákra gyakorolt hatását vizsgáltam mezei juharfákon. Az urbanizáció mértékét az egyes területek 500 méteres sugarú körzetében található mesterséges felületek arányaként határoztam meg. A levéltetvek egyedszámát a növekvő urbanizáció pozitívan, míg a ragadozók számát és azon belül különösen a gyenge diszperziós képességű fajok jelenlétét negatívan befolyásolta. A ragadozók egyedszáma és diszperziós képessége szignifikánsan magyarázta a levéltetvek egyedsűrűségét. A hangyák száma csökkent az urbanizáció növekvő mértékével és nem befolyásolta a levéltetvek



egyedszámát. Eredményeink szerint az urbanizáció negatívan hat a levéltetvek biológiai szabályozására, ami így hozzájárul a levéltetvek városi fákon megfigyelhető jelentős felszaporodásához.

### **1.3. Auszug**

Ahornarten gehören zu häufigsten Baumarten in Städten auch in Europa und Nordamerika. Bergahorn (*Acer pseudoplatanus*), Spitzahorn (*A. platanoides*) und Feldahorn (*A. campestre*) sind einheimisch in Mitteleuropa, und sind oft in Städten gepflanzt. Das Ziel meiner Dissertation war einerseits die faunistische Untersuchung der Arthropodengemeinschaften der Ahornbäumen in Städten, andererseits die Forschung die Rolle verschiedener „bottom-up“ (Wirtspflanze-identität und -zustand) und „top-down“ (Anzahl räuberischen Arthropoden und Komposition der Gemeinschaften) Wirkungen in Regulierung dieser phytophagen Insektengemeinschaften.

Erstens untersuchte ich die laubbewohnende Arthropodenfauna der Ahornbäume. Als Ergebnis wir berichteten über fünf für die ungarische Fauna neue Arten mit deren geteilten Beschreibung.

Zweitens wir verglichen phytophage Insektengemeinschaften drei Ahornarten (Berg-, Spitz- und Feldahorn) in städtischen Umgebung. Wir untersuchten außerdem die physiologische Kondition (Peroxidase [POD] Enzymaktivität, Intensität von Laubfall und Blattnekrose) und ich erforschte deren Beziehung zu Individuenzahl phytophagen Insektengruppen. Die meisten pflanzenfressende Insektenarten waren zu Feldahorn gebündelt, die Individuenzahl von Blattläusen war die größte an Bergahorn, und an Spitzahorn war die Insektengemeinschaft am wenigsten spezifisch mit der niedrigsten Individuenzahl. Die superdominante Zikadenart, *Metcalfa pruinosa* hat die POD-Aktivität der Bäume erhöht, und ihre Individuenzahl hat mit Verbesserung der Kondition der Bäume (verminderte Blattnekrose und Blattfall) zusammengewächst. Ich habe an Grund der Überprüfung von der Kondition der Bäume (Blattnekrose) festgestellt, dass Feldahorn am besten, und Spitzahorn am schlechtesten die städtische Umwelt litt.

In dritten Forschung wir untersuchten die Wirkung der Urbanisation auf Blattläusen, räuberischen Arthropoden und Ameisen an Feldahornbäumen. Wir definierten den Grad der Urbanisation als der Anteil der künstlichen Flächen im Radius von 500 m jeder Modellgebiet. Die steigende Urbanisation beeinflusste die Individuenzahl der Blattläusen positiv, die Anzahl der Zoophagen und zwischen denen besonders die Arten mit schlechten Dispersionsfähigkeit negativ.

Individuenzahl und Dispersionsfähigkeit der Zoophagen erklärte signifikant die Individuenzahl der Blattläuse. Anzahl der Ameisen minderte sich mit steigender Urbanisation, aber es beeinflusste die Individuenzahl der Blattläusen nicht. Die Ergebnisse zeigen, dass die Urbanisierung die biologische Kontrolle von Blattlauspopulationen stört und somit zu der Massenvermehrung der Blattläuse auf städtischen Bäumen beitragen werden kann.

## 2. General introduction

More than half of the world's population is currently living in cities and the rapid growth of human population is accompanied by substantial expansion of urban areas (United Nations, 2014). Although cities represent about 3% of the world's land usage, the proportion of global urban land cover is projected to grow threefold during the first 30 years of the 21st century (Seto et al., 2012). Urbanization changes the landscape considerably by covering natural areas with artificial structures such as buildings, roads and other associated elements, comprising mostly impervious surfaces, and results in reduction and degradation of original habitats. In addition to all these features, alterations that occur with increasing urbanization, involve fragmented vegetation, increased temperature, microclimatic shifts, and altered soil and atmospheric chemistry (Kaye et al., 2006; Grimm et al., 2008; Rizwan et al., 2008; Dobbs et al., 2017).

As an additional consequence, disturbance created by cities has a great local effect on animal communities (Magle et al., 2012). Urban expansion affects not only the habitats of sensitive species (urban avoiders) negatively, but also creates suitable environment for a relatively few species that are able to adapt to changed environmental conditions (urban exploiters and adapters). These two phenomena lead to biodiversity loss and biotic homogenization (McKinney, 2006). Urban avoiders reach highest densities at the most natural sites or in remnant semi-natural habitats and disappear quickly with increasing urban disturbance. They contain mostly habitat specialist and native species. In contrast, urban adapter and exploiter species are mostly habitat generalists, thus they have better capability to use resources and novel habitats provided by cities (Blair & Launer, 1997; McKinney, 2006; Kark et al., 2007). Since cities are important nodes of anthropogenic activities including commerce and transportation, urbanization contributes greatly to the introduction, establishment, and spread of alien and invasive species, which often have negative ecological consequences (Padayachee et al., 2017). According to the most recent projections, there will be distinct increases in alien species numbers, particularly in Europe, and among these, the number of arthropod species is predicted to increase by circa 70 % (more than a thousand species) by the mid-21st century (Seebens et al., 2020).

Arthropods are regarded as suitable indicators of human-induced environmental changes. They are a megadiverse group, relatively easy to sample, and show quick responses to altering environmental conditions due to their short generation times, compared to many other taxonomic groups. In addition, arthropods represent a wide spectrum of trophic levels (i.e., pollinators,

herbivores, parasitoids, predators, and mutualists), thus they are one of the most important components of urban ecosystems (Kremen et al., 1993, McIntyre, 2000; Bang & Faeth, 2011). Among others, factors influencing arthropod community dynamics in urban environment might be bottom-up, such as quality and availability of host plants, and top-down, such as the abundance and community composition of natural enemies (Faeth et al. 2005; Raupp et al., 2010; Miles et al., 2019).

Generally, plants in urban areas are exposed to greater environmental stress compared to natural habitats, due to numerous factors including soil compaction, air pollution, water deficits, and mechanical injuries (Dreistadt et al., 1990; Raupp et al., 2010; Sjöman & Nielsen, 2010; Pautasso et al., 2015). However, response of phytophagous insects to plant stress and condition in urban areas is quite variable. Some studies showed evidence that stressed urban plants provide more suitable nutrient for phytophagous insects than plants growing on natural habitats. For instance, Dale and Frank (2017) found higher fecundity and larger body size in the scale insect, *Melanaspis tenebricosa* on water stressed trees. Similarly, Cregg and Dix (2001) found higher aphid and lace bug densities on oak trees, growing in a downtown area, under severe stress. In contrast, some other studies found that increasing stress and deteriorating condition of urban trees explained negatively the survival of scale insects (Hanks & Denno, 1993) and aphid abundance (Sienkiewicz-Paderewska et al., 2017). Urbanization also leads to fragmented vegetation with altered composition and diversity (Dobbs et al., 2017), and thus results in reduced availability of host plants for phytophagous species (Bagchi et al., 2018). Therefore, host plant specialization might be important factor in shaping herbivore communities in cities as well, and advancing urbanization can contribute to increase in abundance of dietary generalist phytophagous insects at the expense of specialist ones (Clark et al., 2007, Cichocka & Goszczyński, 2008; Miles et al., 2019).

Studying how natural enemies influence herbivore populations is essential, because these top-down forces have direct and indirect effects on biodiversity, ecosystem functions and stability (Faeth et al., 2005; Turrini et al., 2016). Less diverse vegetation in city centers with reduced structural complexity often provides unfavorable conditions for natural enemies, due to decreased number of refuges and alternative food resources (e.g. prey, nectars, and pollen) (Cortesero et al., 2000; Langellotto & Denno, 2004; Shrewsbury & Raupp, 2006). Furthermore, impervious surfaces and artificial structures in cities may act as dispersal barrier for many species at higher trophic levels, especially for poor dispersers (McIntyre, 2000; Raupp et al., 2010; Corcos et al., 2020). All

these factors can modify prey-natural enemy interactions and, thus providing opportunity for herbivores to reach high densities in highly urbanized areas (Denys & Schmidt, 1998; Shrewsbury & Raupp, 2006; Bergerot et al., 2010; Turrini et al., 2016).

For some herbivores, warmer temperature in urban areas compared to natural habitats also can provide temporal escape from their predators and parasitoids (Forrest, 2016). In connection with urbanization, studies showed, that warmer sites can be characterized not only by greater population increase of pest insects (Meineke et al., 2013; Dale & Frank, 2014; Long et al., 2019), but also by their advanced phenology (i.e., earlier development and reproduction) compared to their natural enemies (Meineke et al., 2014). Therefore, increasing level of urbanization may lead to spatial and temporal mismatch between insect herbivores and species at higher trophic levels.

Urban trees provide a range of ecosystem services. Beyond their aesthetic value, they mitigate the urban heat island effect by shading and evapotranspirational cooling and provide more favorable atmospheric composition by absorbing and depositing air pollutants (Livesley et al., 2016). Moreover, cities have dozens of native tree species with diverse and abundant arthropod communities that can greatly contribute to maintaining urban biodiversity (Helden et al., 2012; Burghardt & Tallamy, 2013; Frank, 2019). Among tree species, maples (*Acer* spp.) are commonly planted and appear to predominate the urban green areas with trees in the United States (Cowett & Bassuk, 2014, 2020; Frank, 2019) and Europe (Sæbø et al., 2003; Britt & Johnston 2008; Sjöman et al., 2012) including the Hungarian capital, Budapest (Szaller, 2014). Maple trees support numerous specialist and generalist phytophagous species (e.g. Blackman & Eastop, 1994; Nickel, 2003; Korányi et al., 2015; Frank, 2019) and tolerate urban stress in different degrees (Roloff et al., 2009; Stratópoulos et al., 2019), thus they are ideal choice for studying the direct and indirect effects of urbanization on arthropods.

This thesis comprises three studies conducted in and around the city of Budapest, Hungary with the following aims: (1) to explore the canopy dwelling arthropod fauna of maple trees; (2) to assess the abundance pattern and composition of phytophagous insect communities of three commonly planted maple species (*Acer pseudoplatanus*, *A. platanoides* and *A. campestre*) in urban environment considering their stress level and condition; (3) and finally, to examine the effect of urbanization on aphids, predatory arthropods, and ants as well as their predator-prey-mutualist interactions on field maple (*A. campestre*).

### 3. STUDY I: New records for the Hungarian spider and insect fauna

#### 3.1. *Icius subinermis* Simon, 1937 (Araneae, Salticidae)

This part of the thesis was published as: **Korányi, D.**, Mezőfi, L., & Markó, V. (2017). First record of the jumping spider *Icius subinermis* (Araneae, Salticidae) in Hungary. *Arachnologische Mitteilungen* 54: 38-40. DOI: 10.5431/aramit5408

##### 3.1.1. Introduction

The spider fauna of Hungary is well studied (Samu & Szinetár, 1999). Due to intensive research and more specialized collecting methods, new records frequently emerge. Some of these new species are indigenous, others are newcomers. International trade is one of the most important factors that contribute to the spread of invasive arthropod species, including spiders (Nedvěd et al., 2011). In addition, climate change may also facilitate the establishment of exotic species originating from warmer areas (Nentwig, 2015). Due to warmer climate, Mediterranean spider species have extended their range northwards (e.g. Kumschick et al., 2011; Nedvěd et al., 2011). Among 87 introduced alien spiders, 44 expanded their range from the Mediterranean or the Eastern Palaearctic to western and northern Europe (Kobelt & Nentwig, 2008).

Jumping spiders (Salticidae) are one of the most common spider families (after Theridiidae and Pholcidae) in which species are indicated as alien (Nentwig 2015). Salticidae is the richest family worldwide with over 620 genera and more than 5900 described species (WSC, 2017). Within Salticidae, the genus *Icius* comprises 34 described species (WSC, 2017) and five *Icius* species are confined to the Mediterranean region of Europe (Nentwig et al., 2017). Two of them, *I. hamatus* (C.L. Koch, 1846) (Tomasiewicz & Wesolowska, 2006; Schäfer & Deepen-Wieczorek, 2014) and *I. subinermis* Simon, 1937 (Jäger, 1995; Helsdingen, 2006) have also been reported from Central and Western Europe in recent years. No representatives of *Icius* have been found in Hungary until now (Szűts et al., 2003).

### 3.1.2. *Materials and methods*

The arthropod community of *Acer campestre* L. was surveyed in a green area of Budapest (Mátyás tér, 47°29'32"N, 19°4'48"E, 110 m a.s.l.), Hungary, in the growing season of 2016. This area is covered by trees (e.g. *Acer* spp., *Fraxinus* spp., *Robinia* spp.), small bushes (e.g. *Berberis* spp., *Juniperus* spp., *Rosa* spp.), grassy patches and concrete surfaces, and surrounded by multi-storey buildings and traffic roads.

The specimen was collected on June 22nd 2016 using the beating method. The study was carried out at the Department of Entomology of Szent István University. The specimen was examined with Leica MZ6 and photographed with a Sony XCD-SX90CR camera attached to a Zeiss Stemi stereomicroscope. We used the key available in Alicata & Cantarella (1994) for identification. The female vulva was prepared and macerated with 20% KOH and photographed with a Zeiss Imager A2 light microscope equipped with AxioCam MRc5. Measurements are given in millimetres. The specimen was deposited in the second author's private collection.

### 3.1.3. *Results and discussion*

The adult female jumping spider specimen was collected from the canopy of an *A. campestre* tree and identified as *Icius subinermis* Simon, 1937 (leg. D. Korányi, det. L. Mezőfi). The specimen's general appearance is shown in Fig. 1. The specimen's opisthosoma has a light brown or off-white tincture and reddish-brown spots which form a horseshoe-shaped pattern. The epigyne and vulva are shown in Fig. 2.



Figure 1. *Icius subinermis* female general appearance, dorsal view. (Photo: László Mezőfi)

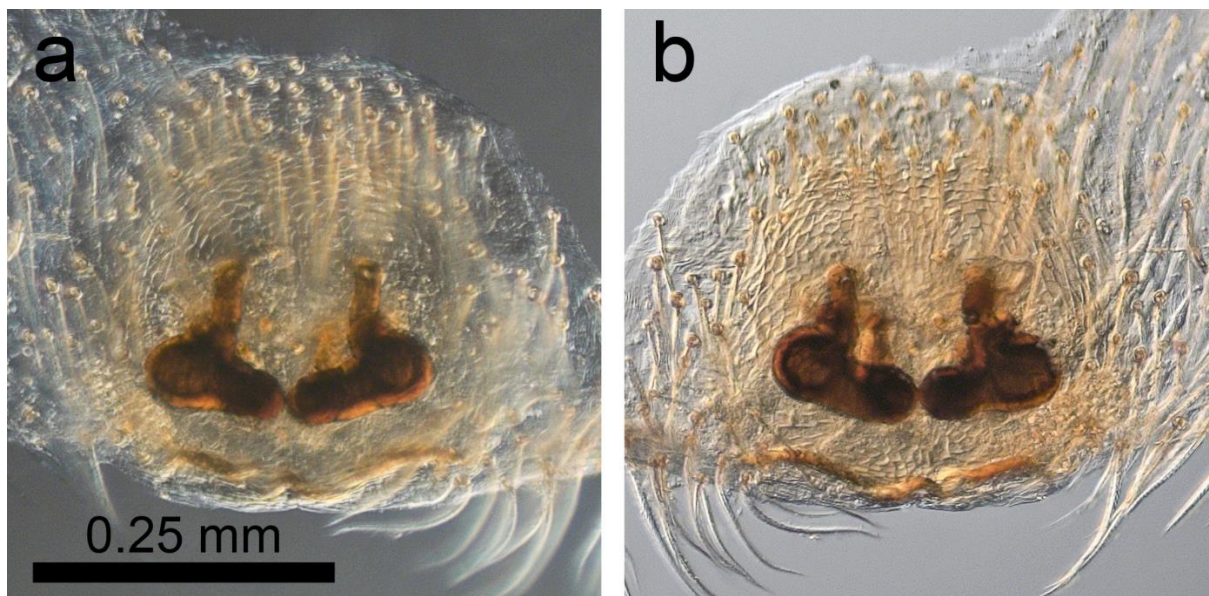


Figure 2. Cleared, dissected epigyne/vulva of *Icius subinermis* female from Hungary; a. epigyne, ventral view; b. vulva, dorsal view. (Photo: László Mezőfi)



*Icius subinermis* is known from Spain, France, Italy, Portugal (Bellmann, 1997), Macedonia (Komnenov, 2005), Slovenia (Kostanjšek & Fišer, 2005), Switzerland (Maurer & Hänggi, 1990), Germany (Blick et al., 2016) and Serbia (Stanković, 2012). In addition, *I. subinermis* was reported from the Netherlands (Helsdingen, 2006) and from the Czech Republic (Šich, 2015) although its establishment has not been confirmed in these two countries. Recently this species was also reported from North America (Philadelphia and Pennsylvania) (Cutler & Parr, 2020).

This species generally occurs in moist habitats, for example near streams or on moist meadows. It builds a silken retreat on rush plants or under rocks near rivers or creeks (Stanković, 2012). It may also occur on trees, especially in the vegetation bordering aquatic environments, but is usually present at the waterside at the time of its reproduction. Females are often seen guarding their eggs (Ledoux, 2007).

Although *I. subinermis* has a Mediterranean origin (Alicata & Cantarella, 1994), it has also been reported from Central and Western Europe (e.g. from Germany and the Netherlands) (Jäger, 1995; Helsdingen, 2006). *Icius subinermis* probably lives in moist habitats under natural conditions (Stanković, 2012; Leroy, et al. 2014). However, it was also observed in urban environments or near residential areas (Jäger, 1995; Komnenov, 2005; Kostanjšek & Fišer, 2005; Helsdingen, 2006; Stanković, 2012). Furthermore, in most cases the specimens were found in buildings (e.g. in a house, greenhouse or apartment) (Jäger, 1995, 1996; Komnenov 2005; Helsdingen 2006). This supports the findings of Nedvěd et al. (2011) that occurrence in buildings is a prerequisite for range expansion in many arachnid species. Moreover, these observations suggest that an urban environment and its microclimate may provide suitable conditions for this species, particularly northwards from the Mediterranean region.

How this specimen of *I. subinermis* got to Hungary is unclear and hard to speculate about. The warming climate and/or human mediation could be suspected. Since the specimen was found in an outdoor habitat in Budapest, it may have an established population here. To confirm this, further surveys are needed, mainly in residential areas and semi-natural habitats nearby.

In Hungary, the most comprehensive checklist of the Salticidae family was published by Szűts et al. (2003), with 70 salticid species from Hungary. Since then several jumping spider species have been reported: *Chalcoscirtus nigrinus* (Thorell, 1875), *Saitis tauricus* Kulczyński, 1904 (Szita et al., 2004), *Sitticus inexpectus* Logunov & Kronstedt, 1997 (Déri et al., 2007), *Euophrys herbigrada* (Simon, 1871), *Talavera parvistyla* Logunov & Kronstedt, 2003 (Kis, 2007,

cited in Kovács et al., 2012), *Talavera aperta* (Miller, 1971) (Batáry et al., 2008), and *Talavera milleri* (Brignoli, 1983) (Szinetár et al., 2012). In total, including the new record of *I. subinermis*, 78 jumping spider species are recorded from Hungary so far.

### 3.2. *Latilica maculipes* (Melichar, 1906) (Hemiptera: Issidae) and *Synophropsis lauri* (Horváth, 1897) (Hemiptera: Cicadellidae)

This part of the thesis was published as: **Korányi, D.**, Markó, V., Haltrich, A., & Orosz, A. (2018). First records of *Latilica maculipes* (Hemiptera: Issidae) and *Synophropsis lauri* (Hemiptera: Cicadellidae) in Hungary. *Opuscula Zoologica* 49: 71–75. DOI: 10.18348/opzool.2018.1.71

#### 3.2.1. Introduction

The number of leafhopper and planthopper species reported from Hungary is continuously increasing, several species have just recently been recorded for the first time. Most of them are native of North America or Asia [e.g. *Scaphoideus titanus* Ball, 1932 and *Orientus ishidae* (Matsumura, 1902)] (Dér et al., 2007; Koczor et al., 2013), or are of Mediterranean origin [e.g. *Fruticidia bisignata* (Mulsant & Rey, 1855) and *Pagiphora annulata* (Brullé, 1832)] (Orosz & Horváth, 2009; Koczor et al., 2011). As a result of faunal surveys in Budapest, another two Mediterranean Auchenorrhyncha species are reported here for the first time from Hungary.

#### 3.2.2. Materials and methods

The arthropod community of ornamental shrubs (*Abelia*, *Lonicera* and *Viburnum* spp.) was assessed in the Botanical Garden of the Szent István University (Botanical Garden Buda) in 2011 and 2012. In a subsequent study, the leafhopper and planthopper assemblages of field maple (*Acer campestre* L.) trees were also surveyed in different public areas of Budapest in 2016 and 2017.

Arthropods were collected by beating the branches of the sampled shrubs and trees over a beating umbrella. The collected individuals were preserved as dry specimens and deposited in the Hemiptera Collection of the Hungarian Natural History Museum, Budapest. All specimens were identified by A. Orosz using characters of the exoskeleton and male genitalia. Photographs of habitus were taken using a Nikon D5000 digital camera.

### 3.2.3. Results and discussion

#### ***Latilica maculipes* (Melichar, 1906)**

*Material examined.* Botanical Garden Buda (47°28'48"N 19°02'21"E), *Lonicera x xylosteoides*, 17.VIII.2012, 1♀, leg. A. Haltrich & A. Karap; Gellért-hegy (47°29'09"N, 19°02'51"E), *Acer campestre*, 27.IX.2017, 1♀, leg. D. Korányi; Ludovika tér (47°28'55"N, 19°05'01"E), *A. campestre*, 16.VII.2017, 1♂, leg. D. Korányi; Mátyás tér (47°29'31"N, 19°04'45"E), *A. campestre*, 13.X.2016, 1♀, leg. D. Korányi; Róbert Károly körút (47°32'08"N, 19°03'47"E), *A. campestre*, 27.IX.2017, 1♀, leg. D. Korányi.

*Distribution.* Described from Croatia, Bosnia-Herzegovina and Italy (Melichar, 1906). It was also reported from Israel, Palestine, Jordan (Linnauori, 1962), Cyprus, Greece, Turkey (Nast, 1972), Southern France, Spain (Balears Islands) (Dlabola, 1975), Southern Russia (Logvinenko, 1975; Gnezdilov, 1999; Gnezdilov et al., 2014) and Slovenia (Seljak, 2004).

*Host.* Very common on Mediterranean vegetation, mostly evergreen trees and shrubs, e.g. evergreen oak (*Quercus ilex* L.), cork oak (*Q. suber* L.), mastic tree (*Pistacia lentiscus* L.), common myrtle (*Myrtus communis* L.) and olive (*Olea europea* L.) (Linnavuori, 1962; Mazzoni, 2005).

*Flight period.* Based on our data, in Hungary, adults are active from middle of July to middle of October.

*Habitus.* Detailed description of the habitus of *L. maculipes* was provided by Melichar (1906) and furthermore, Gnezdilov & Mazzoni (2004) published the description of the genitalia of both sexes. Length of body 4.8–5.2 mm. The general appearance of the adult is shown in Fig. 3.



Figure 3. *Latilica maculipes* (Melichar, 1906) female. a = dorsal view; b = lateral view. Scale bar = 1 mm. (Photo: Dávid Korányi)

### ***Synophropsis lauri* (Horváth, 1897)**

*Material examined.* Botanical Garden Buda (47°28'48"N 19°02'21"E), *Abelia x grandiflora*, 29.VIII.2011, 1♀, *Viburnum tinus*, 07.IX. 2011, 1♂, 16.IX.2011, 1♂, 26.IX.2012, 1♀, *Viburnum x burkwoodii*, 29.VIII.2011, 1♂, 07.IX. 2011, 2♂♂, *Viburnum nitens*, 10.VIII.2011, 1♀, 1♂, 29.VIII. 2011, 1♂, 07.IX.2011, 2♂♂, 10.X. 2011, 1♂, *Viburnum carlesii*, 07.IX.2011, 2♀♀, *Viburnum x pragense*, 07.IX.2011, 2♂♂, *Viburnum setigerum*, 16.IX.2011, 1♀, leg. A. Haltrich & A. Karap; Farkasvölgy (47°29'05"N, 18°59'09"E), *A. campestre*, 13.IX.2016, 1♀, leg. D. Korányi; Vérmező (47°30'05"N, 19°01' 31"E), *A. campestre*, 27.IX.2017, 1♀, leg. D. Korányi.

*Distribution.* *Synophropsis lauri* was described from Croatia (Horváth, 1897). It was also recorded from Greece, Israel, Italy, Jordan, Turkey, Azerbaijan, Ukraine (Nast, 1972), France (Bonfils & Lauriaut, 1975), Southern Russia (Gnezdilov, 1999), Slovenia (Holzinger & Seljak, 2001), Switzerland (Mühlethaler, 2001), Germany (Nickel, 2010), Belgium (Bagnée, 2011), Malta (D'Urso & Mifsud, 2012), Austria (Holzinger et al., 2016), England (Bantock & Botting, 2018), and the Netherlands (Den Bieman & De Haas, 2018).

*Host.* This species was described from specimens collected on bay laurel (*Laurus nobilis* L.) (Horváth, 1897). In the Mediterranean region, *S. lauri* feeds on various evergreen trees and shrubs, in Central Europe, besides *L. nobilis*, common ivy (*Hedera helix* L.) seems to be the most suitable host plant (Nickel, 2010). Based on our records, *Viburnum* species may also be suitable as host plants for this leafhopper species.

*Flight period.* In the studied areas, adults are active from middle of August to middle of October.

*Habitus.* Description of the habitus was given by Horváth (1897) and Bagnée (2011). 6.0–6.5 mm. The general appearance of the adult is shown in Fig. 4.

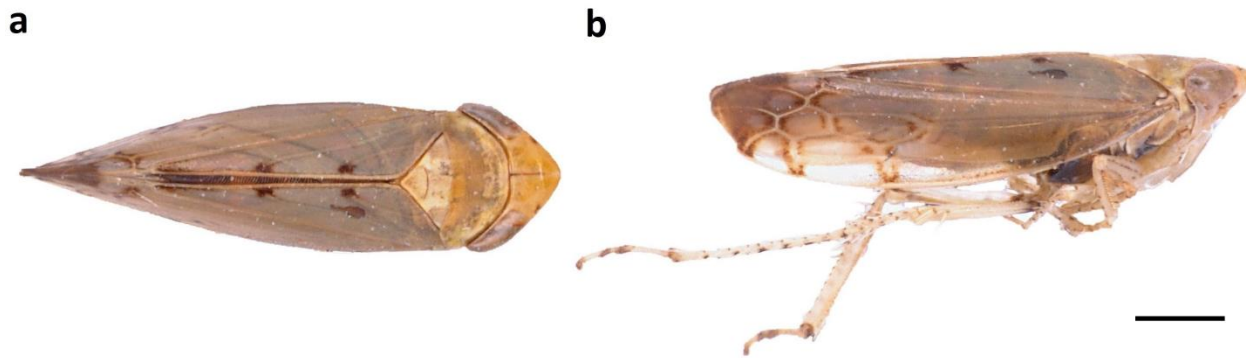


Figure 4. *Synophropsis lauri* (Horváth, 1897) female. a = dorsal view; b = lateral view. Scale bar = 1 mm. (Photo: Dávid Korányi)

The individuals of *Latilica maculipes* and *Synophropsis lauri* were collected from green belt areas in urban environments. Both species might have been introduced to Hungary unintentionally, but considering the climatic variations of the last years, the possibility of a natural expansion of their distribution area could not be excluded. Further surveys are needed to explain their occurrence and frequency in natural habitats.

The last checklist of leafhoppers and planthoppers of Hungary published by Györffy et al. (2009) listed 540 species. Since then several species have been added to the list: *P. annulata* (Koczor et al., 2011), *Graphocephala fennahi* Young, 1977 (Papp et al., 2012), *Liguropia juniperi* (Lethierry, 1876), *Opsius smaragdinus* Emeljanov, 1964 (Koczor et al., 2012), *O. ishidae* (Koczor et al., 2013) and *Tautoneura polymitusa* Oh & Jung, 2016 (Tóth et al., 2017). With the newly recorded *L. maculipes* and *S. lauri* currently 548 Auchenorrhyncha species are reported from Hungary. According to A. Orosz, as a result of different faunal collections (e.g. Hungarian Biodiversity Days and the field program of 5th European Hemiptera Congress) there are some additional unpublished records of Auchenorrhyncha new to Hungary, and therefore, the presumed number of Auchenorrhyncha species in Hungary exceeds 560.

### 3.3. *Psallus assimilis* Stichel, 1956 (Hemiptera: Heteroptera: Miridae)

This part of the thesis was published as: **Korányi, D.**, Markó, V., & Kondorosy, E. (2018). First record of *Psallus assimilis* in Hungary (Hemiptera: Heteroptera: Miridae). *Opuscula Zoologica* 49: 17–22. DOI: 10.18348/opzool.2018.1.17

#### 3.3.1. Introduction

*Psallus* Fieber, 1858 is one of the largest genera of Miridae (Hemiptera: Heteroptera); it comprises almost 140 species in the Palearctic Region (Kerzhner & Josifov, 1999; Aukema et al., 2013), 23 of which have also been recorded from Hungary. Eleven of these species, e.g. *P. anaemicus*, *P. helenae* and *P. pardalis*, were recorded during the last twenty-five years (Kondorosy, 1999, 2005, 2011, 2012).

*Psallus* species are primarily zoophytophagous in the adult stage. Young nymphs feed on pollen, therefore they can only be found on mature, fertile host plants. Later nymphal stages become predatory, and prey mainly on mites and aphids, but also on other insects, e.g. scale insects, psyllids and caterpillars (Wachmann et al., 2004), or eggs of leaf beetles (Björkman et al., 2009). Many species of this genus are associated with oak trees (*Quercus* spp.), while other species are found on other deciduous and coniferous trees and shrubs (e.g. *Picea*, *Larix*, *Fraxinus* and *Fagus* spp.) (Wachmann et al., 2004; Goßner, 2008).

#### 3.3.2. Materials and methods

The arthropod community in the canopies of field maple (*Acer campestre* L.) trees was surveyed in 23 locations of Budapest, Hungary: Alkotás utca (47°29'22"N, 19°01'27"E, 142 m a.s.l.), Botanical Garden Buda (47°28'49"N, 19°02'12"E, 113 m a.s.l.), Csillebérc (47°29'25"N, 18°57'39"E, 447 m a.s.l.), Farkasvölgy (47°29'05"N, 18°59'09"E, 304 m a.s.l.), Gellért-hegy (47°29'09"N, 19°02'51"E, 187 m a.s.l.), Haller park (47°28'28"N, 19°04'49"E, 107 m a.s.l.), Hegyalja út (47°29'07"N, 19°01'00"E, 193 m a.s.l.), Hunyadi tér (47°30'21"N, 19°04'00"E, 104 m a.s.l.), Hűvösvölgy (47°32'30"N, 18°57'49"E, 227 m a.s.l.), Karolina út (47°28'45"N, 19°01'53"E, 110 m a.s.l.), Keleti Pályaudvar (47°29'59"N, 19°05'03"E, 109 m a.s.l.), Ludovika tér (47°28'55"N, 19°05'01"E, 110 m a.s.l.), Margit-sziget (47°31'24"N, 19°02'9"E, 104 m a.s.l.), Mátyás tér

(47°29'31"N, 19°04'45"E, 105 m a.s.l.), Normafa (47°30'24"N, 18°57'42"E, 460 m a.s.l.), Rác Aladár út (47°28'59"N, 18°59'43"E, 253 m a.s.l.), Rákóczi tér (47°29'33"N, 19°04'19"E, 104 m a.s.l.), Róbert Károly körút (47°32'08"N, 19°03'47"E, 107 m a.s.l.), Szent István park (47°31'07"N, 19°03'03"E, 105 m a.s.l.), Széchenyi-hegy (47°29'42"N, 18°58'30"E, 461 m a.s.l.), Városmajor (47°30'30"N, 19°01'02"E, 135 m a.s.l.), Vérmező (47°30'05"N, 19°01'31"E, 125 m a.s.l.), Zugligeti út (47°31'03"N, 18°59'09"E, 180 m a.s.l.) and in Diósd (47°24'44"N, 18°56'17"E, 165 m a.s.l.) and Törökbálint (47°25'58"N, 18°55'37"E, 182 m a.s.l.).

Tree canopies were sampled monthly from April to October in 2015, 2016 and 2017. Arthropods were collected by beating the branches of each sampled field maple trees over beating umbrella. Samples were stored in 70% ethanol, heteropterans were examined in the laboratory of the Department of Entomology of Szent István University (SZIU). Adults of *Psallus* species were identified by D. Korányi using characters of the exoskeleton and male genitalia following the keys of Wagner (1967) and Wyniger (2004). Photographs of habitus and femora (Fig. 5) were taken using a Sony XCD-SX90CR digital interface connected to a Zeiss Stemi 2000 stereomicroscope, those of the vesica (Fig. 6) using a Zeiss Imager A2 light microscope equipped with Axio Cam MRc5.

### 3.3.3. Results and discussion

Among the 5536 heteropteran individuals collected during the study, 714 specimens (226 ♂♂, 488 ♀♀) were identified as *P. assimilis*. Further 354 specimens (73 nymphs, 191 ♂♂ and 90 ♀♀ damaged or teneral adults) of *Psallus* spp. were very similar to *P. assimilis* and likely represented this species, but they could not be unambiguously identified to species level. Collected specimens were deposited in the Hemiptera Collection of the Hungarian Natural History Museum (HNHM) and the insect collection of Department of Entomology, SZIU.

*Material examined.* Alkotás utca, 7.V.2015, 27 ♂♂, 32 ♀♀, 26.IV.2016, 43♀♀; Botanical Garden Buda, 7.V.2015, 13 ♂♂, 25 ♀♀, 26.IV.2016, 35 ♀♀; Csillebérc, 25.V.2016, 8 ♂♂, 5 ♀♀, 22.VI.2016, 1 ♀; Diósd, 25.V.2016, 1 ♂, 2 ♀♀; Farkasvölgy, 25.V.2016, 3 ♂♂, 5 ♀♀; Gellért-hegy, 7.V.2015, 79 ♂♂, 91 ♀♀, 26.IV.2016, 1 ♀, 25.V.2016, 1 ♀; Haller park, 26.IV.2016, 20 ♀♀, 25.V.2016, 1 ♂, 5.V.2017, 1 ♂; Hegyalja út, 25.V.2016, 6 ♀♀; Hunyadi tér, 26.IV. 2016, 1 ♂, 6 ♀♀, 25.V.2016, 1 ♂, 5.V.2017, 4 ♂♂, 10 ♀♀; Hűvösvölgy, 25.V.2016, 2 ♀♀; Karolina út, 7.V.2015, 62 ♂♂, 80 ♀♀, 26.IV.2016, 2 ♂♂, 24 ♀♀, 25.V.2016, 1 ♂, 5.V.2017, 1♀; Keleti



Pályaudvar, 26.IV. 2016, 2 ♂♂, 2 ♀♀; Ludovika tér, 5.V.2017, 1 ♀; Margit-sziget, 26.IV.2016, 3 ♂♂, 35 ♀♀; Mátyás tér, 26.IV.2016, 2 ♀♀, 5.V.2017, 1 ♀; Normafa, 25.V.2016, 2 ♀♀; Rácz Aladár út, 25.V.2016, 4 ♂♂, 15 ♀♀; Rákóczi tér, 26.IV.2016, 12 ♂♂, 9 ♀♀, 5.V.2017, 6 ♀♀; Róbert Károly körút, 26.IV.2016, 6 ♀♀, 5.V.2017, 9 ♀♀; Széchenyi-hegy, 25.V.2016, 7 ♀♀; Törökbálint, 25.V.2016, 1 ♀; Vérmező, 25.V.2016, 1 ♀; Zugligeti út, 25.V.2016, 1 ♂, 1 ♀.

Altogether, 20 males and 183 females were collected in April, 206 males and 304 females in May, and only one female was found in June. For doubtfully identified (presumably *P. assimilis*) specimens, the corresponding values were 68 nymphs, 119 male and 58 female individuals in April and 5 nymphs, 72 male and 32 female individuals in May.

Other *Psallus* species in the same samples were *P. wagneri* Ossiannilsson, 1953 (Botanical Garden Buda, 26.IV.2016, 2 ♂♂; Csillebérc, 25.V.2016, 1 ♂; Farkasvölgy, 25.V.2016, 1 ♂; Hegyalja út, 25.V.2016, 1 ♂), *P. perrisi* Mulsant & Rey, 1852 (Botanical Garden Buda, 26.IV.2016, 1 ♂; Csillebérc, 25.V.2016, 1 ♂) and individuals representing either *P. perrisi* or *P. wagneri*, (Botanical Garden Buda, 26.IV.2016, 3 ♀♀; Csillebérc, 25.V.2016, 3 ♀♀; Karolina út, 7.V. 2015, 1 ♀; Széchenyi-hegy, 25.V.2016, 1 ♀) but doubtfully associated with either of these two species.

*Distribution.* *Psallus assimilis* was first reported from Great Britain (Stichel, 1956–1958; Aukema, 1981). Later it was also found in Germany (Rieger, 1972), Luxembourg (Reichling, 1984), the Netherlands (Aukema, 1986), France (Matocq, 1989), Poland (Gorczyca, 1990), Austria (Melber et al., 1991), Italy (Bacchi & Rizzotti Vlach, 1994), Serbia (Protić, 1999), Belgium and Sweden (Kerzhner & Josifov, 1999), Czech Republic (Kment & Bryja, 2001), Slovakia (Bryja & Kment, 2002), Switzerland (Wyniger & Burckhardt, 2003) and Spain (Pagola-Cardé et al., 2006). *Psallus assimilis* was also mentioned from Finland (Stichel, 1956–1958) and Denmark (Skipper, 2017), though its presence in these countries still needs to be confirmed (Endrestøl & Ødegaard, 2011).

*Habitat and bionomics.* *Psallus assimilis* prefers woody habitats (forests, forest edges and woodlands) and lives on *Acer campestre* (Rabitsch, 2008; Friess, 2011; Heckmann & Blöchlinger, 2011). It is univoltine and overwinters in the egg stage (Wachmann et al., 2004; Rabitsch, 2008) on young twigs of the host plant (Aukema & Hermes, 2009). It is zoophytophagous, reported as a predator of various insects including psyllids (Jerinić-Prodanović & Protić, 2013). In the studied areas, adults are active from the end of April to the beginning of June.

*Adult.* The general appearance of the adults is shown in Figs. 5a–b. Length of body is 3.3–3.9 mm. The yellowish, segment I with two setae. Corium, embolium and cuneus reddish orange, membrane brown. Tibiae yellow, with brown spines arising from brown spots. Tarsus yellowish, third tarsal segment dark (Figs. 5a–b). Ventral surface of metafemora has longitudinally arranged brown spots (Figs. 5c–d).

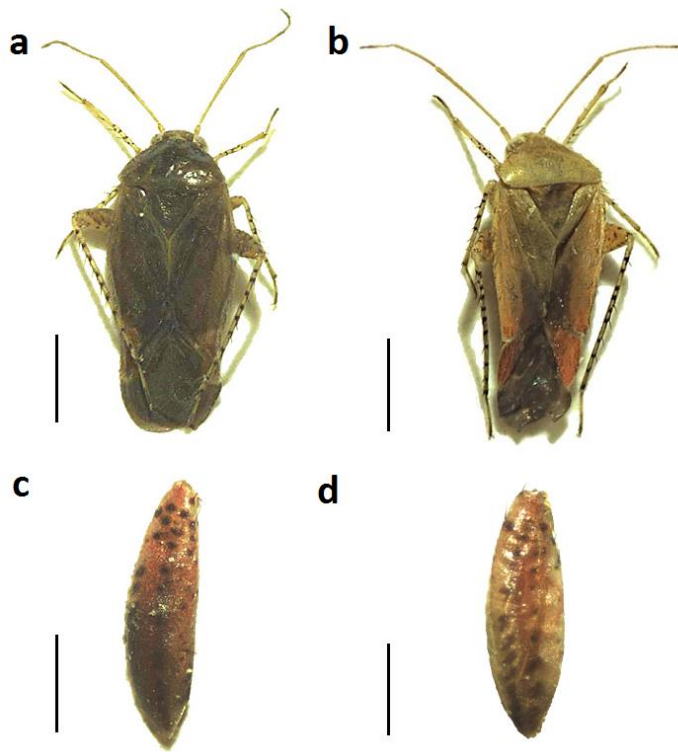


Figure 5. *Psallus assimilis* Stichel, 1956. a = male, dorsal view; b = female, dorsal view; c = male, ventral surface of metafemur; d = female, ventral surface of metafemur. Scale bars = 1 mm (Fig. 1a–b), 0.5 mm (Fig. 1c–d). (Photo: Dávid Korányi)

*Male.* The body is elongate, head, scutellum and clavus are orange-brown, the pronotum is bright brown (Fig. 5a). Femora are brownish, with yellowish apical part (Fig. 5c). Vesica is C-shaped, basal lateral process is long, straight, slightly surpassing apical margin of secondary gonopore, apical lateral process is straight and widened (Figs. 6a–b).

*Female.* The body is roundish, the head, the pronotum, the scutellum and the clavus are yellowish red (Fig. 5b). Femora are yellowish, with brown basal part (Fig. 5d).

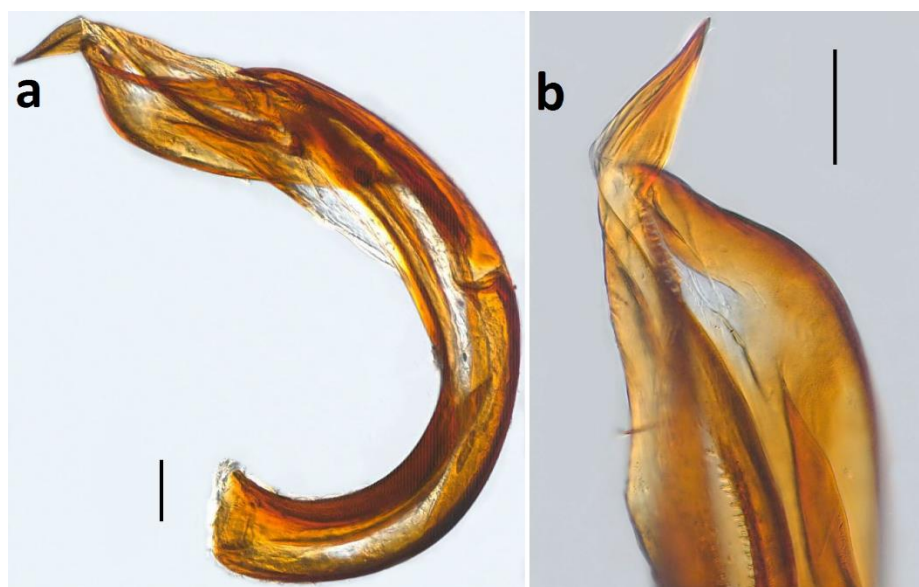


Figure 6. Cleared and dissected vesica of *Psallus assimilis* Stichel, 1956. a = ventral view; b = apex, magnified. Scale bars = 0.1 mm. (Photo: Dávid Korányi)

The large number of individuals of *P. assimilis* collected during the present study suggests that this species is either autochthonous in Hungary (but has not been found yet due to the lack of intensive collecting from maple trees) or it is a recent invader which has already successfully established and it is present since several years. We have reexamined the *Psallus* spp. specimens in the Hemiptera Collection of HNHM and did not find any further specimens of *P. assimilis*. Since other congeners (*P. perrisi*, *P. wagneri*) were found in low abundance, *P. assimilis* can be considered as the dominant (most abundant) *Psallus* species in the canopy of *Acer campestre* in the studied region. Furthermore, based on our results, this species was one of the most common true bug species not only in urban forests (e.g. Csillebérc, Hűvösvölgy, Széchenyi-hegy), but also in urban areas bounded by artificial surfaces (e.g. Alkotás street, Karolina street, Rákóczi tér). Besides of the pollen of its host plant, aphids (*Periphyllus* spp., *Drepanosiphum* spp.) that occurred in large numbers in the canopy of *A. campestre* trees could serve as food for the species at these locations.

With the present new record, the number of *Psallus* species recorded from Hungary is brought to 24; accordingly, *Psallus* is the most species-rich true bug genera in Hungary.

### 3.4. *Cybocephalus nipponicus* Endrődy-Younga, 1971 (Coleoptera: Cybocephalidae)

This part of the thesis was published as: Merkl, O., Károlyi, B., & **Korányi, D.** (2017). First record of *Cybocephalus nipponicus* in Hungary (Coleoptera: Cybocephalidae). *Folia Entomologica Hungarica* 78: 71–76. DOI: 10.17112/FoliaEntHung.2017.78.71

#### 3.4.1. Introduction

The family Cybocephalidae (Coleoptera: Cucujoidea) is a small assemblage of minute (0.5–2.5 mm long) beetles with ca. 150 described species in eight genera – the majority belongs to the genus *Cybocephalus* Erichson, 1844 (Hisamatsu, 2013; Smith & Cave, 2006a). Both larvae and adults are predators, preying mainly on armored scale insects (Hemiptera: Diaspididae). The group was recognized either as a subfamily of Nitidulidae or a distinct family, its taxonomic history was discussed in the introductory parts of Cline et al. (2014) and Hisamatsu (2013). Molecular phylogenetic studies (Bocak et al., 2014; Cline et al., 2014; Robertson et al., 2015) support recognition of the group as a separate family.

Until now, four species of the family have been recorded from Hungary (Endrődy-Younga, 1968; Jelínek & Audisio, 2007): *Cybocephalus fodori* Endrődy-Younga, 1965, *C. politus* (Gyllenhal, 1813), *C. pulchellus* Erichson, 1845, and *C. rufifrons* Reitter, 1874 (occurrence of the last species within present-day Hungary needs confirmation). In the summer of 2015 and the autumn of 2016 and 2017, a fifth species, the scale picnic beetle *Cybocephalus nipponicus* was found in four localities of urban Budapest, the capital city of Hungary.

#### 3.4.2. Materials and methods

On 15th October 2017 the second author (BK) posted photos of a distinctively patterned minute beetle on the website [www.izeltlabuak.hu](http://www.izeltlabuak.hu) operated by him. The original post is found at <https://www.izeltlabuak.hu/talalat/14626>, and shows a specimen observed on a yellow-washed wall of the Békásmegyer housing estate in District III, Budapest. The voucher was donated to the Hungarian Natural History Museum (HNHM), where OM identified it as *Cybocephalus nipponicus*.

The third author (DK) collected beetles in parks and avenues of different locations in Budapest by beating foliage of field maple (*Acer campestre* L.) as part of his PhD research project. In November 2017, several samples of beetles (mainly small-sized, hairy Coccinellidae) were passed on to OM for identification. Individuals of *C. nipponicus* were found in three samples. Seven specimens were collected in Rákóczi tér [square], which is a small (less than one hectare) park around a subway station in District VIII of Budapest, covered by ornamental trees, small shrubs, grassy patches and concrete surfaces and surrounded by multi-storey buildings and roads with heavy traffic. One specimen was collected in Hunyadi tér [square], which is also a small (about one hectare) park in District VI, with vegetation similar to that of Rákóczi tér and also with a small food market. One specimen was collected in the Buda Arboretum of the Szent István University in District XI, which is a 7.5-hectare botanical garden around the buildings of the university, surrounded by roads and old villas with gardens.

### 3.4.3. Results and discussion

*Material examined.* Budapest, XI. district, Budai Arborétum, 47°28'49"N, 19°02'12"E, *Acer campestre*, 29.VII.2015, leg. Dávid Korányi (1 ♂, HNHM); Budapest, VI. district, Hunyadi tér, 47°30'21"N, 19°04'00"E, *Acer campestre*, 14.X.2016, leg. Dávid Korányi (1 ♀, HNHM); Budapest, VIII. district, Rákóczi tér, 47°29'33"N, 19°04'19"E, *Acer campestre*, 27.IX.2017, leg. Dávid Korányi (4 ♂♂, 3 ♀♀, HNHM); Budapest, III. district, Békásmegyér, Heltai Jenő tér, from yellow-washed house wall, 47°35'52"N, 19°03'26"E, 15.X.2017, leg. Balázs Károlyi (1 ♂, HNHM).

*Distribution.* *Cybocephalus nipponicus* was redescribed and its bionomics and distribution were reviewed by Smith & Cave (2006a, 2006b) and Hisamatsu (2013). The species is indigenous in East (Korea, China, Japan), South (India, Sri Lanka) and Southeast Asia (Thailand, Singapore) and in Micronesia (Palau, Mariana Islands) (Endrődy-Younga, 1971; Jelínek & Audisio, 2007). As a biological control agent against various armored scale insect species it was deliberately introduced from Korea and Thailand to the eastern United States (several times), where it has been established and currently is widely distributed (Smith & Cave, 2006a, 2006b). Other documented events of human-mediated introduction include the one from Florida to the West Indies (Smith & Cave, 2007), from Thailand to Taiwan (Smith & Bailey, 2007; Song et al., 2012) and South Africa

(Labuschagne et al., 1996). The species was also found in Hawaii, but its introduction must have been accidental (Ewing, 2004).

In Europe, *C. nipponicus* was recorded for the first time from Italy (Lupi, 2002). Although unpublished, the species was observed in France, according to a post on the forum Le Monde des insectes <<https://www.insecte.org/forum/viewtopic.php?t=149434>> that shows a photo of the unmistakable male of *C. nipponicus* from 21 November 2015. Recently this species was also recorded from the Czech Republic (Vávra, 2020). These records may be results of unintentional introduction.

The same holds for the Hungarian records. The source of introduction is unknown; the four known occurrences in urban environment (in areas of the highest population density in Budapest) suggest that the species might have been accidentally brought in with ornamental plants infested with diaspidid scales.

*Prey species.* Thirteen diaspidid species were listed as hosts of *C. nipponicus* by Smith & Cave (2006a), and further four were added by Song et al. (2012). In a no-choice host-specificity test adults fed also on one species each of Asterolecaniidae, Coccidae and Pseudococcidae, but no oviposition took place on these scales (Song et al., 2012). Adults were observed devouring eggs of citrus red mite, *Panonychus citri* (McGregor, 1916) (Acari: Tetranychidae), but ovaries of such female adults remained undeveloped, and were unable to lay eggs (Tanaka & Inoue, 1980). Consequently, the life cycle of *C. nipponicus* can apparently be completed only with feeding on armored scale species.

The hosts of *C. nipponicus* in Hungary are unknown as yet. DK found the euonymus scale, *Unaspis euonymi* (Comstock, 1881) on wintercreeper, *Euonymus fortunei* (Turcz.) Hand.-Maz. near the maple trees in Rákóczi tér; this diaspidid might be a prey species of the beetle. *Unaspis euonymi* was the first scale species against which *C. nipponicus* was released in the United States (Drea & Carlson, 1988).

*Identification.* *Cybocephalus nipponicus* may be quite easily distinguished from its congeners occurring in Hungary. The male color pattern is distinctive (Fig. 7): head and pronotum are yellow and elytra are black (frons of male *C. politus* and *C. rufifrons* is yellowish red, but their pronotum is black, except ill-defined yellowish translucent lateral margins). Females of all species are unicolored black dorsally, but the punctural interspaces of pronotum and elytra on *C. nipponicus* are smooth and glossy (interspaces, especially on elytra, are microreticulated and alutaceous on the other species). Some male specimens of *C. nipponicus* have dark brown to black

pronotum (Hisamatsu, 2013), but the smooth interspaces separate them from its congeners in Hungary.



Figure 7. *Cybocephalus nipponicus* Endrődy-Younga, 1971. a = live male; b = mounted male. Scale bar = 0.2 mm. (Photo: Tamás Németh)

The proposed Hungarian name of *C. nipponicus* is “japán pajzstetvézbogár” (meaning Japanese scale-hunting beetle).

#### **4. STUDY II: Abundance pattern and composition of phytophagous insects on urban maple trees (*Acer* spp.)**

This part of the thesis was submitted to the journal *Arthropod-Plant Interactions* with the title: **Korányi, D., & Markó, V.** Host plant identity and condition shape phytophagous insect communities on urban maple (*Acer* spp.) trees.

##### **4.1. Introduction**

Although urban areas represent a relatively small proportion of the total Earth surface, the urban land cover continues to grow and is predicted to increase by 1.2 million km<sup>2</sup> in the first 30 years of the 21st century (Seto et al., 2012). Urban expansion and associated land-cover change is considered to be one of the most extreme forms of landscape and habitat transformation. It leads to dramatic changes in the local biotic and abiotic environment, and hence has substantial impacts on ecological systems (McDonnell & Pickett, 1990; McIntyre, 2000; Grimm et al., 2008).

Trees contribute to the mitigation of abiotic environmental changes associated with urbanization, thus have important role in providing a livable environment for humans. Urban trees reduce air temperature by absorbing solar radiation through evapotranspiration and reduce surface temperatures via shading (Rahman et al., 2017). Moreover, trees remove significant amounts of air pollutants originating from traffic and industrial activity, by absorption and by dry deposition on plant surfaces (Nowak et al., 2006). At the same time, trees are highly exposed to different factors associated with urbanization, including heat stress, increased emissions, low air humidity and periods of critical water stress, soil compaction, and de-icing salt (Sjöman & Nielsen, 2010; Pautasso et al., 2015).

Tree species respond to urban stress differently. Species that are poorly adapted to these harsh conditions are increasingly losing their decorative value (Günthardt-Goerg & Vollenweider, 2007; Swoczyna et al., 2015; Stratópoulos et al., 2019), and are becoming particularly susceptible to biotic stress agents (Richards, 1983; Wargo, 1996; Tubby & Webber, 2010). Accordingly, knowledge about different species' tolerance and stress resistance is crucial during the selection of trees for urban sites (Richards, 1983; Roloff et al., 2009; Sjöman & Nielsen, 2010).

Urbanization is often associated with a higher abundance of phytophagous arthropods on trees (Raupp et al., 2010; Youngsteadt et al., 2015; Korányi et al., 2020), which, along with abiotic



stressors, affects negatively their physiological functions and causes visible declines in their condition (Zvereva et al., 2010). For example, piercing-sucking insect pests can cause significant removal of nutrients, leading to reduced growth and survival, and weakened photosynthesis of trees (Dixon, 1971; Kaakeh et al., 1992; Frank et al., 2013). Native species might be more exposed to these effects as they often support more local phytophagous species and receive increased herbivory (Tallamy, 2004; Matter et al., 2012; Clem & Held, 2015; Frank et al., 2019). Differences in abundance and composition of herbivore communities also occur within congener tree species due to numerous reasons, including phenological characteristics (Ekholm et al., 2019) and physiological condition of trees (Dale & Frank, 2017), and host plant specialization of herbivores (Fraser, 1997). Although a number of studies have been conducted examining the effects of the urban environment on plants and herbivores, more studies examining the ecology of plant-herbivore interactions, including how tree species shape herbivore communities in cities, are needed to get a more holistic picture (Raupp et al., 2010; Miles et al., 2019).

Maples (*Acer* spp.) are among the most commonly-planted urban tree species in North America (Cowett & Bassuk, 2014, 2020) and Europe (Sæbø et al., 2003; Britt & Johnston, 2008; Sjöman et al., 2012). In Central Europe, sycamore (*Acer pseudoplatanus* L.), Norway (*A. platanoides* L.), and field maple (*A. campestre* L.) are common native tree species (San-Miguel-Ayanz et al., 2016), and are often selected for urban forestry (Roloff et al., 2009). These tree species have overlapping phytophagous insect communities due to the presence of some generalist and maple specialist species (e.g., Jones, 1945; Nickel, 2003; Wilkaniec & Sztukowska, 2008). However, sycamore, Norway and field maples have distinct ecological preferences (San-Miguel-Ayanz et al., 2016) and tolerate urban stress differently (Roloff et al., 2009; Stratópoulos et al., 2019); therefore, their performances might vary considerably in urban environments resulting in different outcomes in their interactions with herbivorous insects.

In this study, we examined the abundance patterns of phytophagous insects as well as their interactions with physiological condition of these three common *Acer* species in urban areas. Our first objective was to compare the abundance and composition of common pest insects on sycamore, Norway, and field maple trees. Our second objective was to assess how phytophagous insects influence the stress level and condition of trees. Finally, our third objective was to determine whether the condition of these trees may affect the abundance of phytophagous insects.

## 4.2. Materials and methods

### 4.2.1. Study area and arthropod collection

The research was carried out in the city of Budapest between 2014 and 2015. In order to minimize the impact of the urban landscape, we selected four study sites (Arboretum of Buda [47°28'50"N 19°02'16"E], Gellért Hill [47°29'07"N 19°02'38"E], streets around the Buda Campus of Szent István University [47°28'40"N 19°02'06"E], and Alkotás utca [47°29'20"N 19°01'28"E]) that are situated close to each other and have sufficient numbers of field (*A. campestre*), Norway (*A. platanoides*), and Sycamore maples (*A. pseudoplatanus*). We selected 12 individuals (three at each site) in 2014 and 20 individuals (five at each site) per tree species in 2015 for arthropod collection, all of which had similar ages and undamaged trunks.

Arthropods were collected from the canopy of the trees by the beating method (Basset et al., 1997), using a beating funnel 70 cm in diameter and 60 cm in depth, together with a 120 cm long beating stick. Ten branches were sampled per tree. Samples were taken on 14 dates in 2014 (April 6, 20, May 4, 18, June 1, 16, 29, July 13, 26, August 9, 24, September 7, 20 and October 5) and on seven dates in 2015 (May 7, June 16, July 8, 29, August 19, September 10 and October 3). The collected arthropods were counted and deposited at the Department of Entomology of Szent István University. We identified the phytophagous insects i.e. aphids (Hemiptera, Aphididae), psyllids (Hemiptera, Psylloidea), plant- and leafhoppers (Auchenorrhyncha), heteropterans (Heteroptera), and curculionids (Coleoptera, Curculionidae) to species.

### 4.2.2. Stress level and condition of trees

To determine the stress level of the trees, we measured peroxidase (POD) enzyme activity. In 2015, we collected leaves from the selected trees starting after July 29, when the highest abundance of phytophagous insects was detected, and transported the leaves in a cooler box to the laboratory of the Department of Applied Chemistry of Szent István University. For enzyme analyses, leaves were homogenized in 20 mM sodium acetate, pH 7.8 buffer containing 1% polyvinylpyrrolidone, 20% sucrose, 0,035% bovine serum albumin, 10% Triton X100. The tissue extract was centrifuged at 13,000 r/min for 20 minutes. The procedure was carried out at 4 °C and the supernatant was used for further analyses. Peroxidase (POD) activity was determined by spectrophotometry in a H<sub>2</sub>O<sub>2</sub>

substrate with ortho-dianizidine used as chromogenic indicator ( $\epsilon = 11.3$ ) at 460 nm (Shannon et al., 1966). POD activity was expressed in units of peroxidase per ml. A unit of peroxidase was defined as an increase of 0.001 unit of absorbance for 90 seconds.

In 2015, we evaluated visually the degree of leaf necrosis and leaf fall of trees as indicators of environmental stress (Close et al., 1996; Dobrowolska et al., 2001; Schreuder et al. 2001; Günthardt-Goerg & Vollenweider, 2007; Khavaninzadeh et al., 2014). The evaluations were done in the second half of October, when leaf fall and leaf necrosis symptoms became apparent. The evaluations were done in five-point scales along ordinal conditional gradients (leaf necrosis: observed in less than 5% [score: 1], between 5–20% [score: 2], between 20–35% [score: 3], between 35–50% [score: 4], and between 50–70% of the canopy [score 5]; degree of leaf fall: less than 10% [score: 1], between 10–25% [score: 2], between 25–40% [score: 3], between 40–50% [score: 4] and between 50–60% [score: 5]).

#### 4.2.3. Data analyses

We used R version 3.4.4 statistical environment (R Core Team, 2018) for all analyses. Before the analyses, insect abundance and POD activity were log-transformed to meet conditions of normality. The degree of leaf necrosis and leaf fall variables were handled as ordered factors in the models using the function ‘as.ordered’ of R. For the analyses on the relationships between phytophagous insects and stress levels and condition of trees, we included the numbers of the most abundant phytophagous insect species (*Metcalfa pruinosa* [Say],  $n = 15912$ ) and groups (other plant- and leafhoppers [except *M. pruinosa*],  $n = 1886$ ; heteropterans,  $n = 1626$ ; aphids,  $n = 1154$ ) in 2015 and  $p$  values were adjusted using the method of Benjamini and Hochberg (1995).

#### **Effect of tree species on the abundance and composition of phytophagous insects**

To determine the effect of maple species on phytophagous insects, we ran general linear mixed models (GLMMs) using the function ‘lme’ from the ‘nlme’ package version 3.1-143 (Pinheiro et al., 2019). The models included the abundances of the main insect groups (aphids, plant- and leafhoppers and heteropterans) and species as response variables, tree species as an explanatory variable (fixed factor), and site as a random factor. In order to obtain meaningful quantitative responses, only those insect species represented by at least 50 individuals in each year’s samples

were included in the species-level analyses, and their abundance data from the two years (2014 and 2015) were analyzed separately (Table S1.1). Since the leafhopper and other (non-*M. pruinosa*) planthopper samples collected in 2014 were damaged, we analyzed the data for these groups only in 2015. If the model validation plots showed heteroscedasticity, we implemented a variance function ‘varIdent’ in the weight of the models to estimate the within-group variance and account for unequal variances. To evaluate the effect of tree species, ANOVA tests were performed using ‘Anova’ function of the ‘car’ package version 3.0-6 (Fox & Weisberg, 2019). For post-hoc analysis, least square means were calculated using the ‘lsmeans’ function, and pairwise comparisons with Tukey *p* value correction were performed using the ‘pairs’ function from the package ‘lsmeans’ version 2.30-0 (Lenth, 2016).

We performed non-metric multidimensional scaling (NMDS) to examine the effect of tree species on the community composition of abundant phytophagous insect species (Table S1.1) using Bray–Curtis dissimilarity as the distance measure, and the ‘metaMDS’ function of ‘vegan’ package version 2.5-3 (Oksanen et al., 2018). We also ran an indicator species analysis (Dufrêne & Legendre, 1997) to identify potential phytophagous character species for each maple species by using the ‘indval’ function of the ‘labdsv’ package version 2.0-1 (Roberts, 2019). For NMDS and IndVal analyses, the abundance data were pooled across study years.

### **Stress level and condition of maple tree species**

To determine the differences between stress levels and conditions of maple species, we ran GLM and cumulative link mixed models (CLMMs) using the functions ‘lme’ from the ‘nlme’ package and ‘clmm’ from the ‘ordinal’ package version 2019.12-10 (Christensen, 2019). The models included POD activity (GLMM), degree of leaf necrosis, and leaf fall (CLMMs) as response variables, tree species as an explanatory variable (fixed factor), and site as a random factor. To evaluate the differences between tree species, ANOVA tests were performed using the ‘Anova’ function of the ‘car’ package. For post-hoc analysis, least square means were calculated using the ‘lsmeans’ function and pairwise comparisons with Tukey *p* value correction were performed using the ‘pairs’ function from the package ‘lsmeans’.

## **Effect of phytophagous insects on stress level of trees**

We performed two types of analyses (GLMMs) in order to examine the effect of phytophagous insects on tree stress levels using the function ‘lme’ from ‘nlme’ package. In the first analysis, we tested this relationship including all tree individuals ( $n = 60$ ). The model included POD activity as response variable, the abundance of phytophagous insect species and groups as explanatory variables (pooled abundance data across collection dates before the POD measurements in 2015, fixed factors), and tree species and site as random factors. In the following analyses, we ran models for each tree species separately ( $n = 20$ ). The models included POD activity as a response variable, the abundances of phytophagous insect species and groups as explanatory variables (fixed factors), and site as a random factor.

## **Relationships between phytophagous insects and tree condition**

To test the effect of phytophagous insects on the condition of trees, we ran CLMMs using the function ‘clmm’ of the ‘ordinal’ package. The models included the degree of leaf fall and necrosis as response variables, the abundance of phytophagous insect species and groups as explanatory variables (fixed factors), and tree species and site as random factors.

We used GLMMs to assess whether the condition of trees would influence the abundance of phytophagous insects using the function ‘lme’ from ‘nlme’ package. The models included the abundance of phytophagous insect species and groups as response variables, degree of leaf fall and necrosis as explanatory variables (fixed, ordered factors), and tree species and site as random factors.

## **4.3. Results**

### *4.3.1. Taxa recorded*

In total, we identified 33072 phytophagous insects, 12302, 7835 and 12935 individuals from the canopy of sycamore, Norway, and field maple, respectively. The overall abundance was significantly ( $t = -2.186, p = 0.033$ ) and marginally significantly ( $t = -1.966, p = 0.055$ ) lower on

Norway maple than on field and sycamore maple. There was no significant difference between the total number of individuals on field and sycamore maple ( $t = 0.220$ ,  $p = 0.827$ ). The collected individuals consisted mainly of planthoppers (Fulgoromorpha; 66.4%), aphids (17.8%), heteropterans (7.0%), leafhoppers (Cicadomorpha; 5.3%), curculionids (2.5%) and psyllids (0.86%). *Metcalfa pruionosa* ( $n = 21852$ ) was by far the most abundant species, representing 66.1% of all individuals examined, followed by *Periphyllus testudinaceus* (Ferne) ( $n = 2791$ , 8.4%), *Drepanosiphum platanoidis* (Schrank) ( $n = 2502$ , 7.6%), *Halyomorpha halys* (Stål) ( $n = 1182$ , 3.6%), *Phyllobius oblongus* (Linnaeus) ( $n = 571$ , 1.7%), *Nezara viridula* (Linnaeus) ( $n = 566$ , 1.7%), and *Acericerus ribauti* Nickel & Remane ( $n = 549$ , 1.7%) (Table S1.1). (The latter species is listed under the name *Idiocerus rotundifrons* Kirschbaum in the Hungarian checklist of plant- and leafhoppers by Györfy et al. [2009], but following Biedermann and Niedringhaus [2004], we use the name proposed by Nickel and Remane [2002].) For temporal abundances of phytophagous species see Figs. S1.1-S1.4.

#### 4.3.2. *Effect of tree species on the abundance and composition of phytophagous insects*

The total number of aphids was the highest on sycamore and the lowest on Norway maple trees in both years (Fig. S1.5, Table S1.2). Aphid species exhibited a high degree of host specificity. *Drepanosiphum platanoidis* was exclusively, and *Periphyllus acericola* (Walker) and *Periphyllus aceris* (Linnaeus) were mainly associated with sycamore, while *Drepanosiphum aceris* Koch and *Periphyllus obscurus* Mamontova were almost exclusively associated with field maple. *Periphyllus testudinaceus* was abundant on both sycamore and field maple trees. In contrast, no aphid species were associated with Norway maple (Fig. 8, Table S1.3).

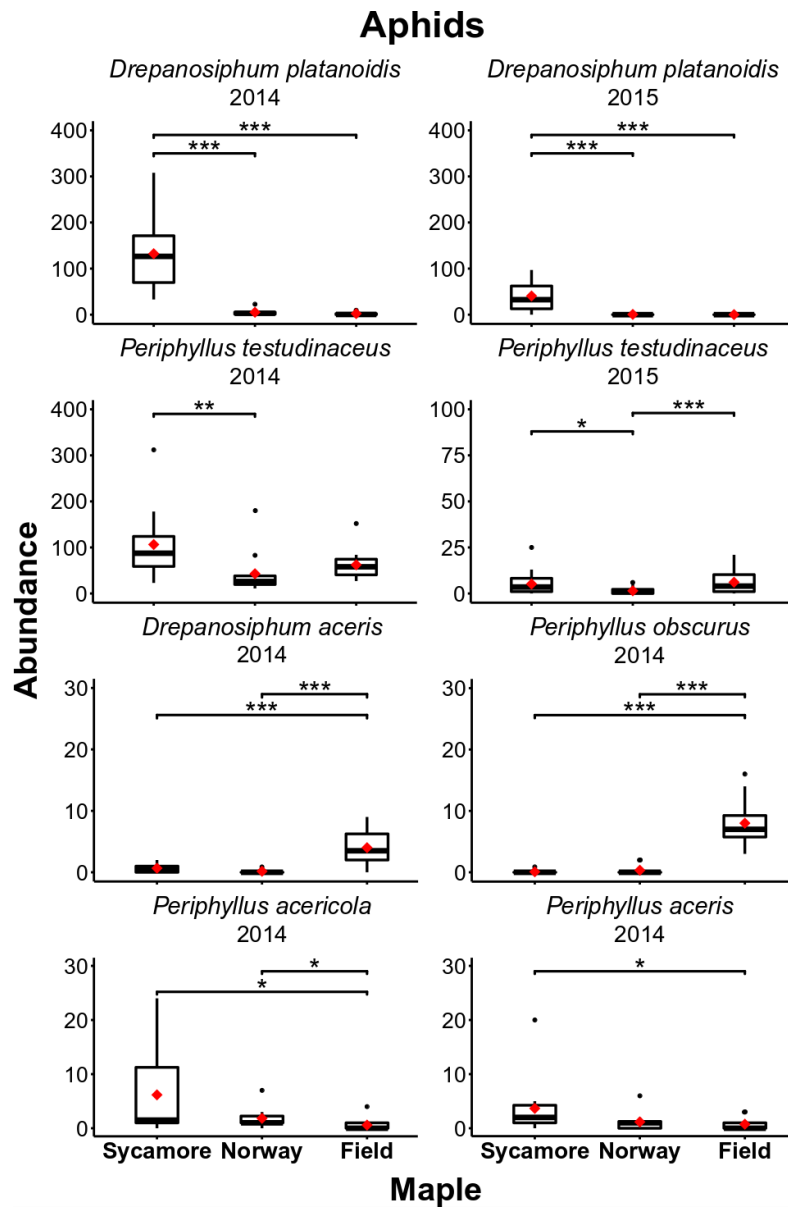


Figure 8. Abundance of aphid species on sycamore, Norway, and field maple trees in 2014 and 2015. On the boxplots red squares indicate means. Significant differences between maple species (least square means, ANOVA, GLMM; \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ ) were calculated for log-transformed data. The main outcomes of pairwise comparisons are summarized in Table S1.3. Note the different scales on the y-axes.

The abundance of the planthopper *M. pruinosa* was the highest on field maple and the lowest on Norway maple. For other planthoppers and leafhoppers, the overall abundance was significantly higher on field maple compared to sycamore maple (Fig. S1.5, Table S1.2). *Latilica maculipes* (Melichar) showed no preference between the three maple species (Fig. 9, Table S1.3).

For leafhoppers, *Japananus hyalinus* (Osborn) was associated with field maple and *Zyginella pulchra* Low with Norway maple, while *A. ribauti* was associated with both (Fig. 9, Table S1.3).

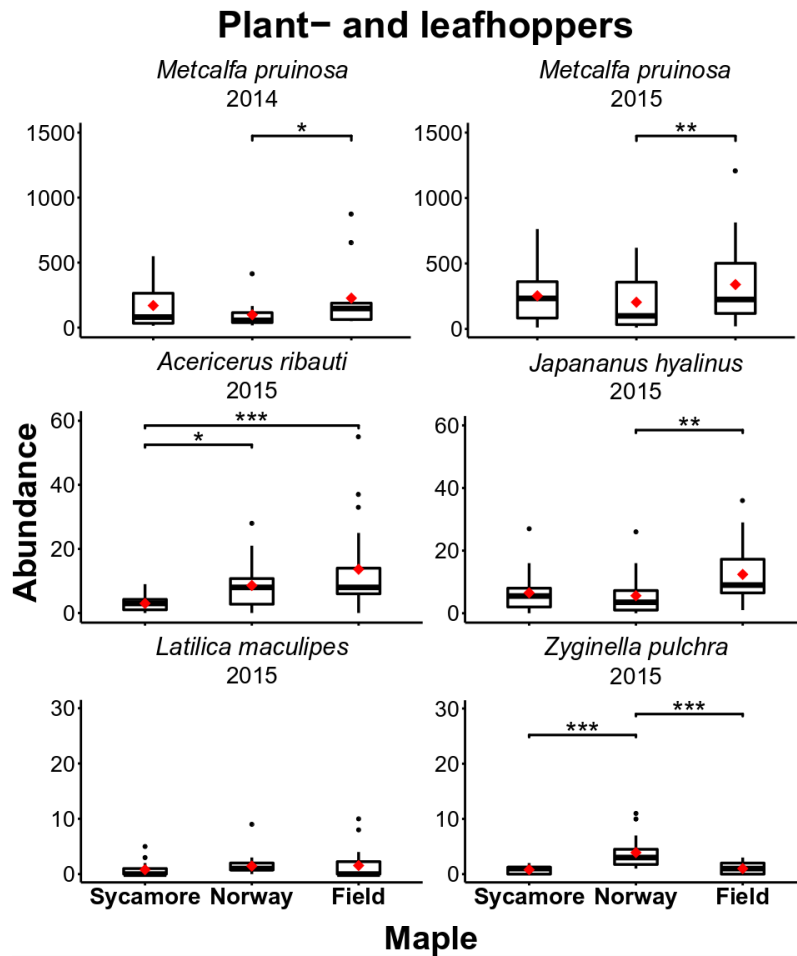


Figure 9. Abundance of plant- and leafhopper species on sycamore, Norway, and field maple trees in 2015. On the boxplots red squares indicate means. Significant differences between maple species (least square means, ANOVA, GLMM;  $*p \leq 0.05$ ,  $**p \leq 0.01$ ,  $***p \leq 0.001$ ) were calculated for log-transformed data. The main outcomes of pairwise comparisons are summarized in Table S1.3. Note the different scales on the y-axes.

The total abundance of heteropterans was significantly higher on field maple than on sycamore maple in 2014, but not in 2015 (Fig. S1.5, Table S1.2). We detected the lowest abundances of *Gonocerus acuteangulatus* (Goeze) and *Nezara viridula* on sycamore maple; however, for the latter species this difference was only significant compared to field maple. *Palomena prasina* (Linnaeus) had higher number of individuals on Norway maple compared to



field maple in 2015. Individuals of *H. halys* occurred in same numbers on all maple species (Fig. 10, Table S1.3).

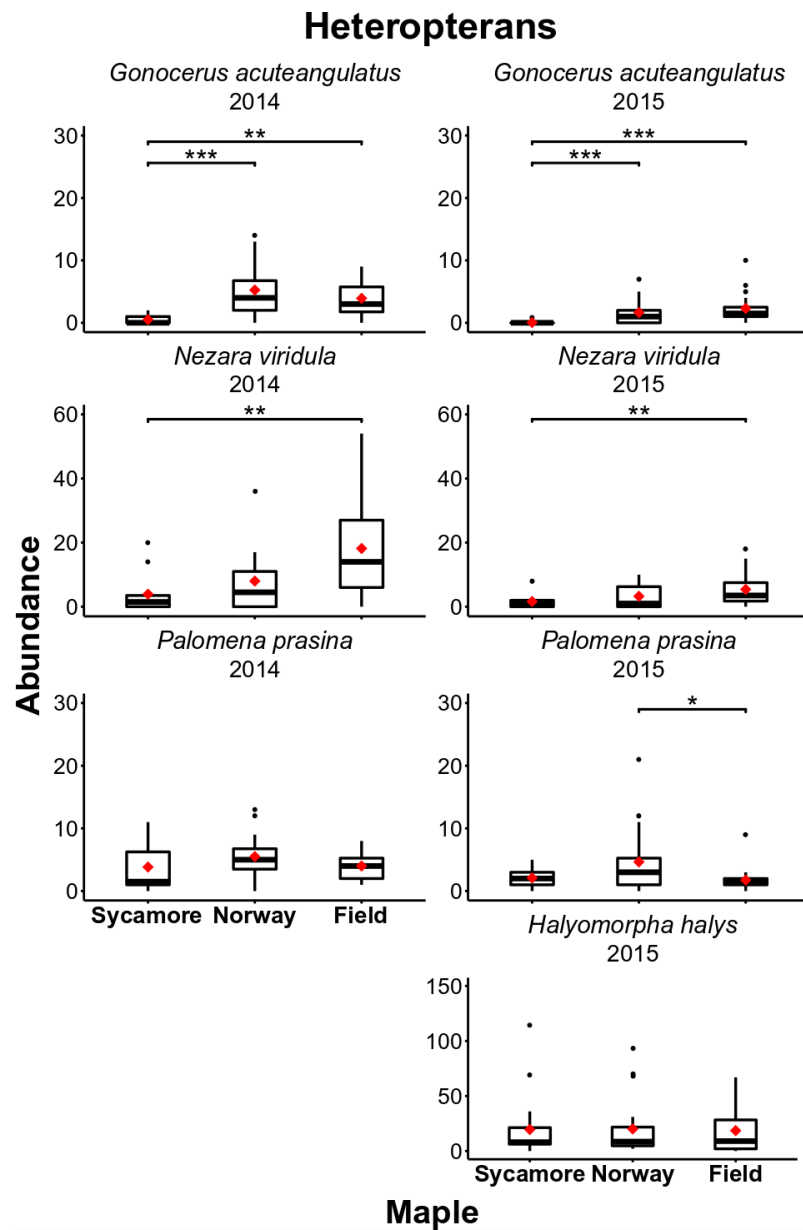


Figure 10. Abundance of heteropteran species on sycamore, Norway, and field maple trees in 2014 and 2015. On the boxplots red squares indicate means. Significant differences between maple species (least square means, ANOVA, GLMM;  $*p \leq 0.05$ ,  $**p \leq 0.01$ ,  $***p \leq 0.001$ ) were calculated for log-transformed data. The main outcomes of pairwise comparisons are summarized in Table S1.3. Note the different scales on the y-axes.

The psyllid *Rhinocola aceris* (Linnaeus) was associated with field maple, while we found no difference between the abundances of *Cacopsylla pulchella* (Low) on the three maple species. Considering curculionids, we found a significantly higher abundance of *P. oblongus* on field maple compared to sycamore maple, with intermediate abundance on Norway maple. *Bradybatus kellneri* Bach was primarily associated with Norway maple (Fig. 11, Table S1.3).

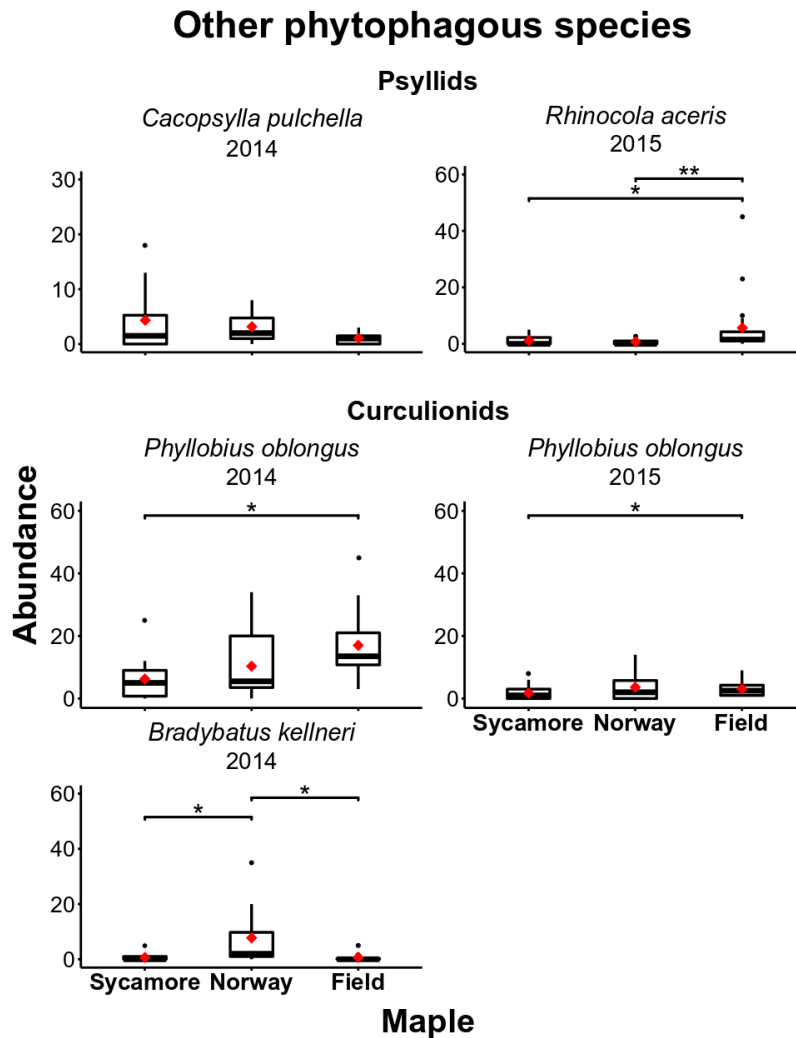


Figure 11. Abundance of psyllid and curculionid species on sycamore, Norway, and field maple trees in 2014 and 2015. On the boxplots red squares indicate means. Significant differences between maple species (least square means, ANOVA, GLMM;  $*p \leq 0.05$ ) were calculated for log-transformed data. The main outcomes of pairwise comparisons are summarized in Table S1.3. Note the different scales on the y-axes.

NMDS analysis clearly separated the phytophagous insect communities of sycamore and field maple, and also showed that Norway maple had the least specific phytophagous insect community, with a high overlap especially with that of field maple (Fig. 12). Indicator species analysis identified two species, *D. platanoidis* and *P. acericola*, as character species of sycamore maple and other two species, *Z. pulchra* and *B. kellneri*, as character species of Norway maple. Seven further indicator species, *D. aceris*, *P. obscurus*, *R. aceris*, *A. ribauti*, *J. hyalinus*, *G. acuteangulatus*, and *N. viridula* showed a preference for field maple (Fig. 12; Table S1.4).

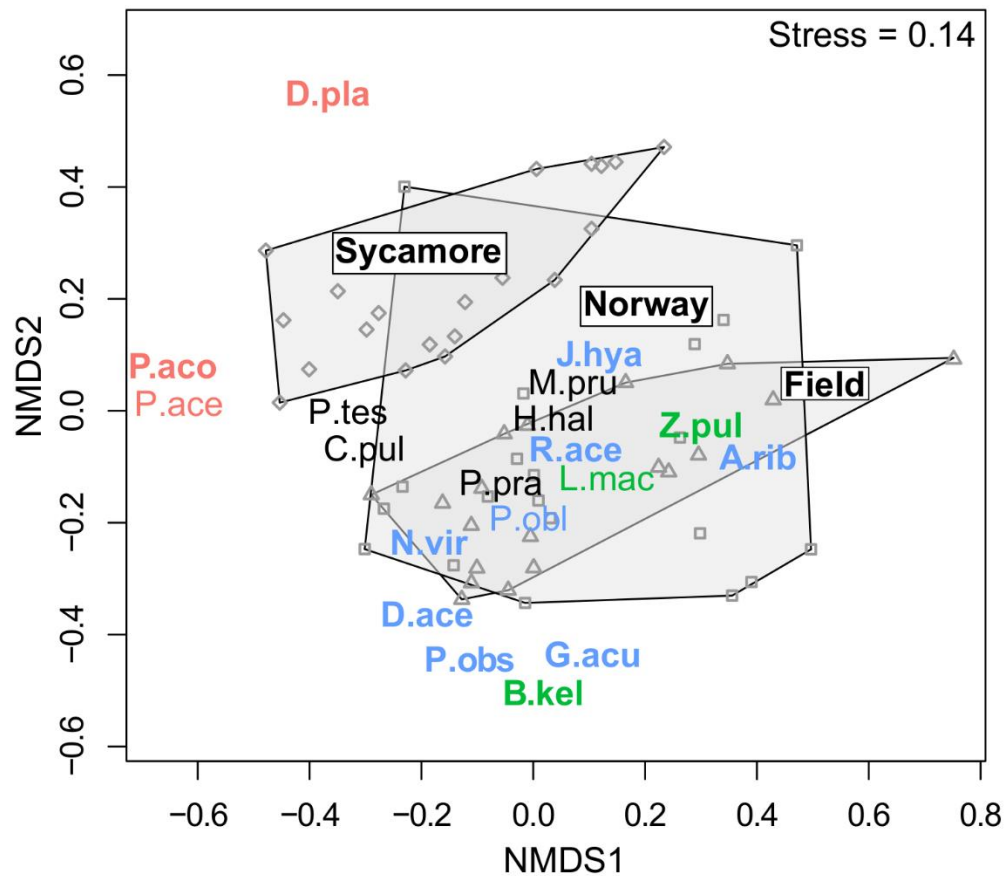


Figure 12. NMDS ordination of trees grouped by maple species based on the community composition of abundant phytophagous insect species. Abbreviations in bold and in color represent character species with significant IndVal values ( $p < 0.05$ ) and abbreviations in color and without bold represent character species with marginally significant IndVal values ( $p \geq 0.05$  and  $p < 0.1$ ) belonging to each maple species; red: sycamore maple, green: Norway maple, blue: field maple. For full names of species and indicator values see Table S1.4.

#### 4.3.3. Stress level and condition of maple tree species

Although on average Norway maple individuals had the highest POD activity values, we did not find significant differences between maple species for this variable. In contrast, we found significant differences in the leaf necrosis levels between the maple species, which were the highest on Norway maple and were lowest on field maple. We found no statistically significant differences in leaf fall between maple species (Fig. 13, Table S1.5).

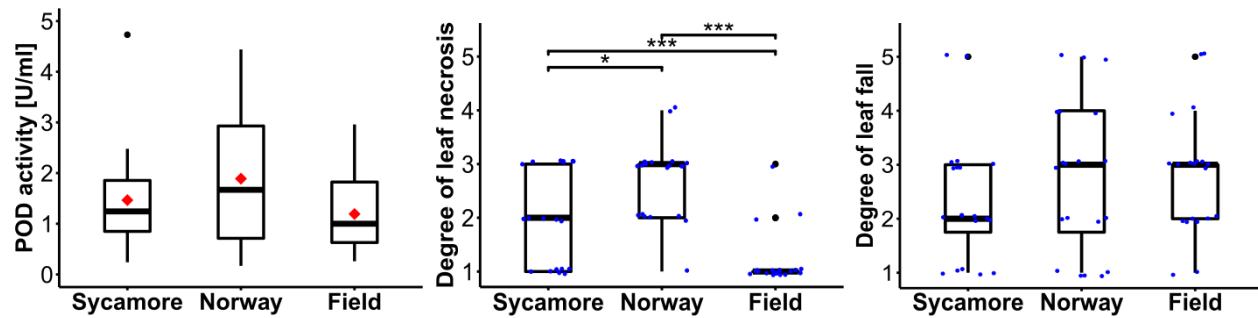


Figure 13. POD enzyme activity, degree of leaf fall, and necrosis of sycamore, Norway, and field maple trees. On the boxplots of POD activity, red squares indicate means. In case of leaf necrosis, asterisks indicate significant differences between maple species (least square means, ANOVA, CLMM; \* $p \leq 0.05$ , \*\*\* $p \leq 0.001$ ). The main outcomes of pairwise comparisons are summarized in Table S1.5.

#### 4.3.4. Effect of phytophagous insects on stress level of trees

Overall, we observed a significant increase in POD activity in maple trees with increasing numbers of *M. pruinosa* individuals, while the abundant phytophagous groups (other plant- and leafhoppers, aphids, and heteropterans) had no effect on this variable (Table 1). We found a significant positive relationship between *M. pruinosa* abundance and POD activity of sycamore and field maple trees, but no such relationship was found for Norway maple (Fig. 14, Table S1.6). The abundance of other phytophagous groups had no effect on POD activity of any of the maple species (Table S1.6).

Table 1. Results of the GLMMs for the POD enzyme activity (log-transformed data) of maple trees depending on the abundance of aphids, *Metcalfa pruinosa*, other (non-*M. pruinosa*) plant- and leafhoppers, and heteropterans. Numbers in bold indicate significant ( $p < 0.05$ ) and number in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values.

| Explanatory variable         | Estimate | SE    | $t$    | Adj. $p^*$   | Unadj. $p$   |
|------------------------------|----------|-------|--------|--------------|--------------|
| <i>M. pruinosa</i>           | 0.000    | 0.000 | 2.753  | <b>0.034</b> | <b>0.008</b> |
| Other plant- and leafhoppers | 0.001    | 0.001 | 1.014  | 0.421        | 0.316        |
| Aphids                       | 0.000    | 0.001 | -0.327 | 0.745        | 0.745        |
| Heteropterans                | 0.007    | 0.003 | 1.913  | 0.124        | <i>0.062</i> |

\* Benjamini-Hochberg correction.

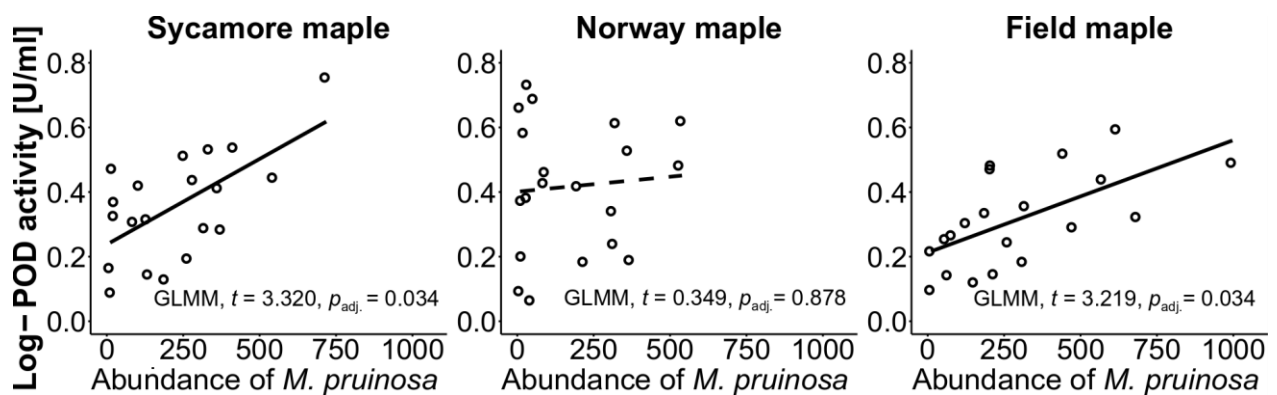


Figure 14. Effect of the abundance of *Metcalfa pruinosa* on POD enzyme activity of sycamore, Norway, and field maple trees. Continuous lines indicate significant ( $p < 0.05$ ) relationships. The main outcomes of phytophagous insect – POD activity relationships are summarized in Table S1.6.

#### 4.3.5. Relationships between phytophagous insects and tree condition

Analyzing the relationship between the abundance of phytophagous insects and tree condition we found that the abundance of phytophagous insect groups had no significant effect on the degree of leaf fall or necrosis of maple trees (Table S1.7). Conversely, advancing degree of leaf fall and leaf necrosis negatively affected the abundance of the super-abundant species *M. pruinosa* (Table 2). The abundance of other insect groups showed no response to the changing conditions of the trees (Table 2).

Table 2. Results of the GLMMs for the abundance of aphids, *Metcalfa pruinosa*, other (non-*M. pruinosa*) plant- and leafhoppers, and heteropterans (log-transformed data), depending on the degree of leaf fall and necrosis of maple trees (ordered factors). Numbers in bold indicate significant ( $p < 0.05$ ) and number in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values.

| Explanatory variable | Response variable            | Estimate* | SE    | $t$    | Adj. $p^{**}$ | Unadj. $p$   |
|----------------------|------------------------------|-----------|-------|--------|---------------|--------------|
| Leaf fall            | <i>M. pruinosa</i>           | -0.332    | 0.113 | -2.939 | <b>0.041</b>  | <b>0.005</b> |
|                      | Other plant- and leafhoppers | -0.005    | 0.080 | -0.060 | 0.960         | 0.952        |
|                      | Aphids                       | -0.183    | 0.108 | -1.697 | 0.257         | <i>0.097</i> |
|                      | Heteropterans                | 0.011     | 0.127 | 0.083  | 0.960         | 0.934        |
| Leaf necrosis        | <i>M. pruinosa</i>           | -0.320    | 0.127 | -2.521 | <b>0.049</b>  | <b>0.013</b> |
|                      | Other plant- and leafhoppers | 0.032     | 0.102 | 0.311  | 0.960         | 0.756        |
|                      | Aphids                       | -0.010    | 0.196 | -0.051 | 0.960         | 0.960        |
|                      | Heteropterans                | 0.232     | 0.187 | 1.242  | 0.442         | 0.221        |

\* Negative values indicate phytophagous groups or species that decreased in abundance with increasing rates of leaf fall and necrosis.

\*\* Benjamini-Hochberg correction.

#### 4.4. Discussion

We observed a higher total abundance of phytophagous insects on field and sycamore maple compared to Norway maple trees. Field maple had the most indicator species and Norway maple had the least characteristic phytophagous insect community. The numbers of the most abundant phytophagous insect species, *M. pruinosa*, were driven by tree conditions, with higher abundances on healthier trees.

##### 4.4.1. Objective 1: Effect of tree species on the abundance and composition of phytophagous insects

In this study, the abundance of aphids was the lowest on Norway maple (Fig. 8; Fig. S1.5). In contrast to our results, Mackoś (2008) found high numbers of aphids, especially those of *P. testudinaceus* and *P. aceris*, on Norway maple in urban environments. This suggests that the urban environmental conditions in our study may have negatively affected the aphid abundances on Norway maple. The abundance of aphids in both years was much higher on sycamore than on

Norway and field maple (Fig. S1.5). The explanation for this latter difference might be that budburst of sycamore starts earlier than field maple (Lechowicz, 1984), providing better phenological synchronization for aphid species with early egg hatch (e.g., for *P. testudinaceus*) (Fig. S1.1) (Dixon, 1998). In line with our results, *D. platanoidis* and *P. acericola* are known to develop primarily on sycamore maple, *D. aceris* and *P. obscurus* on field maple, while *P. testudinaceus* develops mainly on field and sycamore maple (Figs. 8 and 12) (Blackman & Eastop, 1994).

Our results are consistent with earlier findings that leafhopper species *A. ribauti* and *J. hyalinus* feed mainly on field maple, which seems to be the primary host plant for these species in Europe (Nickel, 2003). According to Nickel (2003), *Z. pulchra* feed mainly on sycamore maple and less frequently on its congener species. In contrast, and in line with the observations of Wilson and Mühlethaler (2010), we found that this species can reach higher densities on Norway maple in urban settings (Figs. 9 and 12).

The abundance of most heteropteran species, mainly feeding on fruits of the trees, was the lowest on sycamore maple (Fig. 10). One explanation for this pattern might be the inadequate amount or quality of ripening fruits on sycamore trees during the second half of the growing season, when true bugs reached high abundance in the canopy (Fig. S1.3). The invasive and highly polyphagous stink-bug species *Halyomorpha halys* was first detected in Hungary in 2013 at one of our study sites (Vétek et al., 2014). Our results suggest that this species became the most abundant true bug on all examined maple species within a few years.

The large number of the seed-feeding curculionid, *B. kellneri*, on Norway maple (Fig. 11) was because Norway is the earliest flowering of the three tree species (Weryszko-Chmielewska et al., 2016), and overwintered *B. kellneri* individuals search for flowers of maples after their emergence (Fig. S1.4) (Blake et al., 2018).

We demonstrated that field and sycamore maple have distinct phytophagous communities. At the same time, the community composition of Norway maple was the least characteristic and overlapped with its congener species, especially with field maple, suggesting that these tree species have similar phytophagous communities due to the presence of some oligo- and polyphagous insects (Fig. 12).

#### 4.4.2. Objective 2: Effect of phytophagous insects on stress level and condition of trees

We found that increasing abundance of *M. pruinosa* significantly increased the POD activity of trees, but no such relationship was observed for other insect groups (Table 1). This result could be expected, since *M. pruinosa* was the most abundant phytophagous species in the canopy of maple trees and the POD activity measurements coincided with its activity peak (Fig. S1.2). As antioxidative enzymes, PODs play important role in reducing perturbations caused by reactive oxidative species, which induce oxidative damages under environmental stress conditions in plant cells (Sharma et al., 2012; War et al., 2012). PODs also regulate a number of processes that have a direct or indirect role in plant defense, including lignification or wound healing, and are known to become more active when herbivore damage occurs (Tschardt et al., 2001; Zhang et al., 2008; War et al., 2012). In contrast to field and sycamore maple, *M. pruinosa* abundance did not affect POD activity in Norway maple, where we found trees with high stress levels even at low *M. pruinosa* densities (Fig. 14, Table S1.6). One reason for this may be that other, presumably abiotic factors may have increased the stress level of this tree species.

The degree of leaf necrosis, an indicator of a tree's condition, was by far the lowest in field maple and the highest in Norway maple (Fig. 13, Table S1.5). Although tree condition was assessed only in the second year, this pattern was already apparent in the first year of this study (DK personal observation). Prior studies reported that the appearance of necrosis in leaves is directly or indirectly induced by abiotic stress factors, such as air pollution, drought, heavy metal contamination of soil, and salt stress (Paludan-Müller et al., 2002; Günthardt-Goerg & Vollenweider, 2007; Khavaninzadeh et al., 2014). For instance, increased necrotic leaf injury was observed on Norway maple as a response to salinity stress (Marosz & Nowak, 2008), elevated concentrations of particulate matter in city air (Mitrović et al., 2006), and soil alkalization (Bach & Pawłowska, 2006). Furthermore, biotic factors like pathogens can also cause necrotic spotting (Hudelson et al., 2008; Held et al., 2018), although we observed a low disease (e.g., *Sawadea bicornis* [Wallr.] Homma or *Rhytisma acerinum* [Pers.] Fries) incidence on the studied trees.

We found that field maple trees were in better condition than the other maple species (Fig. 13). Field maple is considered one of the most tolerant tree species to urban conditions due to its wide ecological plasticity, winter robustness, and resistance to drought and adverse soil conditions (Roloff et al., 2009; Swoczyna et al., 2015; Stratópoulos et al., 2019). In contrast to our expectations, Norway maple showed the most severe necrosis symptoms (Fig. 13). Norway maple



is often considered to be resistant to urban conditions tolerating heat, drought, salt, and air pollution (reviewed by Sjöman et al., 2010). However, in accordance with our results, under certain circumstances, Norway maple responds negatively to urban conditions. For instance, *A. platanoides* can express low vitality in urban areas with high proportion of impervious surfaces and heavy traffic due to the combined effect of relatively high soil pH and extensive application of de-icing salt (Fostad & Pedersen, 1997) and higher temperature in summer periods associated with extremely dry conditions (Uhrin et al., 2018).

#### 4.4.3. Objective 3: Effect of condition of trees on phytophagous insects

The deteriorating condition of trees (i.e., advanced leaf necrosis and leaf fall) negatively influenced the abundance of the super-dominant planthopper species *M. pruinosa* (Table 2). Although we did not find a significant relationship between tree condition and aphid abundance, the total number of aphids was the lowest on Norway maple (Fig. S1.5, Table S1.2). However, we measured the condition of the trees in autumn and it is therefore hard to speculate about its effect on phytophagous insects in the first half of the season.

Although many authors claim that stressed trees in urban areas have a greater susceptibility to attack by sap-sucking insects (e.g., Cregg & Dix, 2001; Raupp et al., 2010; Dale & Frank 2017), some studies showed that these insect groups prefer trees with better conditions and healthier leaves (Hanks & Denno, 1993; Huberty & Denno, 2004; Sienkiewicz-Paderewska et al., 2017). *Metcalfa pruinosa* is a highly polyphagous, devastating pest of ornamental trees in Europe (Alma et al., 2005, Strauss, 2010). Our results suggest that its abundance in the canopy of maple trees is determined primarily by the tree condition and to a lesser extent by the species of the studied maple hosts.

## 5. Study III: Effect of urban landscape on aphids and their predator communities on urban trees

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### 5.1. Introduction

The number of people living in cities continues to grow, and the expansion of urban land cover is predicted to increase by 1.2 million km<sup>2</sup> by 2030 (Seto et al., 2012). As a result, a landscape with heterogeneous elements, from semi-natural remnant forests and public green areas to concrete surfaces and artificial structures is created, which has a wide range of functional characteristics and environmental conditions. This landscape provides an opportunity for studying complex ecological systems operating under strong human influence (Alberti, 1999; McDonnell & Pickett, 1990; McDonnell & Hahs, 2008).

Although the number of studies examining the effects of urban landscapes on ecological patterns and processes has increased considerably in the past years, fewer studies have focused on arthropods compared to other taxa (Muderere et al., 2018). Arthropods are an ideal choice for studying the effects of urbanization as they (1) show quick responses to changed conditions, (2) have great biological diversity, (3) have relatively short generation time, and (4) represent a broad spectrum of trophic levels (McIntyre, 2000). Arthropods show various responses to increasing levels of urbanization. While species that are less mobile or habitat specialist decrease in abundance or disappear altogether with increased urbanization, species that are highly mobile, or habitat generalists can reach high densities (McIntyre, 2000; Niemelä & Kotze, 2009; Comont et al., 2014). This process can lead to biotic homogenization (McKinney, 2006). Urbanization can also influence the abundance (Denys & Schmidt, 1998; Corcos et al., 2019; Rocha & Fellowes, 2020) and composition (Burkman & Gardiner, 2014; Argañaraz et al., 2018; Lövei et al., 2019) of species at higher trophic levels, which might affect the top-down control of some herbivorous species, such as sap-sucking insects, and result in outbreaks of their populations (Shrewsbury & Raupp, 2006; Raupp et al., 2010; Meineke et al., 2017).

Within the sap sucking insects, aphids (Hemiptera, Aphididae) are important worldwide pests of more than 400 plant species, including agricultural crops and ornamental plants (Blackman & Eastop, 2000). They are also appropriate model organisms for studying how urbanization might affect predator-prey-mutualist systems because they (1) can reach high densities in urban areas (Denys & Schmidt, 1998; Honěk et al., 2018; Parsons & Frank, 2019), (2) have a wide range of natural enemies (Nagy et al., 2015), and (3) often have a mutualistic relationship with ants (Dixon, 1998).

Aphidophagous arthropods have a strong tendency to aggregate on aphid colonies, and they can play a key role in setting the density of aphid populations (Dixon, 1998; Markó et al., 2013; Piñol et al., 2009b; Roy et al., 2016). However, the level of predation pressure on aphids depends on several factors including the spatial and temporal distribution of aphids, their natural enemies, and mutualistic ants. Predatory arthropods can be more detrimental to aphids at the beginning of aphid population development when colonies are small, and the per capita predation risk is high (Boreau de Roince et al., 2013; Nagy et al., 2015; Gómez-Marco et al., 2016). Highly mobile predators usually arrive in greater numbers when aphid colonies are already large and are therefore often tracking rather than driving their abundance, while more sedentary predators that have a lower dispersal ability and higher degree of habitat fidelity might stay at the sites even when aphid density is low and can thus suppress the aphid population increase more effectively (Piñol et al., 2009b; Markó et al., 2013; Welch & Harwood, 2014).

Aphid abundance can also be affected by the presence of ants, which can act as mutualists by protecting aphid species that provide sugar-rich honeydew for them (Dixon, 1998). Skinner and Whittaker (1981) showed that the abundance of ant-tended species, such as *Periphyllus testudinaceus* (Ferne), increased in the presence of the ant *Formica rufa* L. on sycamore trees (*Acer pseudoplatanus* L.). Predators and ants might respond differently to urbanization, which could lead to different outcomes for aphid species. However, despite the importance of natural enemies in shaping herbivorous insect communities, only a few studies have investigated the effects of urbanization on predator-prey-mutualist systems (Eötvös et al., 2018; Rocha & Fellowes, 2018, 2020).

Turrini et al. (2016) studied how the abundance of a non-ant-tended (non-myrmecophilous) aphid species, the vetch aphid (*Megoura viciae* Buckton), changed on potted broad bean (*Vicia faba* L.) plants in agricultural versus urban ecosystems. They applied treatments with and without predator exclusion and found that aphid abundance was determined by predation, which was less

intense in city centers than in agricultural fields. As a consequence, aphids showed a pattern opposite to predators, being more abundant in the city centers. In a similar study Rocha and Fellowes (2018) examined an ant-tended (myrmecophilous) aphid species, the black bean aphid (*Aphis fabae* Scopoli), on the same host plant and found that the presence of mutualist ant species (*Myrmica rubra* L. and *Lasius niger* L.) overrode the effect of predators and, therefore, aphid abundance showed no difference between highly-urbanized and semi-natural areas.

In this study, we examined the abundance pattern and interactions of aphids, predatory arthropods, and ants in the canopy of field maple (*Acer campestre* L.) trees along an urbanization gradient. We chose *A. campestre* because it is highly tolerant of urban conditions (Roloff et al., 2009) and common both in rural and urban habitats with a rather uniform distribution in Hungary (Bartha et al., 2018). Moreover, *A. campestre* is fed on by several aphid species, which are preyed on by a large number of predatory arthropods. More specifically, we tested the following hypotheses: along the urbanization gradient (1) the abundance of aphids, predators and ants would increase, decrease and not change, respectively; (2) considering the whole growing season, the predatory arthropods would affect negatively while ants, through their negative effect on predators, would affect positively the abundance of aphids; (3) during the peaks in aphid abundance, the populations of predatory arthropods and ants would track the abundance of aphids; (4) the composition of the predator community would change along the urban gradient. Finally, we also hypothesized (5) that a shift in predator community composition towards species with high dispersal ability would lead to higher aphid abundance.

## 5.2. Materials and methods

### 5.2.1. Study area and arthropod collection

We selected 22 sites for this study in or near the city of Budapest, Hungary (Fig. S2.1), representing a range of seminatural rural, suburban, and urban areas. We chose three field maple (*A. campestre*) trees at each site for arthropod collection by having similar trunk and canopy diameters and the shortest distance between them. The distance between the trunks of the sampled trees was 2–15 m. There was no significant effect of urbanization (defined as the proportion of impervious surfaces) on the trunk diameters (diameter at breast height) (Pearson  $r = 0.24$ ,  $p = 0.28$ ) and on the distance between the selected trees (Pearson  $r = 0.14$ ,  $p = 0.55$ ).

A beating funnel 70 cm in diameter, 60 cm in depth, together with a 120 cm long beating stick, was used to collect arthropods from the canopy of the trees (Basset et al., 1997). In order to standardize sampling effort, ten branches were sampled per tree. Branches were sampled monthly on seven dates in 2016 (April 26, May 25, June 22, July 18, August 15, September 13, and October 14). In 2017, we also sampled on three additional dates (May 5, July 16, and September 27). On all sample dates, we identified and counted all collected aphids (Aphididae) to species. Predatory arthropods (Hemiptera, Coccinellidae, Dermaptera, Neuroptera, and Araneae) were identified to species or, if not possible, to genus or family, using characters of the exoskeleton or genitalia. The collected arthropods were deposited at the Department of Entomology of Szent István University. Because of the low aphid parasitism rates observed, parasitoids were not included in this study.

### 5.2.2. *Dispersal ability of predators*

Aphidophagous predator species were classified into five dispersal groups following the methodology described by Gossner et al. (2015) using data of different literature sources (Duffey, 1956; Bell et al., 2005; Wachmann et al., 2004–2012; Blandenier, 2009; Gossner et al., 2015). We considered wing morphology for true bugs, ladybirds, and lacewings (always brachypterous, predominantly brachypterous, equally brachypterous and macropterous, predominantly macropterous, and always macropterous; coded 0.00, 0.25, 0.50, 0.75 and 1.00 respectively), and ballooning ability for spiders (non-ballooning species [code:0.00], species with weak ballooning propensity [code: 0.25], ballooning species observed outside the main habitat less frequently [code: 0.50] and frequently [0.75], and species with the highest ballooning propensity and dispersal distances [code: 1.00]). For juvenile spider individuals which were identified to genus or species group (e.g. *Philodromus aureolus* and *rufus* group) level, we used the dispersal trait values of adult individuals representing the same genus or species group weighted by their relative abundances. The collected dermapteran species were considered as species with the lowest dispersal category (code: 0.00) as *Apterygida media* (Hagenbach) and *Chelidurella acanthopygia* (Géné) are apterous species, and although *Forficula auricularia* L. has wings, it hardly ever uses them (Crumb et al., 1941) and the mobility of this species is very low (Moerkens et al., 2010). For the assigned dispersal trait values, see Table S2.1.

### 5.2.3. *Landscape structure*

We calculated landscape composition around each sampling site within a 500 m radius buffer with the OpenStreetMap land cover map, using OpenLayers plugin of Quantum GIS 2.16 software (Quantum GIS Development Team, 2018). This radius has been found to be appropriate spatial scale for analyzing the relationship between landscape pattern and aphid-ant-predator relationships (Stutz & Entling, 2011; Schüepp et al., 2014). The geographic center (centroid) of a triangle formed by the sampled trees was used as the center of each study site. To characterize the landscape composition of the study sites, we considered six land cover types (buildings, roads, forests, gardens, meadows, and parks) and calculated their percentage cover in a buffer around each site (Table S2.2). We excluded water bodies from our analyses due to their low abundance within the sampled landscapes.

### 5.2.4. *Data analyses*

First, to explore the correlations among the six landscape variables, we calculated the Kendall rank correlation coefficients for all pairs of the six land cover variables. We found significant correlations between most landscape variables (Table S2.3); therefore, we used only the proportion of impervious surfaces (pooled proportion of buildings and roads) as an explanatory variable in further analyses. Finally, a gradient was created from this variable among the sites that ranged between 2 and 95% surface with impervious cover (Table S2.2) indicating the degree of urbanization. For all analyses, we pooled the number of individuals collected (from three trees) at each site. For analysis of annual abundance, we pooled data across sampling dates in both years and analyzed them separately. The spatial autocorrelation in the residuals of our models was tested by Moran's I tests with inverse distance weighting using 'spdep' package version 1.1–3 (Bivand & Wong, 2018). There was no evidence of residual spatial autocorrelation in any model ( $p > 0.21$  in all cases), and therefore we did not add an auto-covariate to our models. We used R 3.4.4 statistical environment (R Core Team, 2018) for all analyses.

## **Hypothesis 1: Effects of urbanization on the abundance patterns of aphids, predators and ants**

To test how annual and monthly abundance of aphids, predators, and ants (response variables) depended on the proportion of impervious surfaces (explanatory variable), we used Poisson-distributed generalized linear models (GLMs). The models included the percentage of impervious surfaces as a fixed factor. Because we detected overdispersion in the abundance data, we corrected the standard errors using generalized linear models with quasi-Poisson distribution (quasi-GLMs) (Zuur et al., 2009). In case of monthly analyses,  $p$  values were adjusted using the method of Benjamini and Hochberg (1995).

## **Hypotheses 2 and 3: Aphid-predator-ant interactions**

Since the effects of predators and mutualistic ants on aphid population development might be accumulated and delayed, we tested how annual aphid abundance (response variable) depended on annual and monthly abundance of predators and ants (explanatory variables) using quasi-GLMs. We fitted the models separately for each sample year and month. The full models included predator and ant abundance as fixed factors, and model selection retained only the models with significant variables ( $p < 0.05$ ). In the analyses, where monthly abundances of predators were considered as explanatory variables,  $p$  values were adjusted with the Benjamini-Hochberg method. To determine whether there is any relationship between predator and ant abundances in each year, we built quasi-GLMs including the abundance of predators as response variable and the abundance of ants as explanatory variable (fixed factor).

We also tested how abundance of predators and ants was influenced by the abundance of aphids (tracking) in different years and seasons using generalized linear mixed effects models with quasi-Poisson errors (penalized quasi-likelihood GLMM, GLMMPQL) in the package ‘MASS’ version 7.3–51.4 (Venables & Ripley, 2002). In order to obtain a meaningful quantitative response, only the months of peak aphid abundance were considered (April, May and October in 2016; May and September in 2017). In the model, the response variable was the abundance of predators or ants, and abundance of aphids, season, and year were entered as fixed factors. To control for the possible effect of sampling location on the response variables, we included sampling site as a random intercept factor.

## **Hypothesis 1 and 4: Species of aphids and predators and taxonomic composition of predator community**

To analyze how the observed number of aphid or predatory species, the number of species groups, and genera (response variables) responded to the proportion of impervious surfaces (explanatory variable), we used quasi-GLMs. Only those arthropod groups (species, species groups, or genera) represented by at least 50 individuals in each year's samples were included in the analyses (for species groups and genera, see Table S2.4). In the case of *Harmonia axyridis* Pallas, juvenile and adult stages were analyzed separately. The full model included percentage of impervious surfaces as a fixed factor. The data from the two years (2016 and 2017) were analyzed separately. In these analyses, *p* values were adjusted using the Benjamini-Hochberg method.

We performed non-metric multidimensional scaling (NMDS) to examine the differences in composition for the predator community and within the three largest predatory assemblages: true bugs (Heteroptera), aphidophagous ladybirds (Coccinellidae), and spiders (Araneae), each separately. We used the Bray-Curtis distance measure to compute the resemblance matrix among sites. The resulting matrix was the basis for creating a NMDS ordination, in which sites were ranked based on their similarity and then plotted in 2-dimensional ordination space. The analyses were based on species-level abundance data. Because we collected samples in both years only in May, July, and September, the abundance data of these three months were pooled across years for the NMDS analyses of true bugs, aphidophagous ladybirds, and spiders. We generated smooth surfaces along impervious surface gradient with generalized additive models (GAMs). This function automatically selects the degree of smoothing by generalized cross-validation and interpolates the fitted values on the NMDS plot. NMDS was performed using 'metaMDS' function, while GAMs were run using 'odisurf' function of the package 'vegan' version 2.5–3 (Oksanen et al., 2018).

## **Hypothesis 5: Effect of dispersal ability of predators on aphids**

We calculated community weighted means (CWM) for dispersal trait of predators using the averages of trait values weighted by the relative abundances of each predator species at each study site ( $n = 22$ ) (Ricotta & Moretti, 2011). We used the 'FD' package version 1.0–12 to calculate



CWM indices (Laliberte & Legendre, 2010). In case of some spider individuals, dispersal trait classification was not possible, due to the family level identification ( $n = 23$ ) or the lack of adult representatives of the genus ( $n = 24$ ) (Table S2.1), thus these individuals were excluded from the analyses. We used general linear models to test whether percentage of impervious surfaces (explanatory variable, fixed factor) had a significant effect on CWM of dispersal trait (response variable) in 2016 and 2017 separately.

Quasi-GLMs were used to assess whether predators with lower dispersal ability would have a more important role in aphid suppression than those with higher dispersal ability. The models included annual abundance of aphids as a response variable and CWM of dispersal ability of predator community as an explanatory variable (fixed factor) for each year.

Finally, predators were classified into eleven groups based on their taxonomic status and abundance: (1) Dermaptera, (2) *Deraeocoris lutescens*, (3) other heteropterans (all Heteroptera except *D. lutescens*), (4) *H. axyridis* larvae, (5) *H. axyridis* adults, (6) other coccinellids, (7) Neuroptera, (8) web building spiders, (9) the *Philodromus aureolus* group, (10) the *Philodromus rufus* group, and (11) other hunting spiders (for detailed data see Table S2.1). We used NMDS to analyze how these species and groups were associated to aphid abundance using ‘metaMDS’ function. For this analysis, we summed data for the two sample years for the abundance of aphids and for each predator species or group. We used Euclidean distance measure for comparing similarities and generated smooth surfaces along aphid infestation with GAMs using ‘odisurf’ function.

## 5.3. Results

### 5.3.1. Taxa recorded

In total, we collected 10,197 individual aphids (Sternorrhyncha, Aphididae), 8955 predators, and 3555 ants (Hymenoptera, Formicidae) from the canopy of *A. campestre* trees. The collected aphids belonged to four genera and nine species. Among these, two ant-tended species, *Periphyllus testudinaceus* and *Periphyllus obscurus* Mamontova, were collected in the largest numbers (59.5% and 30.9% of total aphid abundance, respectively) followed by two non-ant-tended species, *Drepanosiphum aceris* Koch and *Drepanosiphum platanoidis* (Schrank), which occurred only in small numbers (2.1% and 1.8% of the total aphid abundance, respectively). The most abundant ant

species were *Prenolepis nitens* (Mayr), *L. niger*, and *Lasius emarginatus* (Olivier) (32.7%, 21.6%, and 10.4% of the ants collected, respectively). These ant species are known for honeydew utilization and having mutualistic relationships with aphids (Miñarro et al., 2010; Purkart et al., 2019), thus we assumed that they have mutualistic interactions with the myrmecophilous aphid species (90.5% of aphids collected).

The predators we collected comprised 24 families, 103 genera, and 145 species. They consisted mainly of spiders (Araneae; 32.4%), coccinellids (28.2%), mirid bugs (25.9%), forficulid earwigs (9.3%), and, to a lesser degree, lacewings (Neuroptera, Chrysopidae, and Hemerobiidae; 1.6%), anthocorid flower bugs (1.6%), and other species (1.3%). The most abundant predator species were *Deraeocoris lutescens* (Schilling) (Miridae,  $n = 1450$ ), *Harmonia axyridis* (Coccinellidae,  $n = 1439$ ), *Forficula auricularia* (Forficulidae,  $n = 675$ ), and two species groups of spiders – *Philodromus aureolus* group ( $n = 752$ ) and *Ph. rufus* group ( $n = 692$ ) (Philodromidae) (Tables S2.1 and S2.4).

### 5.3.2. *Effects of urbanization on the abundance of aphids, predators and ants*

Aphids were abundant in spring and autumn, while in summer they were almost absent. Predator abundance was lowest in spring and increased throughout the growing season. The monthly abundances of ants showed a less clear pattern. They were abundant in April and June in 2016 and in May and September in 2017 (Fig. 15). For the monthly abundances of each aphid species and predatory groups, see Fig. S2.2.

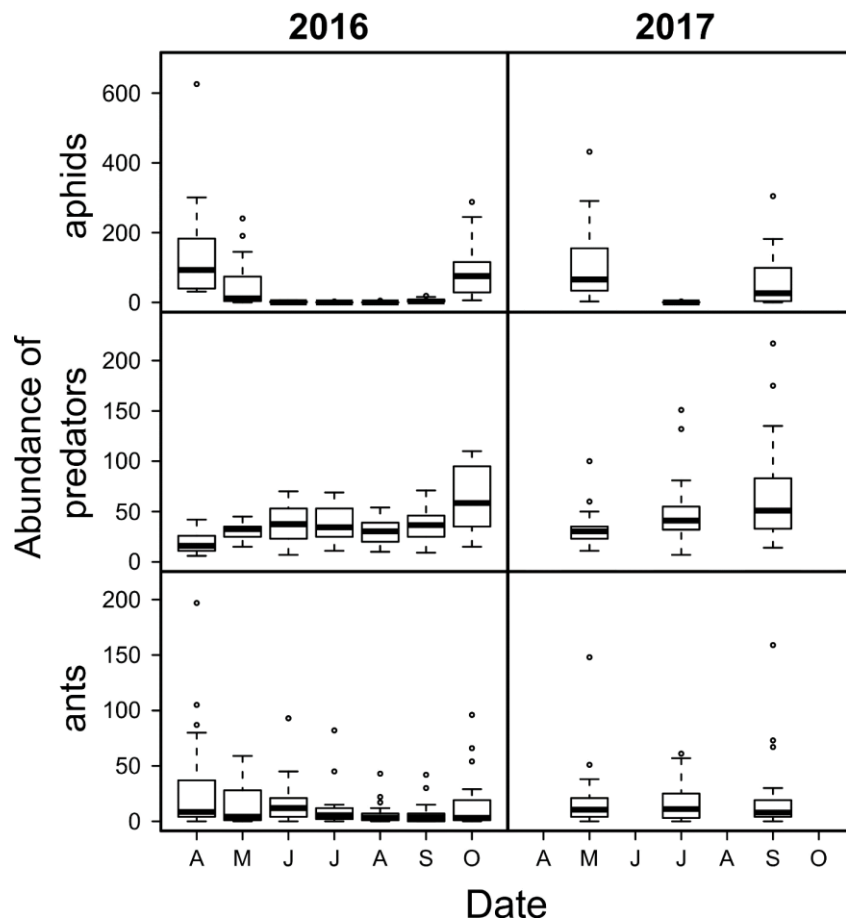


Figure 15. Monthly abundance of aphid, predator, and ant assemblages in 2016 and 2017. Boxplots show medians, lower, and upper quartiles, whiskers include the range of data without outliers. Note the different scales on the y-axes.

The annual abundance of aphids increased significantly with increase in the percentage of impervious surfaces in both years (2016:  $p = 0.008$ ; 2017:  $p < 0.001$ ). In contrast, the abundance of predators and ants was negatively affected by the percentage of impervious surfaces, and these relationships were also significant for both groups ( $p = 0.039$  and  $0.013$ , respectively) in 2016 and nearly significant for ants ( $p = 0.073$ ) in 2017 (Table 3, Fig. 16).

Table 3. Results of quasi-GLMs for the annual abundance of aphids, predators, and ants (total abundance per site, response variables) depending on the percentage of impervious surfaces (explanatory variable). Numbers in bold indicate significant ( $p < 0.05$ ) and numbers in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values.

| Response variable | Estimate | SE    | Exp. Estimate | $p$          | Pseudo- $R^2$ |
|-------------------|----------|-------|---------------|--------------|---------------|
| <b>2016</b>       |          |       |               |              |               |
| Sum aphids        | 0.011    | 0.004 | 1.011         | <b>0.008</b> | 30.7          |
| Sum predators     | -0.005   | 0.002 | 0.995         | <b>0.039</b> | 20.3          |
| Sum ants          | -0.021   | 0.008 | 0.979         | <b>0.013</b> | 31.3          |
| <b>2017</b>       |          |       |               |              |               |
| Sum aphids        | 0.022    | 0.004 | 1.023         | <b>0.000</b> | 62.7          |
| Sum predators     | -0.003   | 0.004 | 0.997         | 0.472        | 3.0           |
| Sum ants          | -0.017   | 0.009 | 0.983         | <i>0.073</i> | 19.7          |

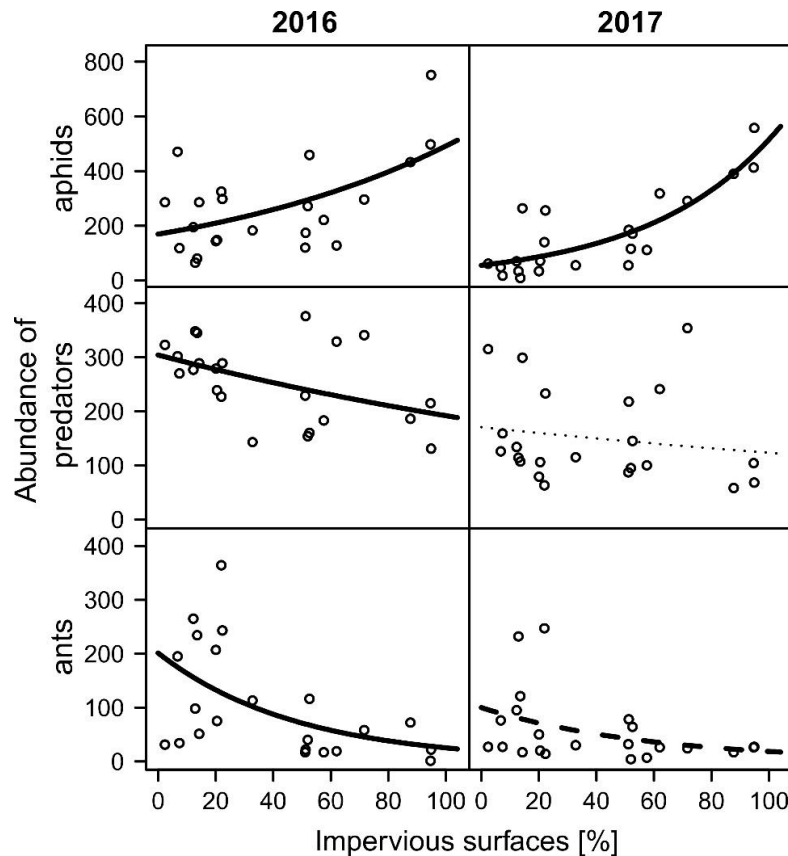


Figure 16. Effect of impervious surface percentage on the abundance of aphid, predator, and ant assemblages in 2016 and 2017. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces. Note the different scales on the y-axes. Fitted lines are from quasi-Poisson GLMs.

The pattern of insects along the urbanization gradient also varied over time. Aphid abundance was positively affected by the percentage of impervious surfaces in spring and autumn, but not in May 2016, when this relationship was negative but not significant ( $p = 0.054$ ) (Figs. 17 and 18, Table S2.5).

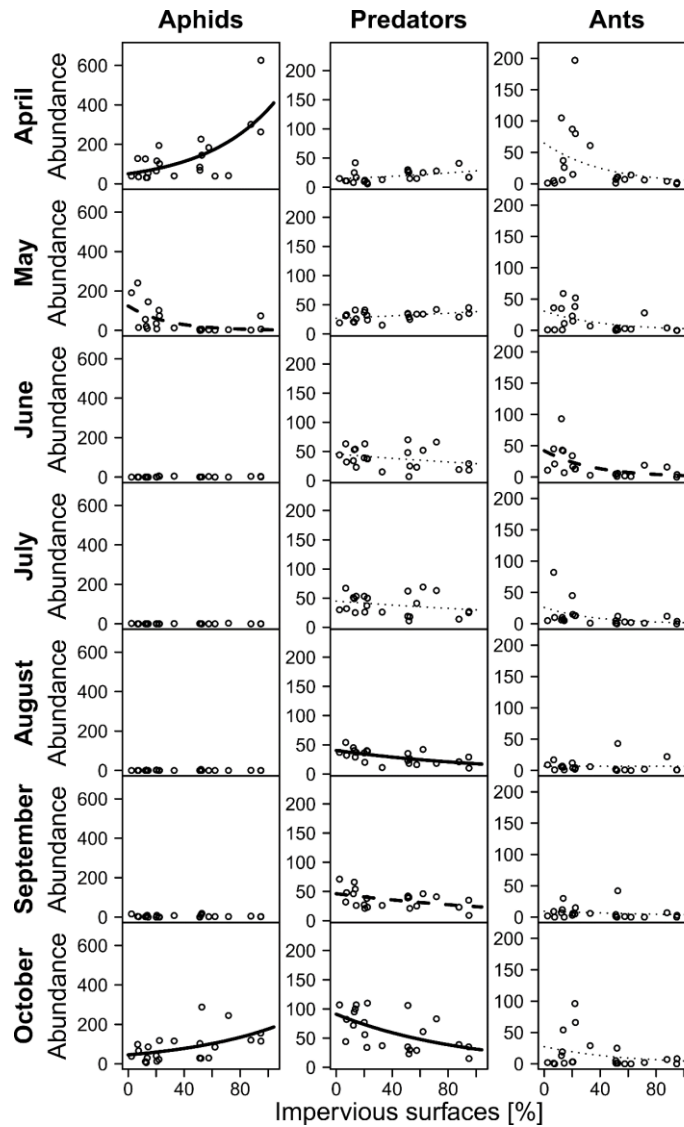


Figure 17. Effect of impervious surface percentage on the abundance of aphid, predator, and ant assemblages in different months in 2016. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted  $p$  values). Between June and September, the aphid numbers were insufficient for statistical analysis. Note the different scales on the y-axes. Fitted lines are from quasi-Poisson GLMs.

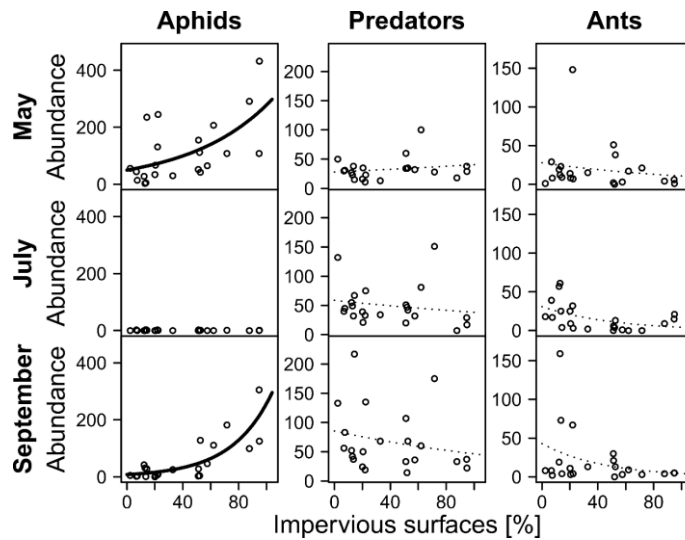


Figure 18. Effect of impervious surface percentage on the abundance of aphid, predator, and ant assemblages in different months in 2017. Continuous lines indicate significant ( $p < 0.05$ ), thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted  $p$  values). Aphid numbers were insufficient for statistical analysis in July. Note the different scales on the y-axes. Fitted lines are from quasi-Poisson GLMs.

We found only a weak correlation between aphid abundances in autumn 2016 and spring 2017 (Spearman  $r = 0.39$ ,  $p = 0.07$ ). For predators, abundance increased slightly with increasing levels of urbanization in spring, but this pattern changed from the beginning of summer, and the abundance was higher in semi-natural habitats for the rest of the season. This temporal pattern was more pronounced in 2016 than in 2017. The abundance of ants slightly decreased with the increasing percentage of impervious surfaces on all sampling occasions. Surprisingly, predators and ants did not follow the spatial abundance pattern of aphids in spring and even less in autumn (Figs. 17 and 18, Table S2.5).

### 5.3.3. Aphid-predator-ant interactions

According to the best models, the presence of predators negatively affected the total abundance of aphids in 2016 ( $p = 0.013$ , Table S2.6). We found significant negative relationship between monthly predator and total aphid abundance in September and October in 2016. However, there was no association between the yearly or monthly abundances of ants and the total aphid density, either in 2016 or in 2017 (Tables 4 and S2.7). We did not find any significant relationship between

yearly abundances of predators and ants in either year (Quasi-GLMs: 2016:  $t = 0.593$ ,  $p = 0.560$ ; 2017:  $t = -1.176$ ,  $p = 0.253$ ).

Table 4. Results of the best quasi-GLMs (after model selection) for the annual abundance of aphids (response variable) depending on the monthly abundance of predators and ants (explanatory variables). Only significant ( $p < 0.05$ , numbers in bold) and marginally significant ( $p \geq 0.05$  and  $< 0.1$ , number in italics) results are shown for the best models (in 2016). The main outcomes of the best and full models are summarized in Table S2.7.

| Explanatory variable | Month     | Estimate | SE    | Exp. Estimate | Adj. $p$     | Unadj. $p$   | Pseudo- $R^2$ |
|----------------------|-----------|----------|-------|---------------|--------------|--------------|---------------|
| Predators            | June      | -0.013   | 0.007 | 0.987         | 0.148        | <i>0.089</i> | 14.9          |
| Predators            | September | -0.024   | 0.008 | 0.976         | <b>0.030</b> | <b>0.006</b> | 34.4          |
| Predators            | October   | -0.010   | 0.004 | 0.990         | <b>0.035</b> | <b>0.014</b> | 27.5          |

During the months of peak aphid abundance, number of aphids had no significant effect on the abundance of predators ( $p = 0.483$ ) or ants ( $p = 0.408$ ), i.e. predators and ants did not track aphid abundance (Table S2.8).

#### 5.3.4. *Species of aphids and predators and taxonomic composition of predator community*

The main aphid species showed a positive response to percentage of impervious surfaces. This relationship was significant in the cases of *P. testudinaceus* in 2016 and *P. obscurus* in 2017 (Table 5, Fig. S2.3).

The earwig *Apterygida media* was strongly associated with sites with the lowest percentage of impervious surfaces (where there was a high percentage of forests). In contrast, *F. auricularia* were most abundant at sites with high percentages of gardens or urban parks and showed no relationship to the degree of urbanization (Table 5, Fig. S2.4, for the percentage of each landscape element see Table S2.2).

Among the true bugs, the abundance of *Deraeocoris flavilinea* (A. Costa) increased with the increasing level of impervious surfaces. Urbanization had no significant effect on the abundance of the rest of the true bug species (Table 5, Fig. S2.4).

Among aphidophagous coccinellids, the density of *H. axyridis* larvae increased significantly with urbanization, while that of *H. axyridis* adults decreased slightly, in 2016. Urbanization had no effect on the density of the rest of the coccinellid species (Table 5, Fig. S2.5).

Table 5. Relationships between impervious surface percentage and the abundance of aphid and predator taxa. Summary of the quasi-GLM results by species and years. Numbers with bold indicate significant ( $< 0.05$ ) and numbers with italic indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ )  $p$  values. Numbers in parentheses are the unadjusted  $p$  values.

| Taxon                             | 2016     |       |               |                        |               | 2017     |       |               |                        |               |
|-----------------------------------|----------|-------|---------------|------------------------|---------------|----------|-------|---------------|------------------------|---------------|
|                                   | Estimate | SE    | Exp. Estimate | Adj. $p$               | Pseudo- $R^2$ | Estimate | SE    | Exp. Estimate | Adj. $p$               | Pseudo- $R^2$ |
| <b>Sternorrhyncha</b>             |          |       |               |                        |               |          |       |               |                        |               |
| <i>Drepanosiphum aceris</i>       | 0.008    | 0.012 | 1.008         | 0.514 (0.514)          | 3.1           | -        | -     | -             | -                      | -             |
| <i>Drepanosiphum platanoidis</i>  | 0.018    | 0.008 | 1.018         | <i>0.096 (0.048)</i>   | 23.9          | -        | -     | -             | -                      | -             |
| <i>Periphyllus obscurus</i>       | 0.008    | 0.005 | 1.008         | 0.192 (0.144)          | 11.0          | 0.032    | 0.005 | 1.033         | <b>0.000 (0.000)</b>   | 74.5          |
| <i>Periphyllus testudinaceus</i>  | 0.011    | 0.004 | 1.011         | <b>0.049 (0.012)</b>   | 28.0          | 0.011    | 0.006 | 1.011         | 0.111 (0.111)          | 13.2          |
| <b>Dermaptera</b>                 |          |       |               |                        |               |          |       |               |                        |               |
| <i>Apterygida media</i>           | -0.112   | 0.049 | 0.894         | <i>0.068 (0.034)</i>   | 53.3          | -0.133   | 0.046 | 0.876         | <b>0.019 (0.010)</b>   | 55.6          |
| <i>Forficula auricularia</i>      | -0.008   | 0.007 | 0.992         | 0.270 (0.270)          | 6.3           | -0.002   | 0.009 | 0.998         | 0.820 (0.820)          | 0.3           |
| <b>Heteroptera</b>                |          |       |               |                        |               |          |       |               |                        |               |
| <i>Deraeocoris flavilinea</i>     | 0.021    | 0.007 | 1.021         | <b>0.035 (0.005)</b>   | 34.8          | -        | -     | -             | -                      | -             |
| <i>Deraeocoris lutescens</i>      | -0.005   | 0.005 | 0.995         | 0.490 (0.350)          | 4.9           | -0.003   | 0.009 | 0.997         | 0.761 (0.761)          | 0.6           |
| <i>Orius</i> spp.                 | 0.000    | 0.007 | 1.000         | 0.992 (0.992)          | 0.0           | -0.003   | 0.007 | 0.997         | 0.761 (0.733)          | 0.5           |
| <i>Phytocoris tiliae</i>          | 0.018    | 0.008 | 1.018         | 0.103 ( <b>0.044</b> ) | 18.7          | -        | -     | -             | -                      | -             |
| <i>Pilophorus perplexus</i>       | -0.036   | 0.016 | 0.964         | 0.103 ( <b>0.034</b> ) | 33.7          | -        | -     | -             | -                      | -             |
| <i>Psallus assimilis</i>          | 0.006    | 0.005 | 1.006         | 0.424 (0.242)          | 6.3           | 0.029    | 0.015 | 1.030         | 0.199 ( <i>0.066</i> ) | 27.5          |
| <i>Reuteria marqueti</i>          | -0.007   | 0.014 | 0.993         | 0.708 (0.606)          | 1.8           | -        | -     | -             | -                      | -             |
| <b>Coleoptera</b>                 |          |       |               |                        |               |          |       |               |                        |               |
| <i>Coccinella septempunctata</i>  | -0.005   | 0.014 | 0.995         | 0.755 (0.717)          | 1.2           | -        | -     | -             | -                      | -             |
| <i>Exochomus quadripustulatus</i> | -0.002   | 0.007 | 0.998         | 0.755 (0.755)          | 0.5           | 0.004    | 0.006 | 1.004         | 0.490 (0.490)          | 2.2           |
| <i>Harmonia axyridis</i> larvae   | 0.015    | 0.004 | 1.015         | <b>0.019 (0.003)</b>   | 35.1          | -        | -     | -             | -                      | -             |
| <i>Harmonia axyridis</i> adults   | -0.011   | 0.005 | 0.989         | 0.121 ( <b>0.047</b> ) | 21.5          | -0.004   | 0.004 | 0.996         | 0.490 (0.380)          | 4.2           |
| <i>Oenopia conglobata</i>         | 0.014    | 0.007 | 1.014         | 0.121 ( <i>0.072</i> ) | 15.7          | 0.018    | 0.012 | 1.018         | 0.466 (0.155)          | 12.2          |
| <i>Scymnus</i> spp.               | 0.013    | 0.007 | 1.013         | 0.121 ( <i>0.080</i> ) | 13.0          | -        | -     | -             | -                      | -             |
| <b>Neuroptera</b>                 |          |       |               |                        |               |          |       |               |                        |               |
| <i>Chrysoperla</i> spp.           | -0.016   | 0.008 | 0.984         | <i>0.078 (0.078)</i>   | 15.3          | -        | -     | -             | -                      | -             |



Table 5. continued.

| Taxon                                       | <u>2016</u> |       |                  |                      |                                  | <u>2017</u> |       |                  |                      |                                  |
|---|-------------|-------|------------------|----------------------|----------------------------------|-------------|-------|------------------|----------------------|----------------------------------|
|   | Estimate    | SE    | Exp.<br>Estimate | Adj. <i>p</i>        | Pseudo-<br><i>R</i> <sup>2</sup> | Estimate    | SE    | Exp.<br>Estimate | Adj. <i>p</i>        | Pseudo-<br><i>R</i> <sup>2</sup> |
| <b>Araneae</b>                              |             |       |                  |                      |                                  |             |       |                  |                      |                                  |
| <i>Anelosimus vittatus</i>                  | -           | -     | -                | -                    | -                                | 0.002       | 0.014 | 1.002            | 0.880 (0.880)        | 0.2                              |
| ‘other Theridiidae’                         | -0.017      | 0.005 | 0.983            | <b>0.012 (0.001)</b> | 41.7                             | -0.020      | 0.009 | 0.981            | <i>0.072 (0.040)</i> | 26.8                             |
| <i>Anyphaena accentuata</i>                 | -0.087      | 0.039 | 0.917            | <i>0.091 (0.040)</i> | 70.2                             | -0.091      | 0.030 | 0.913            | <b>0.023 (0.008)</b> | 62.3                             |
| <i>Araniella</i> spp.                       | -0.022      | 0.010 | 0.978            | <i>0.091 (0.038)</i> | 26.2                             | -0.032      | 0.010 | 0.968            | <b>0.018 (0.004)</b> | 48.0                             |
| <i>Cheiracanthium</i> spp.                  | 0.005       | 0.006 | 1.005            | 0.470 (0.418)        | 3.1                              | -0.003      | 0.005 | 0.997            | 0.624 (0.485)        | 1.9                              |
| <i>Philodromus</i> spp. <i>aureolus</i> gr. | -0.007      | 0.003 | 0.993            | <i>0.091 (0.035)</i> | 20.2                             | -0.009      | 0.004 | 0.991            | <i>0.078 (0.052)</i> | 18.1                             |
| <i>Philodromus</i> spp. <i>rufus</i> gr.    | 0.004       | 0.008 | 1.004            | 0.585 (0.585)        | 1.9                              | 0.003       | 0.008 | 1.003            | 0.820 (0.729)        | 0.7                              |
| <i>Xysticus</i> spp.                        | -           | -     | -                | -                    | -                                | 0.013       | 0.005 | 1.014            | <b>0.032 (0.014)</b> | 22.6                             |
| ‘other Thomisidae’                          | -0.088      | 0.058 | 0.916            | 0.213 (0.142)        | 56.0                             | -0.052      | 0.016 | 0.949            | <b>0.018 (0.004)</b> | 56.4                             |

Most of the spider species responded negatively to the increase of impervious surfaces. This was particularly true for *Anyphaena accentuata* (Walckenaer), *Araniella* spp. [mainly *A. cucurbitina* (Clerck), and *A. opisthographa* (Kulczyński)], and for the groups ‘other Theridiidae’ (mostly juveniles), ‘other Thomisidae’, but to a lesser extent for *Ph. aureolus* group. Only *Xysticus* spp. (mostly juveniles) had significantly higher abundance in built-up areas. *Anelosimus vittatus* (CL Koch), *Cheiracanthium* spp. (mainly *C. mildei* L. Koch) and the *Ph. rufus* group showed no response to urbanization (Table 5, Fig. S2.6, for further information on the species groups and genera, see Table S2.4).

Lacewing abundance (mostly of *Chrysoperla carnea* [Stephens]) decreased slightly with increasing levels of urbanization in 2016 (Table 5, Fig. S2.5).

NMDS ordination revealed that the community composition of predators changed along the urbanization gradient in both 2016 and 2017 (NMDS, Stress = 0.186,  $R^2 = 0.674$ ; Stress 0.203,  $R^2 = 0.715$ , respectively) (Figs. 19a–b). This pattern was most typical for the spider assemblage (NMDS, Stress = 0.173,  $R^2 = 0.539$ ) and to a lesser extent for true bugs and coccinellids (NMDS, Stress = 0.203,  $R^2 = 0.600$ ; Stress = 0.198,  $R^2 = 0.547$ , respectively) (Figs. 19c–e). The composition of coccinellids did not separate clearly along the first axis, although it showed differences between the most natural (impervious surface < 20%) and highly urbanized sites (impervious surface > 60%) (Fig. 19d).

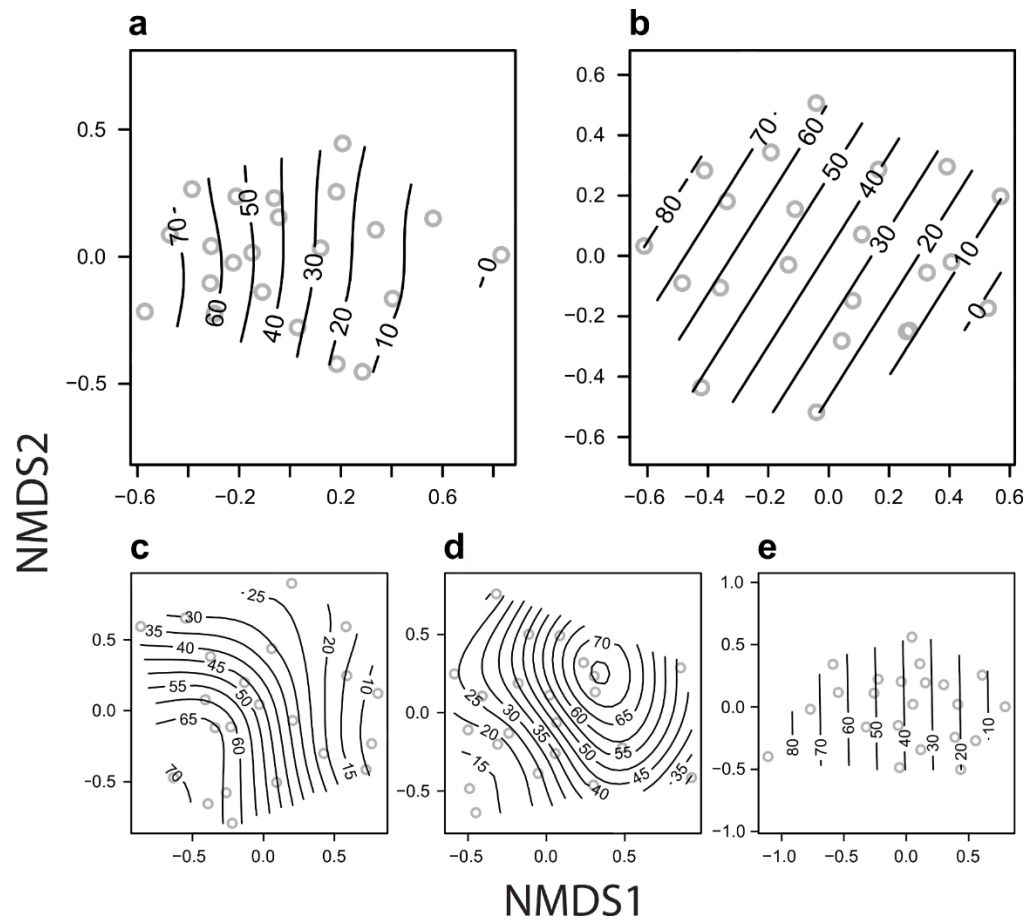


Figure 19. NMDS ordination of the 22 sites based on community composition of all predators in (a) 2016 and (b) 2017; in case of (c) true bugs, (d) aphidophagous ladybirds and (e) spiders. For the three predator groups, the data of May, July, and September in 2016 and 2017 were pooled. Grey circles represent study sites. GAM fitted isoclines represent impervious surface percentages.

### 5.3.5. Effect of dispersal ability of predators on aphids

We found a significant shift in the CWM trait values for predator dispersal ability along the urbanization gradient in both years, where the proportion of predatory species with higher dispersal ability increased with the increasing level of impervious surfaces (GLMs: 2016:  $t = 3.156$ ,  $p = 0.005$ ; 2017:  $t = 2.448$ ,  $p = 0.024$ ) (Fig. 20), and the annual abundance of aphids decreased significantly when the predator community contained more low-dispersing predators (Quasi-GLMs: 2016:  $t = 3.05$ ,  $p = 0.006$ ; 2017:  $t = 2.385$ ,  $p = 0.027$ ).

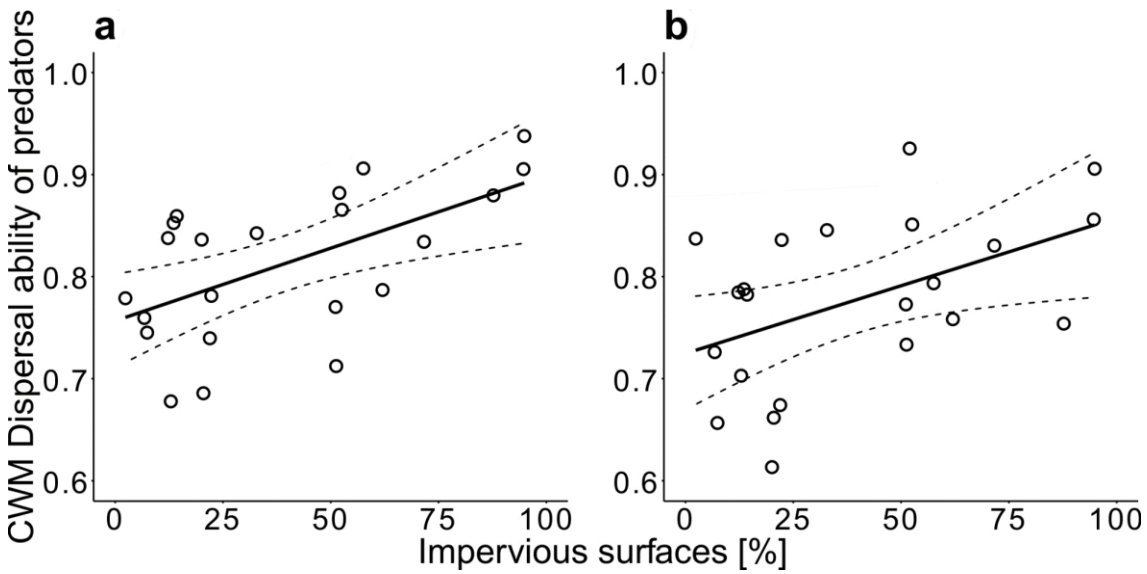


Figure 20. Effect of impervious surface percentage on community weighted mean (CWM) dispersal values of predators in (a) 2016 and (b) 2017.

According to the NMDS ordination based on the association between the abundance of aphids and predatory groups, earwigs (mean dispersal value of the group: 0.0,  $n = 831$ ) and web building spiders (0.61, 649) were associated with the sites with the lowest, while *H. axyridis* larvae (1.0, 255) and other coccinellids (1.0, 1082) were associated with the sites with the highest aphid abundances (NMDS, Stress = 0.113,  $R^2 = 0.227$ ; Stress = 0.155,  $R^2 = 0.359$ , respectively) (Fig. 21).

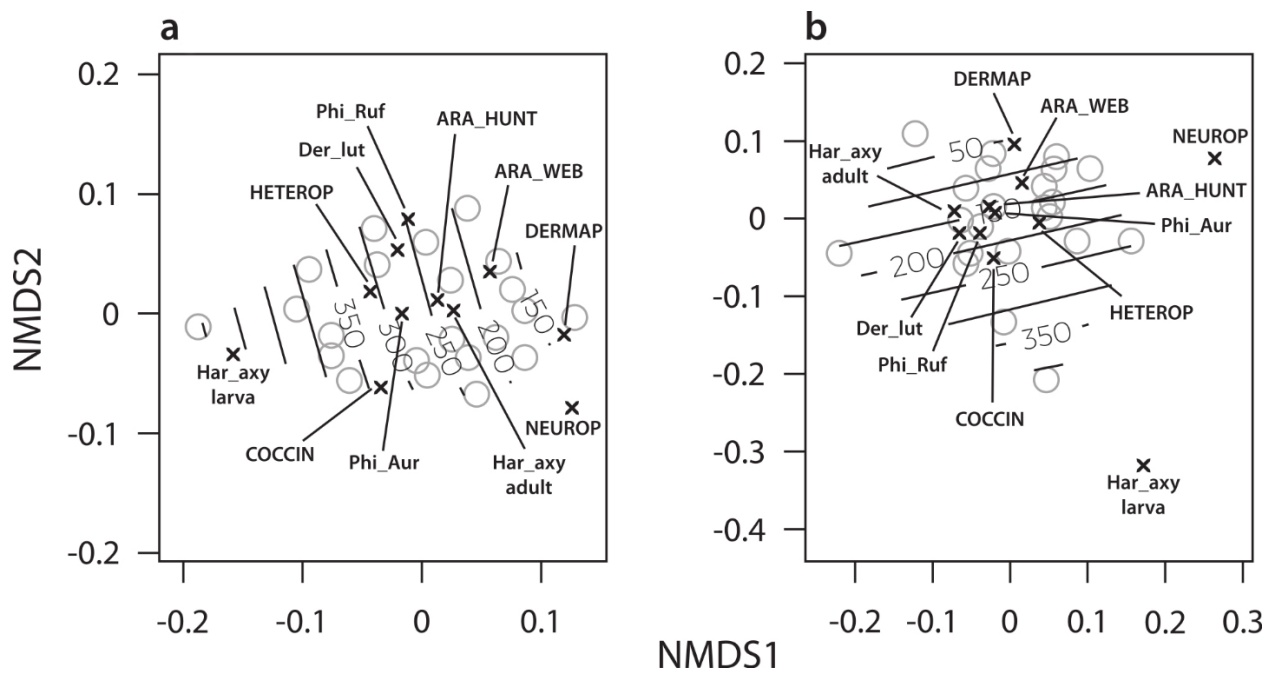


Figure 21. NMDS ordination of total abundances of predators in (a) 2016 and (b) 2017. Grey circles represent study sites and abbreviations correspond to the most abundant natural enemy groups (DERMAP: Dermaptera, HETEROP: other heteropterans (except *D. lutescens*), Der\_lut: *Deraeocoris lutescens*, COCCIN: other coccinellids (except *Harmonia axyridis* larvae and adults), Har\_axy larva: *Harmonia axyridis* larvae, Har\_axy adult: *Harmonia axyridis* adults, NEURO: Neuroptera, ARA\_WEB: web building spiders, ARA\_HUNT: other hunting spiders (except *Philodromus aureolus* and *rufus* groups), Phi\_Aur: *Philodromus aureolus* group, Phi\_Ruf: *Philodromus rufus* group). GAM fitted isoclines represent aphid abundances.

#### 5.4. Discussion

The aphid-predator-ant system we studied changed markedly both in space, along the urbanization gradient, and in time, across the season, in both study years. Aphids and predatory arthropods showed species-specific abundance patterns. There was a negative relationship between predator and aphid abundances in one of the two study years and the abundance of aphids decreased significantly with increasing number of low-dispersing individuals in the predator community in both years.

#### 5.4.1. *Effects of urbanization on the abundance of aphids, predators and ants*

Aphids exhibited the most consistent pattern in this study. In line with our first hypothesis, we found high aphid abundances in highly urbanized areas, in contrast to semi-natural landscapes where their abundance remained low (Table 3, Fig. 16). Aphids benefit from urbanization disturbance due to the environmental conditions and characteristics of their hostplants in cities (Hall & Ehler, 1980; Braun & Flückiger, 1985; Butler & Trumble, 2008) coupled with their enormous reproductive potential and multiple generations per year, which allows them to rapidly take advantage of favorable conditions (Harrington et al., 2007; Durak et al., 2016; Parsons & Frank, 2019).

In contrast to aphids, the overall number of predators decreased towards the city center (Table 3, Fig. 16), which can be explained by several factors. Highly urbanized areas are generally characterized by fragmented habitats with reduced plant density, diversity, and structural complexity (Raupp et al., 2010). This may create an unfavorable environment for predators due to reduced numbers of prey (and alternative resources), refuges, and suboptimal climatic conditions (Langellotto & Denno, 2004). Moreover, the increasing proportion of human-made structures might act as a dispersal barrier for predatory arthropods (Mader et al., 1990; Denys & Schmidt, 1998; Turrini et al., 2016).

Lessard and Buddle (2005) found the highest ant abundance in residential backyards compared to forests while Rocha and Fellowes (2018) showed that ants were present in high numbers even at the most urbanized sites. Contrary to their findings, we observed that ants had the highest abundance in semi-natural areas and the lowest in the city center (Table 3, Fig. 16). Although we did not determine the species composition of ants along the gradient, we assume that highly urbanized areas are less suitable habitats for most of the ant species. The explanation for this could be colonization limitation, as individual ants may have more limited opportunities to spread to more isolated areas from source populations (Pacheco & Vasconcelos, 2007), but also may be due to a lack of necessary resources for nesting sites (Vepsäläinen et al., 2008) and a decline in soil moisture (Clarke et al., 2008).

Generally, the activity of tree-dwelling aphids is characterized by two seasonal peaks (Dixon, 1977; Piñol et al., 2009a, 2009b), and we found the same pattern here (Fig. 15). *Periphyllus* species aestivate during summer months as first instar nymphs, while *Drepanosiphum* species aestivate as adults (Dixon, 1977; Furuta, 1985; Dixon, 1998; Junkiert et al., 2011). Although the

total abundance of aphids increased towards the city center in both years, their monthly abundance showed a less consistent pattern. The abundance of aphids greatly increased in April, but slightly decreased in May towards the city center in 2016 (Fig. 17, Table S2.5). Highly urbanized areas generally have higher temperatures than the surrounding semi-natural habitats due to the urban heat island effect caused by the high proportion of impervious surfaces (Rizwan et al., 2008; Long et al., 2019). Since temperature is considered one of the most important factors in aphid development (Harrington et al., 2007; Durak et al., 2016), it is possible that warmer temperatures resulted in faster nymphal development (phenological shift) at these sites compared to semi-natural habitats (Fig. 17, Table S2.5). Higher temperature can also lead to delayed appearance of sexual generations and reproduction of aphids at the end of summer (Durak et al., 2016). Based on these factors, we expected an earlier peak in aphid abundance in semi-natural habitats compared to highly urbanized ones in this period, but such a pattern was not observed (Fig. 17). The lack of a phenological shift in the later part of the season may be explained by greater predator abundances and therefore higher predation rates in semi-natural areas that might obscure the impact of climate on aphids.

The overall number of predators was relatively low and only increased slightly towards the city center in spring (mostly due to *H. axyridis* larvae and some true bugs). Predator abundance started to increase towards the semi-natural areas from the beginning of June (mostly due to earwigs and coccinellids, including *H. axyridis* adults), and this pattern was most pronounced in autumn (mostly due to spiders and coccinellids) (Figs. 17 and 18, Table S2.5, Fig. S2.2).

Predatory insects with high dispersal ability and ants exhibit positive density-dependent numerical responses to aphid density (Brown, 2004; Stutz & Entling, 2011; Markó et al., 2013; Leigh & van Emden, 2017). However, in our study, predatory arthropods and ants showed a reverse pattern compared to aphids, i.e. the abundance of predators and ants did not track the abundance of aphids along the urbanization gradient even at the aphid peaks in spring and autumn (Figs. 17 and 18, Tables S2.5 and S2.8). This finding indicates that urbanization may lead to a spatial mismatch between aphids, their predators, and mutualistic ants.

#### 5.4.2. *Aphid-predator-ant interactions*

In line with our second hypothesis, high predator numbers were accompanied by low aphid abundance in 2016, but contrary to our expectations (and hypothesis 3), there was no relationship between ant and aphid abundance (Tables 4 and S2.7), and predatory arthropods and ants varied

independently of each other. One explanation for the observed higher aphid densities in more urbanized areas may be that urbanization disrupted predators, resulting in weakened top-down control on aphids (Turrini et al., 2016). Predators reached their highest abundance in autumn (Fig. 15; Table S2.8), and predator abundances were the best predictors of the total aphid abundance in this period in 2016 (Tables 4 and S2.7). This suggests that number of aphids is primarily regulated by predators before and during their second activity peak in semi-natural areas. Furuta (1985) pointed out that aestivating populations of *Periphyllus californiensis* (Shinji) on maple trees seem to face high predation in the second half of the growing season, and this may have a stronger effect on their survival than other factors such as unfavorable climatic conditions.

The highest aphid densities were coincided with the lowest predator densities at the beginning of the growing season. This implies that aphid species with early egg hatch (especially *P. testudinaceus*) are exposed to lower predation in spring (Dixon, 1998), and therefore the peak in aphid density early in the season might be determined more by aphid abundance in the previous autumn than by predation in early spring. Rocha and Fellowes (2018) reported that instead of predation, the abundance of mutualistic ants drove the abundance of myrmecophilous aphids along the urbanization gradient. Contrary to their results and to those of Skinner and Whittaker (1981), we found that the supposed positive effect of ants on aphids did not override the predation pressure on aphids (almost exclusively ant-tended *Periphyllus* spp.) in semi-natural areas.

#### 5.4.3. *Species of aphids and predators and taxonomic composition of predator community*

The ant-tended aphid species (*P. obscurus*, *P. testudinaceus*) responded positively, while the non-ant-tended species (*D. aceris*, *D. platanoidis*) showed no or weak responses to increasing level of urbanization. In contrast, and in line with hypothesis 4, predatory species showed definitive species-specific responses (Table 5). Seven predatory groups responded negatively, whereas three groups responded positively to urbanization in at least one of the studied years. Fourteen groups showed no response to urbanization and were occasionally abundant in moderately built-up sites but less often in highly built-up areas.

One earwig species and most of the spider groups were negatively affected by urbanization. In contrast, most true bugs and coccinellids showed no response or responded positively to increasing levels of urbanization (Table 5, Figs. S2.4, S2.5, and S2.6).



In accordance with species-specific responses, the composition of spiders changed more along the urbanization gradient than that of true bugs or coccinellids (Figs. 19c–e), and based on this, spiders contributed most significantly to the changing composition pattern of the total predator community in both years (Figs. 19a–b). These results suggest that although some spider groups have a wide habitat range and good dispersal ability (Duffey, 1956; Alaruikka et al., 2002; Blandenier, 2009), they are less capable of target-oriented movement than the winged species with relatively high mobility and short residency time such as coccinellids and true bugs (Egerer et al., 2016; Piñol et al., 2009b). Therefore, spiders can be highly sensitive to habitat isolation and its consequences caused by urbanization (Langellotto & Denno, 2004; Meineke et al., 2017; Argañaraz et al., 2018).

It is important to mention that in some cases we also recorded high predator densities (e.g. *F. auricularia*, *D. lutescens*, *P. assimilis*, *E. quadripustulatus*, *O. conglobata*, and *Scymnus* spp.) in moderately built-up sites with relatively high share of parks and gardens (Table S2.2, Figs. S2.4 and S2.5). These kind of green areas in cities are complex, resource-rich habitats, and are preferred by certain predatory species such as coccinellids (Egerer et al., 2016; Honěk et al., 2017) and other aphidophagous predators (Parsons & Frank, 2019). However, a high proportion of impervious surfaces in the surrounding environment may influence the colonization success even of these species (Comont et al., 2014; Rocha et al., 2018).

#### 5.4.4. *Effect of dispersal ability of predators on aphids*

We found that the dispersal capacity of predator community significantly increased with increasing level of urbanization, suggesting that urbanization filters predatory species based on their dispersal ability (Piano et al., 2017; Merckx & Van Dyck, 2019). Furthermore, our observations are consistent with hypothesis 5 and suggest that generalist predators with low dispersal ability such as earwigs and some spiders may play a major role in the biological control of aphids. Some of these predators can be present constantly on the trees, even at early aphid population growth and low aphid density (Piñol et al., 2009b), which can be an important prerequisite for successful aphid suppression (Boreau de Roinceé et al., 2013; Nagy et al., 2015; Gómez-Marco et al., 2016).

Earwigs are voracious predators of aphids and play a key role in the top-down control of these pests (Carroll and Hoyt, 1984; Mueller et al., 1988; Piñol et al., 2009a). They are characterized by low dispersal ability and a preference for habitats with higher humidity (Kirstová

et al., 2019). Therefore, increasing isolation of trees from forests is associated with lower earwig numbers and, as a consequence, greater density of aphids (Stutz & Entling, 2011). There are a few examples where hunting spiders (e.g. *Anyphaena*, *Philodromus* spp.) contributed to the early biological control of aphids (Boreau de Roince et al., 2013; Lefebvre et al., 2017). Moreover, studies showed that web-building spiders can substantially reduce the number of aphids, especially in autumn when density of their webs is high and winged aphids are present. This can lead to fewer aphid fundatrices the following spring (Wyss et al., 1995; Cahenzli et al., 2017).

Our results are in accordance with the finding that predators with high dispersal capacity such as lady beetles and true bugs can be generally less effective at keeping aphid populations at low levels, as they mostly track aphid density rather than control it (Piñol et al., 2009a, b).

## 6. Summary

Urbanization alters dramatically the landscape and natural habitats and has a substantial local effect on animal communities and ecological systems. Although arthropods are suitable indicators of human-induced environmental changes, they are less studied in terms of urbanization compared to other taxa. Arthropods are influenced by numerous factors in urban environment, including bottom-up or top-down effects which greatly influence their community dynamics. In addition, human activities associated with cities contribute to the introduction and establishment of alien species, which might have a significant impact on the abundance and community composition of arthropods in urban environment. Urban trees provide numerous ecosystem services including air cleaning and temperature regulation. Native tree species harbor diverse arthropod communities and thus can greatly contribute to urban biodiversity, but are also attacked by several pest species. Urban trees therefore are ideal choice for studying the direct and indirect effects of urbanization on complex arthropod communities.

In this thesis, we examined the community of canopy dwelling arthropods of urban maple trees in three separate studies. In the first study we made a multi-annual faunal in and around the city of Budapest, Hungary. In the second study we characterized the phytophagous insect communities in the canopy of three native maple species (sycamore, Norway, and field maple), considering their stress level and condition. In the third study we assessed the effect of urbanization on aphids, predatory arthropods, and ants, as well as their interactions on field maple trees. Arthropods were collected by beating method and were identified to the lowest identifiable taxonomic unit. The stress level and condition of trees were expressed as peroxidase enzyme (POD) activity, degree of leaf necrosis and leaf fall. As an index of the degree of urbanization we calculated the percentage of impervious surfaces within a 500 m radius. To evaluate our results, we used linear and cumulative link models, indicator species analysis, and non-metric multidimensional scaling as statistical methods.

As a result of the faunal surveys we reported one spider (*Icius subinermis*) and four insect species (*Latilica maculipes*, *Synophropsis lauri*, *Psallus assimilis*, and *Cybocephalus nipponicus*) for the first time from Hungary. Most of these species might have been introduced to Hungary unintentionally by human mediation, but the possibility of a natural expansion of their distribution area due to the warming climate could not be excluded. Two species, *P. assimilis*, and *C. nipponicus* might have role in control of some pests such as aphids, psyllids and scale insects.

The results of the second study showed that the three maple species support characteristic phytophagous insect communities, which are primarily determined by the species of the host plant. Maple trees differed markedly in their condition, expressed as degree of leaf necrosis, where field maple was in the best and Norway maple in the worst condition in the urban environment. Consistent with that finding, field maple had the most indicator species while Norway maple had the least characteristic phytophagous insect community, with the lowest abundance. Numbers of the super-abundant planthopper species, *M. pruinosa*, were driven by tree condition, reaching higher abundances on healthier trees. Our results suggest that field maple can cope better with the negative effects of urbanization, including abiotic stressors or outbreaks of phytophagous insects than the other two maple species, and that therefore this species is well-suited to urban habitats.

The most important finding of the third study is that an increasing level of urbanization resulted in increasing aphid infestations on urban maple trees, while predators showed opposite abundance pattern. Overall dispersal ability of predator community was positively related to urbanization, i.e. predatory species with low dispersal but high aphid control ability (such as earwigs and some spiders) decreased in abundance toward city centers. In contrast, species with higher dispersal potential but a lower ability to prevent aphid outbreaks such as coccinellids and true bugs did not aggregate in sufficient number on the abundant aphid colonies to compensate for the lack of early aphid control in the city centers by other predators. We concluded that aphid populations in semi-natural habitats are primarily regulated at low aphid densities by predators with low dispersal ability. In this study, ants were less abundant in urban than in the semi-natural habitats and did not drive aphid density. These results suggest that pest control services provided by predatory arthropods decrease markedly towards city centers and are associated with aphid outbreaks on urban trees. To confirm this, further field studies combined with experimental approaches are needed.

## 7. References

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## 8. Theses

### 8.1. Theses

Based on the results of my dissertation, I conclude the following theses:

- 1) I reported one spider (*I. subinermus*) and four insect species (*L. maculipes*, *S. lauri*, *P. assimilis*, and *C. nipponicus*) for the first time from Hungary.
- 2) I characterized the phytophagous insect communities in the canopy of three maple species (*A. pseudoplatanus*, *A. platanoides*, and *A. campestre*) in urban environment. I showed that most herbivorous species were associated with field maple, sycamore had the highest aphid densities, and Norway maple had the least abundant and least characteristic phytophagous insect community.
- 3) I assessed the physiological condition of maple trees and showed that field maple has the highest and Norway maple has the lowest stress tolerance, with sycamore being intermediate, in urban conditions in the city of Budapest, Hungary.
- 4) I reported *Metcalfa pruinosa* to be by far the most abundant phytophagous species on urban maples. I also showed that its abundance was primarily driven by tree condition, i.e. this species reached higher abundances on healthier trees.
- 5) I found increasing aphid and decreasing ant abundances with increasing level of urbanization. I also found that abundance of predatory arthropods and occurrence of poorly dispersing species within the predator community are negatively related to urbanization and identified these two independent factors as significant predictors of aphid abundances.
- 6) Altogether, I showed that urbanization, by altering the abundance and composition of predator communities, can disrupt biological control of aphid populations, and thus may contribute to the aphid outbreaks on urban trees.

## 8.2. Tézisek

A disszertációm eredményei alapján az alábbi téziseket fogalmazom meg:

- 1) Elsőként mutattam ki egy pókfajt (*I. subinermus*) és négy rovarfajt (*L. maculipes*, *S. lauri*, *P. assimilis* és *C. nipponicus*) Magyarország területéről.
- 2) Jellemeztem három juharfaj (*A. pseudoplatanus*, *A. platanoides* és *A. campestre*) lombozatlakó fitofág rovaregyüttesét városi környezetben. Kimutattam, hogy a legtöbb fitofág faj a mezei juharhoz kötődött, hegyi juharon volt a legnagyobb a levéltetvek egyedsűrűsége, míg a korai juharfákon alakult ki a legkisebb egyedsűrűségű és legkevésbé sajátos fitofág rovaregyüttes.
- 3) Felmértem a juharfák fiziológiai állapotát és kimutattam a mezei juhar jó, a hegyi juhar közepes és a korai juhar rossz várostűrő képességét Budapesten.
- 4) Kimutattam, hogy a *Metcalfa pruinosa* messze a leggyakoribb fitofág faj városi juharfákon. Megállapítottam továbbá, hogy a faj egyedszámának alakulását elsősorban a fák kondíciója határozta meg, vagyis nagyobb egyedszámban fordult elő az egészségesebb fákon.
- 5) Az urbanizáció mértékének növekedésével a levéltetvek növekvő, míg a hangyák csökkenő egyedszámát mutattam ki. Szintén megfigyeltem, hogy a ragadozók számát és azon belül a gyenge diszperziós képességű fajok jelenlétét az urbanizáció negatívan befolyásolta és ez a két, egymástól független faktor szignifikánsan magyarázta a levéltetvek egyedsűrűségét.
- 6) Összeségében megállapítottam, hogy az urbanizáció a ragadozók egyedszámára és közösség-összetételére gyakorolt hatásával megzavarhatja a levéltetvek biológiai szabályozását, hozzájárulva a levéltetvek városi fákon megfigyelhető jelentős felszaporodásához.

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Finally, I would like to express my gratitude to my family for supporting me during this difficult and challenging period.

# Appendices

## Supplementary material for STUDY II

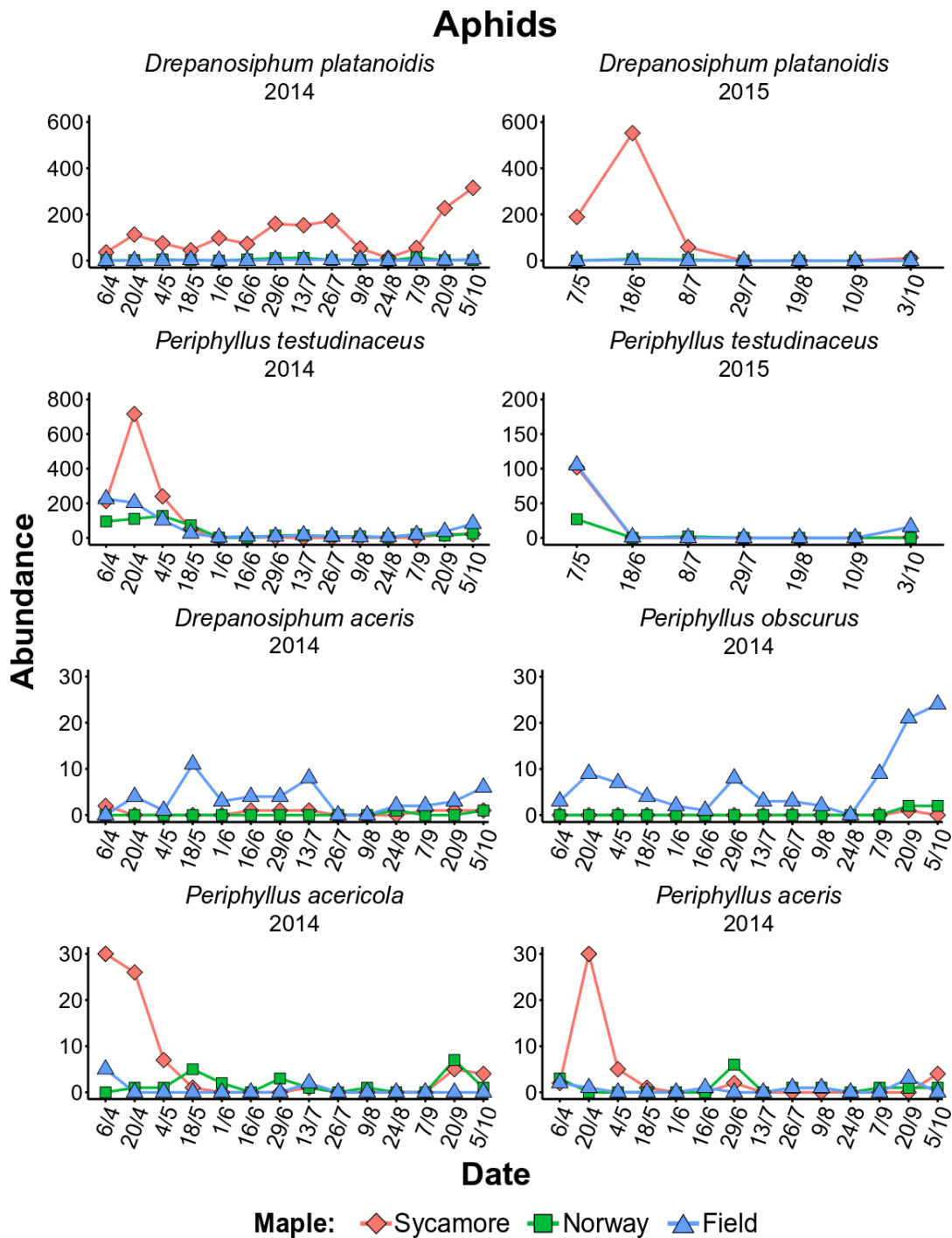


Figure S1.1. Temporal abundance patterns of aphid species on sycamore, Norway, and field maple trees in 2014 and 2015. Note the different scales on the y-axes.

# Plant- and leafhoppers

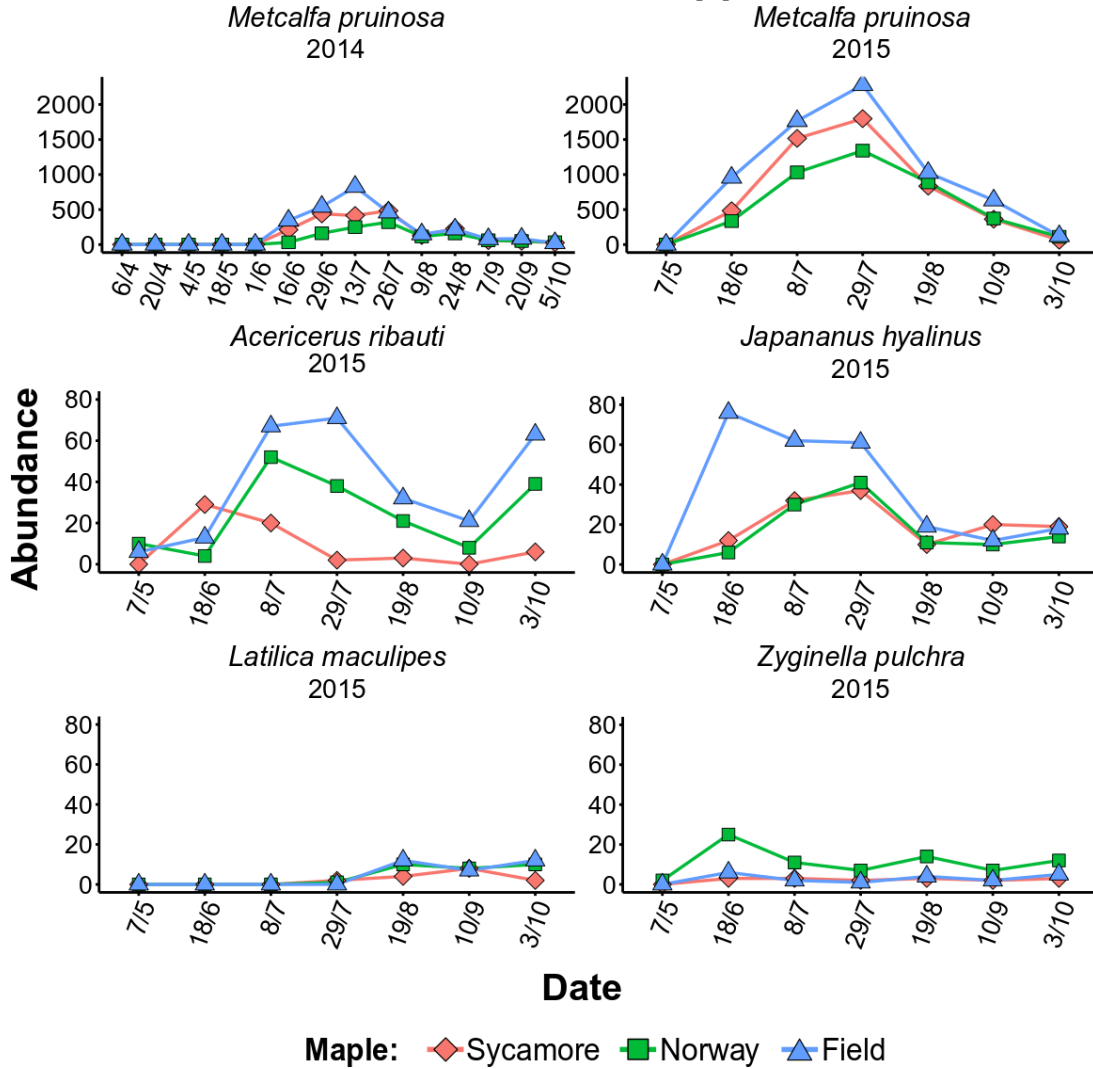


Figure S1.2. Temporal abundance patterns of plant- and leafhopper species on sycamore, Norway, and field maple trees in 2014 and 2015. Note the different scales on the y-axes.

# Heteropterans

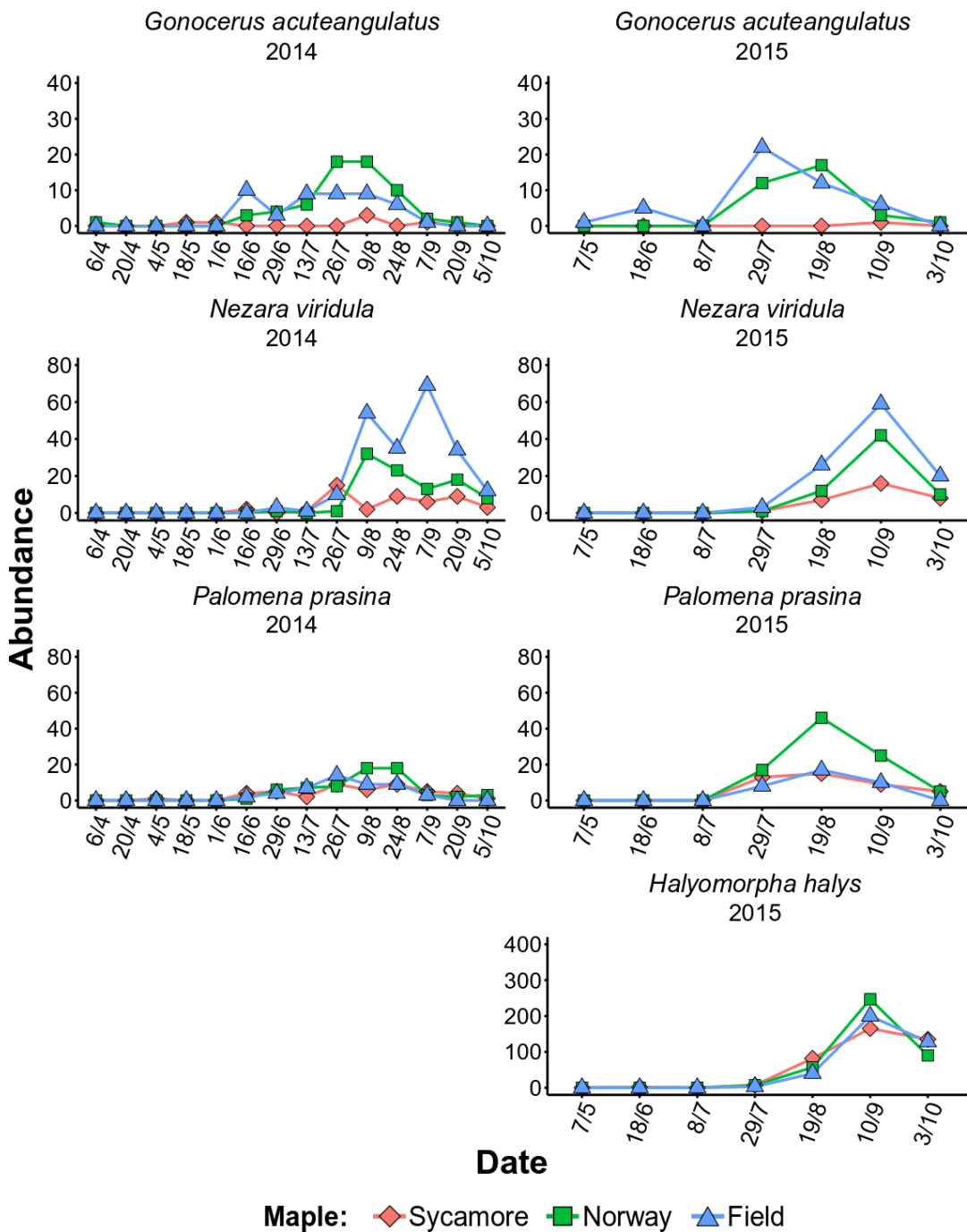


Figure S1.3. Temporal abundance patterns of heteropteran species on sycamore, Norway, and field maple trees in 2014 and 2015. Note the different scales on the y-axes.

## Other phytophagous species

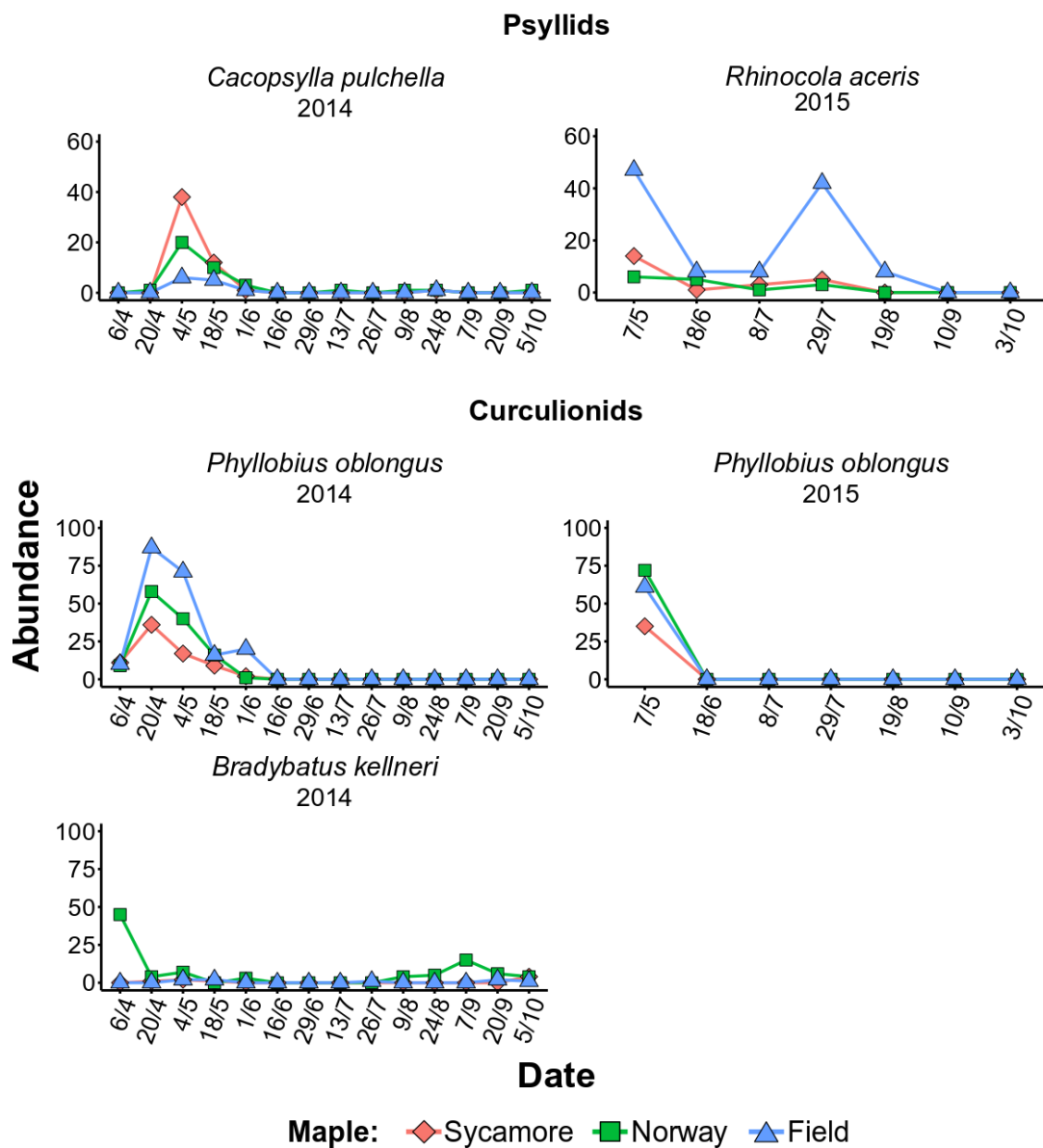
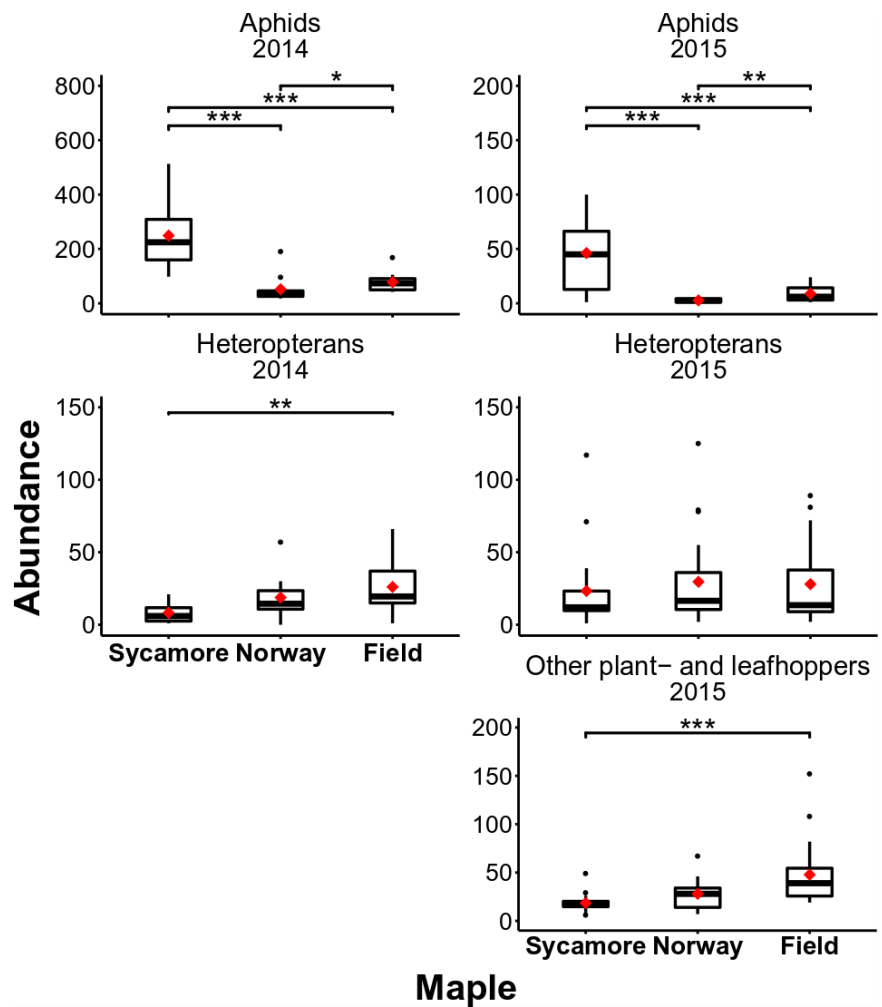


Figure S1.4. Temporal abundance patterns of psyllid and curculionid species on sycamore, Norway, and field maple trees in 2014 and 2015. Note the different scales on the y-axes.



### Maple

Figure S1.5. Abundance of aphids, and heteropterans, and other (non-*M. pruinosa*) plant- and leafhoppers on sycamore, Norway, and field maple trees in 2014 and 2015. On the boxplots red squares indicate means. Significant differences between maple species (least squares means, ANOVA, GLMM; \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ ) were calculated for log-transformed data. The main outcomes of pairwise comparisons are summarized in Table S1.2. Note the different scales on the y-axes.



Table S1.1. List of the abundant phytophagous species and their yearly and total abundance across all trees and sites.

| Order/family           | Species                          | Abundance<br>in 2014 | Abundance<br>in 2015 | Total<br>abundance |
|------------------------|----------------------------------|----------------------|----------------------|--------------------|
| <b>Sternorrhyncha</b>  |                                  |                      |                      |                    |
| Aphididae              | <i>Drepanosiphum aceris</i>      | 58                   | 17                   | 75                 |
|                        | <i>Drepanosiphum platanoidis</i> | 1677                 | 825                  | 2502               |
|                        | <i>Periphyllus acericola</i>     | 103                  | 9                    | 112                |
|                        | <i>Periphyllus aceris</i>        | 67                   | 8                    | 75                 |
|                        | <i>Periphyllus obscurus</i>      | 101                  | 31                   | 132                |
|                        | <i>Periphyllus testudinaceus</i> | 2537                 | 254                  | 2791               |
| Psylloidea             | <i>Cacopsylla pulchella</i>      | 103                  | 21                   | 124                |
|                        | <i>Rhinocola aceris</i>          | 8                    | 151                  | 159                |
| <b>Auchenorrhyncha</b> |                                  |                      |                      |                    |
| Cicadellidae           | <i>Acericerus ribauti</i>        | NA                   | 549                  | 549                |
|                        | <i>Japananus hyalinus</i>        | NA                   | 490                  | 490                |
|                        | <i>Zyginella pulchra</i>         | NA                   | 114                  | 114                |
| Flatidae               | <i>Metcalfa pruinosa</i>         | 5940                 | 15912                | 21852              |
| Issidae                | <i>Latilica maculipes</i>        | NA                   | 76                   | 76                 |
| <b>Heteroptera</b>     |                                  |                      |                      |                    |
| Coreidae               | <i>Gonocerus acuteangulatus</i>  | 116                  | 80                   | 196                |
| Pentatomidae           | <i>Halyomorpha halys</i>         | 19                   | 1163                 | 1182               |
|                        | <i>Nezara viridula</i>           | 361                  | 205                  | 566                |
|                        | <i>Palomena prasina</i>          | 160                  | 170                  | 330                |
| <b>Coleoptera</b>      |                                  |                      |                      |                    |
| Curculionidae          | <i>Bradybatus kellneri</i>       | 109                  | 21                   | 130                |
|                        | <i>Phyllobius oblongus</i>       | 403                  | 168                  | 571                |

Table S1.2. Results of pairwise comparisons of least square mean values (obtained from GLMMs) for the abundance of aphids, heteropterans, and other (non-*M. pruinosa*) plant- and leafhoppers between maple species in 2014 and 2015. Numbers in bold indicate significant ( $p < 0.05$ ) and numbers in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values (with Tukey's correction).

| Species                      | Comparison        | 2014     |       |                |              | 2015     |       |                |              |
|------------------------------|-------------------|----------|-------|----------------|--------------|----------|-------|----------------|--------------|
|                              |                   | Estimate | SE    | <i>t</i> ratio | <i>p</i>     | Estimate | SE    | <i>t</i> ratio | <i>p</i>     |
| Aphids                       | Sycamore - Norway | 0.741    | 0.091 | 8.137          | <b>0.000</b> | 1.035    | 0.111 | 9.312          | <b>0.000</b> |
|                              | Sycamore - Field  | 0.494    | 0.091 | 5.418          | <b>0.000</b> | 0.627    | 0.111 | 5.637          | <b>0.000</b> |
|                              | Norway - Field    | -0.248   | 0.091 | -2.719         | <b>0.028</b> | -0.409   | 0.111 | -3.675         | <b>0.002</b> |
| Heteropterans                | Sycamore - Norway | -0.336   | 0.146 | -2.308         | <i>0.070</i> | -0.094   | 0.114 | -0.823         | 0.691        |
|                              | Sycamore - Field  | -0.495   | 0.146 | -3.401         | <b>0.005</b> | -0.083   | 0.114 | -0.725         | 0.750        |
|                              | Norway - Field    | -0.159   | 0.146 | -1.093         | 0.526        | 0.011    | 0.114 | 0.098          | 0.995        |
| Other plant- and leafhoppers | Sycamore - Norway | -        | -     | -              | -            | -0.141   | 0.066 | -2.132         | <i>0.093</i> |
|                              | Sycamore - Field  | -        | -     | -              | -            | -0.279   | 0.066 | -4.207         | <b>0.000</b> |
|                              | Norway - Field    | -        | -     | -              | -            | -0.138   | 0.066 | -2.075         | 0.105        |

Table S1.3. Results of pairwise comparisons of least square mean values (obtained from GLMMs) for the abundance of phytophagous insect species between maple species in 2014 and 2015 (see Fig. 8-11). Numbers in bold indicate significant ( $p < 0.05$ ) and numbers in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values (with Tukey's correction).

| Species                          | Comparison        | 2014     |       |           |              | 2015     |       |           |              |
|----------------------------------|-------------------|----------|-------|-----------|--------------|----------|-------|-----------|--------------|
|                                  |                   | Estimate | SE    | $t$ ratio | $p$          | Estimate | SE    | $t$ ratio | $p$          |
| <b>Aphids</b>                    |                   |          |       |           |              |          |       |           |              |
| <i>Drepanosiphum aceris</i>      | Sycamore - Norway | 0.130    | 0.066 | 1.956     | 0.137        | -        | -     | -         | -            |
|                                  | Sycamore - Field  | -0.440   | 0.102 | -4.306    | <b>0.001</b> | -        | -     | -         | -            |
|                                  | Norway - Field    | -0.569   | 0.091 | -6.243    | <b>0.000</b> | -        | -     | -         | -            |
| <i>Drepanosiphum platanoidis</i> | Sycamore - Norway | 1.454    | 0.147 | 9.858     | <b>0.000</b> | 1.288    | 0.132 | 9.756     | <b>0.000</b> |
|                                  | Sycamore - Field  | 1.741    | 0.147 | 11.802    | <b>0.000</b> | 1.366    | 0.125 | 10.917    | <b>0.000</b> |
|                                  | Norway - Field    | 0.287    | 0.147 | 1.945     | 0.144        | 0.078    | 0.057 | 1.361     | 0.351        |
| <i>Periphyllus acericola</i>     | Sycamore - Norway | 0.197    | 0.158 | 1.247     | 0.426        | -        | -     | -         | -            |
|                                  | Sycamore - Field  | 0.455    | 0.158 | 2.884     | <b>0.018</b> | -        | -     | -         | -            |
|                                  | Norway - Field    | 0.257    | 0.092 | 2.801     | <b>0.022</b> | -        | -     | -         | -            |
| <i>Periphyllus aceris</i>        | Sycamore - Norway | 0.253    | 0.121 | 2.086     | 0.110        | -        | -     | -         | -            |
|                                  | Sycamore - Field  | 0.327    | 0.121 | 2.702     | <b>0.029</b> | -        | -     | -         | -            |
|                                  | Norway - Field    | 0.075    | 0.121 | 0.616     | 0.812        | -        | -     | -         | -            |
| <i>Periphyllus obscurus</i>      | Sycamore - Norway | -0.054   | 0.056 | -0.979    | 0.596        | -        | -     | -         | -            |
|                                  | Sycamore - Field  | -0.896   | 0.056 | -16.112   | <b>0.000</b> | -        | -     | -         | -            |
|                                  | Norway - Field    | -0.842   | 0.056 | -15.134   | <b>0.000</b> | -        | -     | -         | -            |
| <i>Periphyllus testudinaceus</i> | Sycamore - Norway | 0.431    | 0.108 | 3.973     | <b>0.001</b> | 0.303    | 0.101 | 3.009     | <b>0.011</b> |
|                                  | Sycamore - Field  | 0.175    | 0.108 | 1.609     | 0.257        | -0.092   | 0.101 | -0.918    | 0.631        |
|                                  | Norway - Field    | -0.256   | 0.108 | -2.364    | 0.062        | -0.395   | 0.101 | -3.927    | <b>0.001</b> |
| <b>Plant- and leafhoppers</b>    |                   |          |       |           |              |          |       |           |              |
| <i>Metcalfa pruinosa</i>         | Sycamore - Norway | 0.132    | 0.118 | 1.120     | 0.510        | 0.167    | 0.097 | 1.716     | 0.208        |
|                                  | Sycamore - Field  | -0.210   | 0.118 | -1.785    | 0.192        | -0.158   | 0.097 | -1.623    | 0.245        |
|                                  | Norway - Field    | -0.342   | 0.118 | -2.904    | <b>0.018</b> | -0.325   | 0.097 | -3.340    | <b>0.004</b> |
| <i>Acericerus ribauti</i>        | Sycamore - Norway | -        | -     | -         | -            | -0.323   | 0.118 | -2.733    | <b>0.023</b> |
|                                  | Sycamore - Field  | -        | -     | -         | -            | -0.489   | 0.118 | -4.134    | <b>0.000</b> |
|                                  | Norway - Field    | -        | -     | -         | -            | -0.166   | 0.118 | -1.401    | 0.348        |

Table S1.3. continued.

| Species                         | Comparison        | 2014     |       |                |              | 2015     |       |                |              |
|---------------------------------|-------------------|----------|-------|----------------|--------------|----------|-------|----------------|--------------|
|                                 |                   | Estimate | SE    | <i>t</i> ratio | <i>p</i>     | Estimate | SE    | <i>t</i> ratio | <i>p</i>     |
| <b>Plant- and leafhoppers</b>   |                   |          |       |                |              |          |       |                |              |
| <i>Japananus hyalinus</i>       | Sycamore - Norway | -        | -     | -              | -            | 0.126    | 0.113 | 1.115          | 0.509        |
|                                 | Sycamore - Field  | -        | -     | -              | -            | -0.261   | 0.113 | -2.319         | 0.062        |
|                                 | Norway - Field    | -        | -     | -              | -            | -0.387   | 0.113 | -3.434         | <b>0.003</b> |
| <i>Latilica maculipes</i>       | Sycamore - Norway | -        | -     | -              | -            | -0.143   | 0.092 | -1.548         | 0.277        |
|                                 | Sycamore - Field  | -        | -     | -              | -            | -0.066   | 0.092 | -0.712         | 0.757        |
|                                 | Norway - Field    | -        | -     | -              | -            | 0.077    | 0.092 | 0.836          | 0.682        |
| <i>Zyginella pulchra</i>        | Sycamore - Norway | -        | -     | -              | -            | -0.402   | 0.075 | -5.374         | <b>0.000</b> |
|                                 | Sycamore - Field  | -        | -     | -              | -            | -0.030   | 0.075 | -0.403         | 0.915        |
|                                 | Norway - Field    | -        | -     | -              | -            | 0.372    | 0.075 | 4.972          | <b>0.000</b> |
| <b>Heteropterans</b>            |                   |          |       |                |              |          |       |                |              |
| <i>Gonocerus acuteangulatus</i> | Sycamore - Norway | -0.533   | 0.119 | -4.472         | <b>0.000</b> | -0.300   | 0.069 | -4.375         | <b>0.000</b> |
|                                 | Sycamore - Field  | -0.472   | 0.119 | -3.966         | <b>0.001</b> | -0.402   | 0.069 | -5.843         | <b>0.000</b> |
|                                 | Norway - Field    | 0.060    | 0.119 | 0.506          | 0.869        | -0.102   | 0.095 | -1.074         | 0.522        |
| <i>Halyomorpha halys</i>        | Sycamore - Norway | -        | -     | -              | -            | -0.041   | 0.139 | -0.293         | 0.954        |
|                                 | Sycamore - Field  | -        | -     | -              | -            | 0.010    | 0.139 | 0.072          | 0.997        |
|                                 | Norway - Field    | -        | -     | -              | -            | 0.051    | 0.139 | 0.365          | 0.929        |
| <i>Nezara viridula</i>          | Sycamore - Norway | -0.234   | 0.183 | -1.278         | 0.419        | -0.121   | 0.087 | -1.391         | 0.353        |
|                                 | Sycamore - Field  | -0.657   | 0.183 | -3.593         | <b>0.003</b> | -0.269   | 0.087 | -3.082         | <b>0.009</b> |
|                                 | Norway - Field    | -0.423   | 0.183 | -2.316         | 0.069        | -0.148   | 0.087 | -1.691         | 0.218        |
| <i>Palomena prasina</i>         | Sycamore - Norway | -0.163   | 0.098 | -1.661         | 0.237        | -0.159   | 0.091 | -1.755         | 0.195        |
|                                 | Sycamore - Field  | -0.097   | 0.098 | -0.983         | 0.593        | 0.060    | 0.091 | 0.665          | 0.785        |
|                                 | Norway - Field    | 0.067    | 0.098 | 0.678          | 0.778        | 0.219    | 0.091 | 2.419          | <b>0.049</b> |
| <b>Psyllids</b>                 |                   |          |       |                |              |          |       |                |              |
| <i>Capopsylla pulchella</i>     | Sycamore - Norway | -0.027   | 0.151 | -0.176         | 0.983        | -        | -     | -              | -            |
|                                 | Sycamore - Field  | 0.224    | 0.151 | 1.485          | 0.312        | -        | -     | -              | -            |
|                                 | Norway - Field    | 0.250    | 0.151 | 1.661          | 0.237        | -        | -     | -              | -            |

Table S1.3. continued.

| Species                    | Comparison        | 2014     |       |                |              | 2015     |       |                |              |
|----------------------------|-------------------|----------|-------|----------------|--------------|----------|-------|----------------|--------------|
|                            |                   | Estimate | SE    | <i>t</i> ratio | <i>p</i>     | Estimate | SE    | <i>t</i> ratio | <i>p</i>     |
| <b>Psyllids</b>            |                   |          |       |                |              |          |       |                |              |
| <i>Rhinocola aceris</i>    | Sycamore - Norway | -        | -     | -              | -            | 0.054    | 0.101 | 0.535          | 0.854        |
|                            | Sycamore - Field  | -        | -     | -              | -            | -0.287   | 0.101 | -2.845         | <b>0.017</b> |
|                            | Norway - Field    | -        | -     | -              | -            | -0.341   | 0.101 | -3.380         | <b>0.004</b> |
| <b>Curculionids</b>        |                   |          |       |                |              |          |       |                |              |
| <i>Bradybatus kellneri</i> | Sycamore - Norway | -0.325   | 0.124 | -2.634         | <b>0.032</b> | -        | -     | -              | -            |
|                            | Sycamore - Field  | 0.018    | 0.072 | 0.257          | 0.963        | -        | -     | -              | -            |
|                            | Norway - Field    | 0.344    | 0.125 | 2.751          | <b>0.025</b> | -        | -     | -              | -            |
| <i>Phyllobius oblongus</i> | Sycamore - Norway | -0.226   | 0.177 | -1.276         | 0.419        | -0.152   | 0.109 | -1.392         | 0.347        |
|                            | Sycamore - Field  | -0.534   | 0.177 | -3.010         | <b>0.014</b> | -0.222   | 0.079 | -2.808         | <b>0.018</b> |
|                            | Norway - Field    | -0.308   | 0.177 | -1.734         | 0.209        | -0.070   | 0.096 | -0.729         | 0.744        |

Table S1.4. Characteristic phytophagous insect species of each maple tree species using IndVal approach. The ‘IndVal’ column shows the species character value and ‘Max. value’ column shows maple species for which insect species displayed the highest IndVal value. Numbers in bold indicate significant ( $p < 0.05$ ) and numbers in italics indicate marginally significant ( $p \geq 0.05$  and  $p < 0.1$ )  $p$  values.

| Abbreviation                  | Species name                     | IndVal | Max. value | $p$          |
|-------------------------------|----------------------------------|--------|------------|--------------|
| <b>Aphids</b>                 |                                  |        |            |              |
| D.ace                         | <i>Drepanosiphum aceris</i>      | 0.401  | Field      | <b>0.003</b> |
| D.pla                         | <i>Drepanosiphum platanoidis</i> | 0.739  | Sycamore   | <b>0.001</b> |
| P.aco                         | <i>Periphyllus acericola</i>     | 0.567  | Sycamore   | <b>0.001</b> |
| P.ace                         | <i>Periphyllus aceris</i>        | 0.271  | Sycamore   | 0.082        |
| P.obs                         | <i>Periphyllus obscurus</i>      | 0.539  | Field      | <b>0.001</b> |
| P.tes                         | <i>Periphyllus testudinaceus</i> | 0.361  | Field      | 0.282        |
| <b>Plant- and leafhoppers</b> |                                  |        |            |              |
| M.pru                         | <i>Metcalfa pruinosa</i>         | 0.352  | Field      | 0.258        |
| A.rib*                        | <i>Acericerus ribauti</i>        | 0.405  | Field      | <b>0.026</b> |
| J.hya*                        | <i>Japananus hyalinus</i>        | 0.423  | Field      | <b>0.003</b> |
| L.mac*                        | <i>Latilica maculipes</i>        | 0.327  | Norway     | 0.058        |
| Z.pul*                        | <i>Zyginella pulchra</i>         | 0.576  | Norway     | <b>0.001</b> |
| <b>Heteropterans</b>          |                                  |        |            |              |
| G.acu                         | <i>Gonocerus acuteangulatus</i>  | 0.444  | Field      | <b>0.006</b> |
| H.hal                         | <i>Halyomorpha halys</i>         | 0.343  | Norway     | 0.683        |
| N.vir                         | <i>Nezara viridula</i>           | 0.385  | Field      | <b>0.044</b> |
| P.pra                         | <i>Palomena prasina</i>          | 0.375  | Norway     | 0.158        |
| <b>Psyllids</b>               |                                  |        |            |              |
| C.pul                         | <i>Caposylla pulchella</i>       | 0.204  | Norway     | 0.496        |
| R.ace                         | <i>Rhinocola aceris</i>          | 0.444  | Field      | <b>0.009</b> |
| <b>Curculionids</b>           |                                  |        |            |              |
| B.kell                        | <i>Bradybatus kellneri</i>       | 0.356  | Norway     | <b>0.002</b> |
| P.obl                         | <i>Phyllobius oblongus</i>       | 0.398  | Field      | 0.055        |

\* Data were available only for the year 2015.

Table S1.5. Results of pairwise comparisons of least square mean values for POD enzymatic activity (obtained from GLMM), degree of leaf fall, and necrosis (obtained from CLMMs) between maple species. Numbers in bold indicate significant ( $p < 0.05$ )  $p$  values (with Tukey's correction).

| Variable*     | Comparison        | Estimate | SE    | $t/z$ ratio** | $p$          |
|---------------|-------------------|----------|-------|---------------|--------------|
| POD activity  | Sycamore - Norway | -0.057   | 0.054 | -1.069        | 0.537        |
|               | Sycamore - Field  | 0.043    | 0.054 | 0.804         | 0.702        |
|               | Norway - Field    | 0.100    | 0.054 | 1.874         | 0.156        |
| Leaf fall     | Sycamore - Norway | -0.618   | 0.583 | -1.059        | 0.540        |
|               | Sycamore - Field  | -0.747   | 0.560 | -1.333        | 0.377        |
|               | Norway - Field    | -0.129   | 0.564 | -0.228        | 0.972        |
| Leaf necrosis | Sycamore - Norway | -1.600   | 0.645 | -2.478        | <b>0.035</b> |
|               | Sycamore - Field  | 3.290    | 0.873 | 3.774         | <b>0.001</b> |
|               | Norway - Field    | 4.890    | 0.963 | 5.081         | <b>0.000</b> |

\* POD activity: log-transformed data.

\*\* POD activity:  $t$  ratio, leaf fall and necrosis:  $z$  ratio.

Table S1.6. Results of the GLMMs for the POD enzymatic activity (log-transformed data) of sycamore, Norway, and field maple trees depending on the abundance of aphids, *Metcalfa pruinosa*, other (non-*M. pruinosa*) plant- and leafhoppers, and heteropterans. A random variable = (1|site) was added to the intercept of all models, but only fixed effects are reported here. Numbers in bold indicate significant (< 0.05) *p* values.

| Maple species  | Explanatory variable         | Estimate | SE    | <i>t</i> | Adj. <i>p</i> * | Unadj. <i>p</i> |
|----------------|------------------------------|----------|-------|----------|-----------------|-----------------|
| Sycamore maple | <i>M. pruinosa</i>           | 0.001    | 0.000 | 3.320    | <b>0.034</b>    | <b>0.005</b>    |
|                | Other plant- and leafhoppers | 0.005    | 0.005 | 1.016    | 0.559           | 0.326           |
|                | Aphids                       | 0.000    | 0.001 | -0.354   | 0.878           | 0.728           |
|                | Heteropterans                | 0.016    | 0.006 | 2.835    | 0.050           | <b>0.013</b>    |
| Norway maple   | <i>M. pruinosa</i>           | 0.000    | 0.000 | 0.349    | 0.878           | 0.732           |
|                | Other plant- and leafhoppers | 0.005    | 0.004 | 1.110    | 0.559           | 0.285           |
|                | Aphids                       | 0.001    | 0.022 | 0.026    | 0.979           | 0.979           |
|                | Heteropterans                | -0.001   | 0.006 | -0.133   | 0.977           | 0.896           |
| Field maple    | <i>M. pruinosa</i>           | 0.000    | 0.000 | 3.219    | <b>0.034</b>    | <b>0.006</b>    |
|                | Other plant- and leafhoppers | 0.002    | 0.001 | 1.396    | 0.439           | 0.183           |
|                | Aphids                       | 0.004    | 0.005 | 0.757    | 0.691           | 0.461           |
|                | Heteropterans                | 0.009    | 0.005 | 1.714    | 0.321           | 0.107           |

\* Benjamini-Hochberg correction.



Table S1.7. Results of the CLMMs for the degree of leaf fall and necrosis of maple trees depending on the abundance of aphids, *Metcalfa pruinosa*, other (non-*M. pruinosa*) plant- and leafhoppers, and heteropterans. Random variables = (1|site) and (1|tree\_species) were added to the intercept of all models, but only fixed effects are reported here. Number in bold indicate significant ( $< 0.05$ )  $p$  value.

| Explanatory variable         | Response variable | Estimate* | SE    | $z$    | Adj. $p^{**}$ | Unadj. $p$   |
|------------------------------|-------------------|-----------|-------|--------|---------------|--------------|
| <i>M. pruinosa</i>           | Leaf fall         | -0.002    | 0.001 | -2.198 | 0.223         | <b>0.028</b> |
| Other plant- and leafhoppers |                   | 0.008     | 0.011 | 0.724  | 0.723         | 0.469        |
| Aphids                       |                   | -0.013    | 0.009 | -1.529 | 0.504         | 0.126        |
| Heteropterans                |                   | -0.005    | 0.009 | -0.500 | 0.723         | 0.617        |
| <i>M. pruinosa</i>           | Leaf necrosis     | -0.001    | 0.002 | -0.478 | 0.723         | 0.633        |
| Other plant- and leafhoppers |                   | 0.015     | 0.014 | 1.040  | 0.723         | 0.298        |
| Aphids                       |                   | -0.008    | 0.015 | -0.514 | 0.723         | 0.607        |
| Heteropterans                |                   | 0.004     | 0.011 | 0.341  | 0.733         | 0.733        |

\* Positive value means advanced leaf fall and necrosis with increasing abundance of phytophagous groups or species.

\*\* Benjamini-Hochberg correction.

Supplementary material for STUDY III

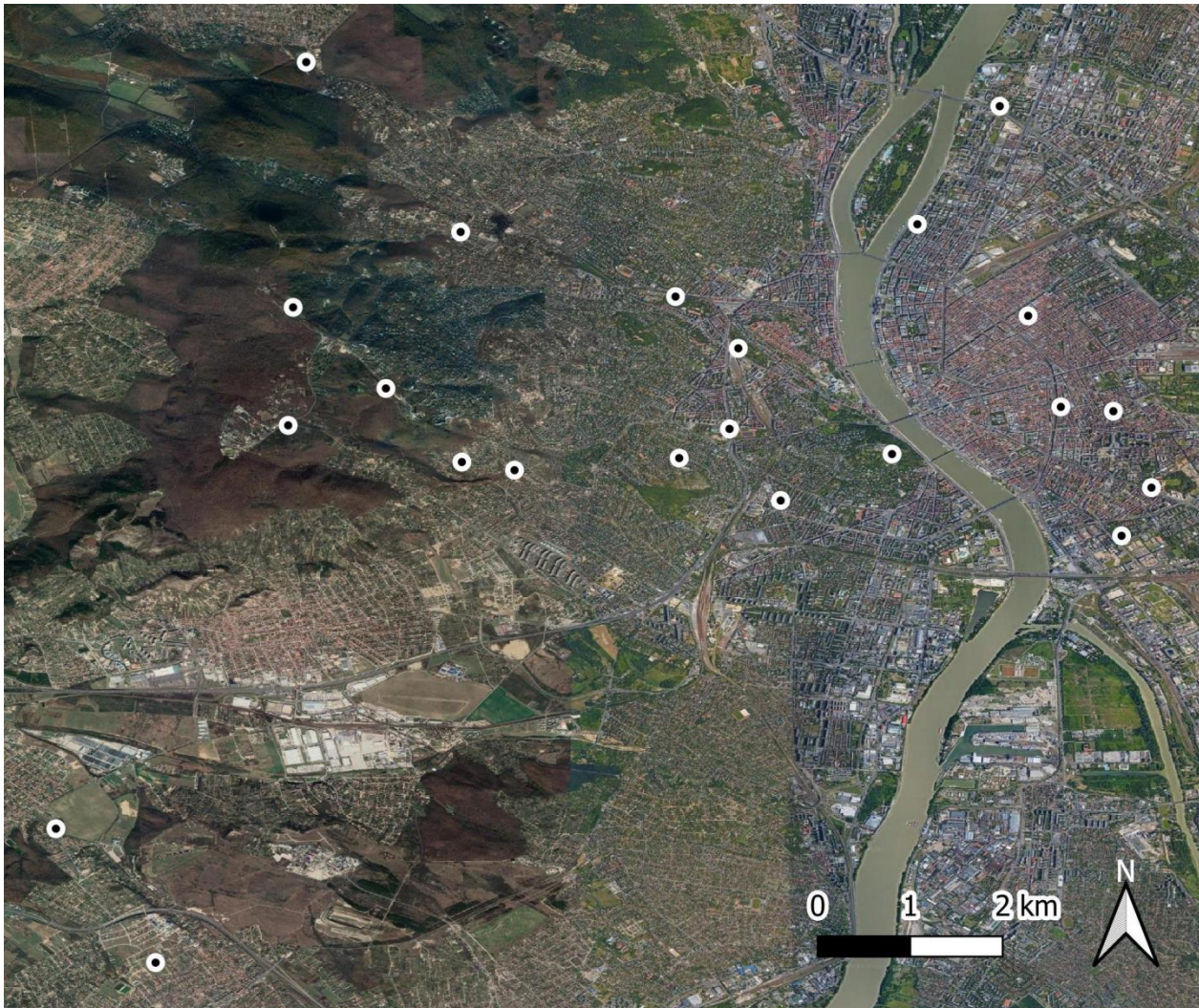


Figure S2.1. Study site locations ( $n = 22$ ) in and near the city of Budapest, Hungary. Aerial image was obtained from Google Earth.

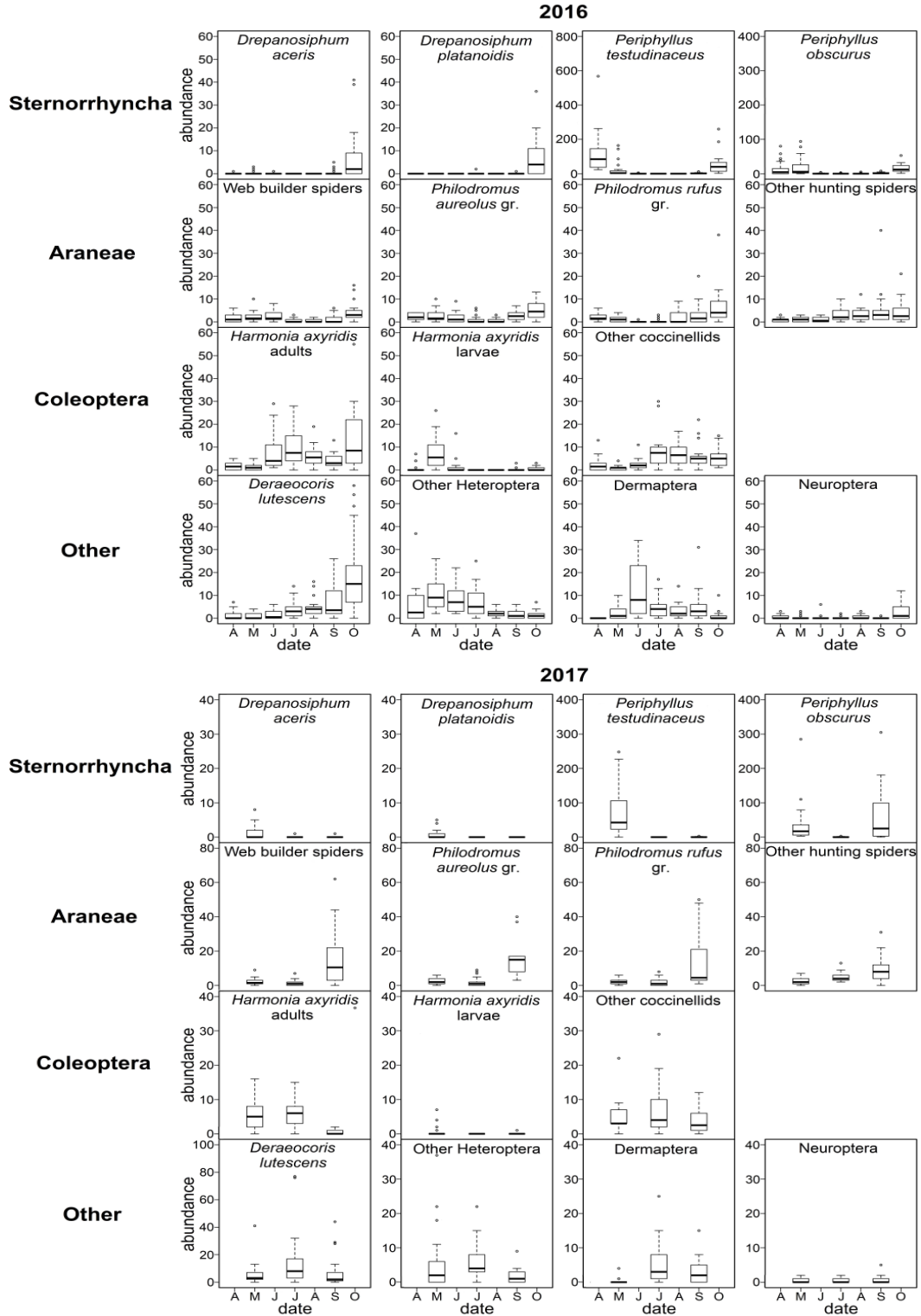


Figure S2.2. Monthly abundance of the most abundant aphid and predator species and predator groups in 2016 and 2017. The predator groups are as in Fig. 21. Boxplots show medians, lower, and upper quartiles, whiskers include the range of data without outliers. Note the different scales on the y-axes.

## Sternorrhyncha

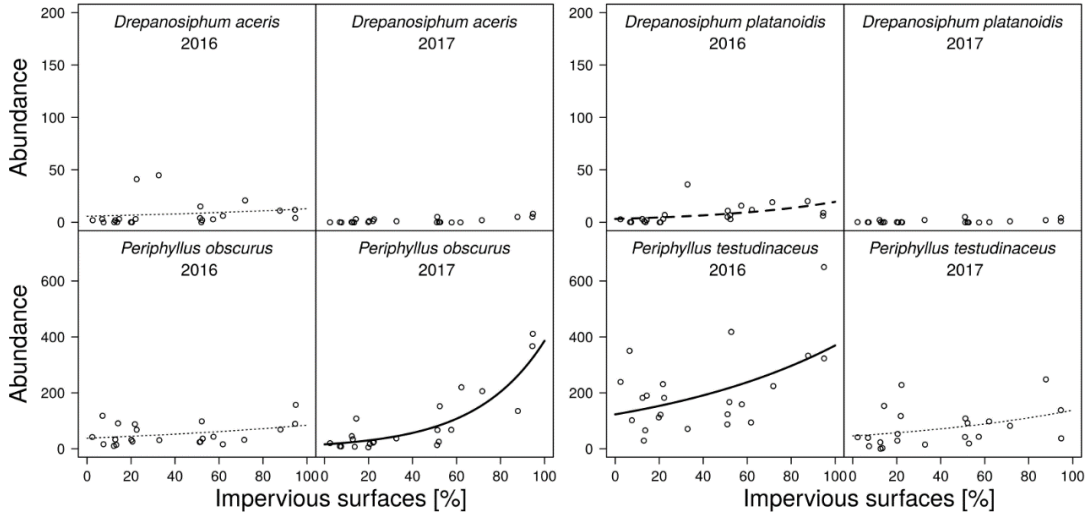
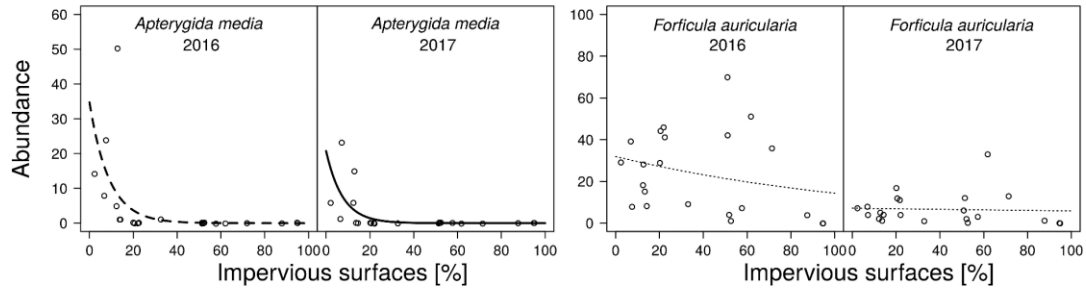


Figure S2.3. Effect of impervious surface percentage on the abundance of aphid species in 2016 and 2017. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted  $p$  values). In plots without lines, the number of individuals was insufficient for statistical analysis. Fitted lines are from quasi-Poisson GLMs. Note the different scales on the y-axes.

### Dermaptera



### Heteroptera

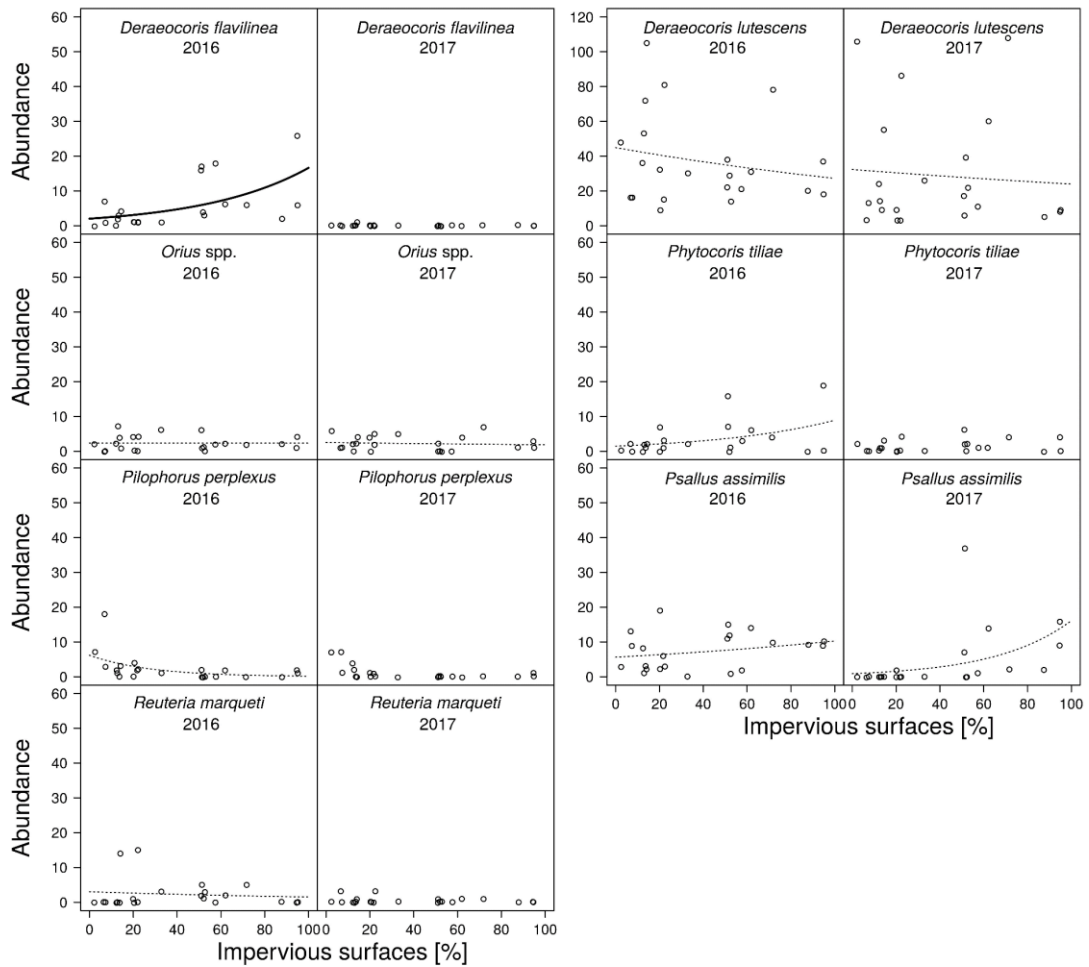
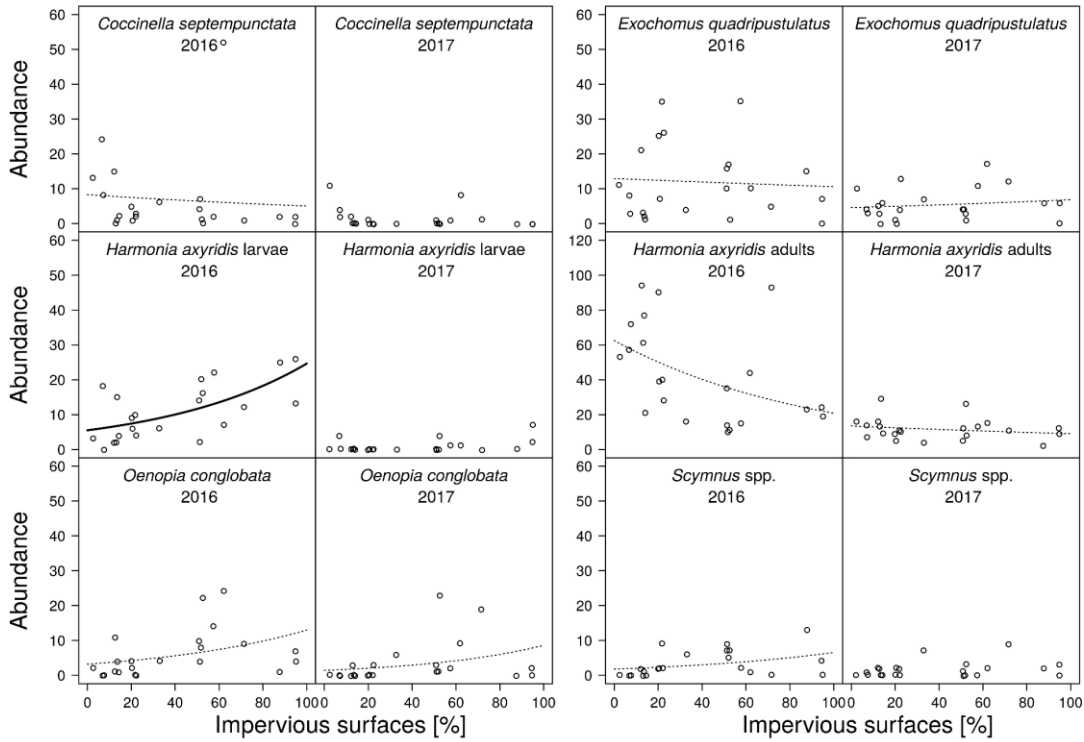


Figure S2.4. Effect of impervious surface percentage on the abundance of earwig and predatory true bug taxa in 2016 and 2017. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted  $p$  values). In plots without lines, the number of individuals was insufficient for statistical analysis. Fitted lines are from quasi-Poisson GLMs. Note the different scales on the y-axes.

## Coleoptera



## Neuroptera

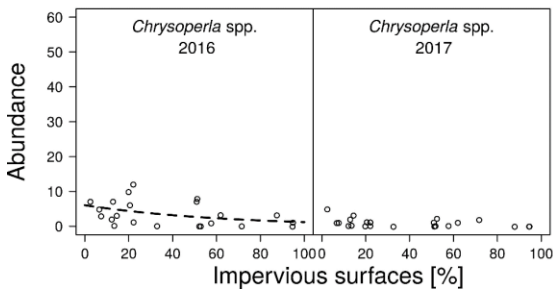


Figure S2.5. Effect of impervious surface percentage on the abundance of predatory ladybird and lacewing taxa in 2016 and 2017. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted  $p$  values). In plots without lines, the number of individuals was insufficient for statistical analysis. Fitted lines are from quasi-Poisson GLMs. Note the different scales on the y-axes.

## Araneae

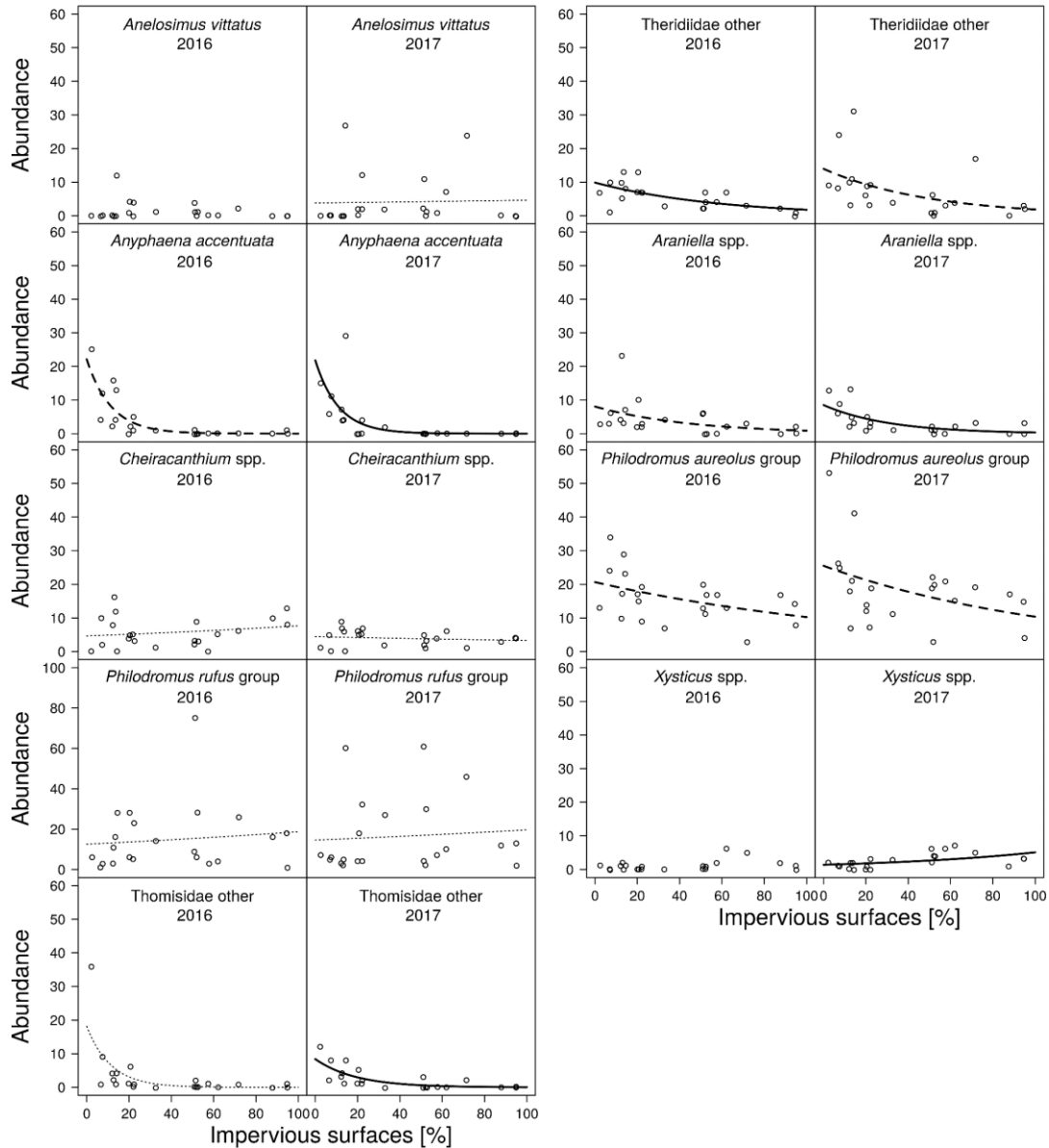


Figure S2.6. Effect of impervious surface percentage on the abundance of spider taxa in 2016 and 2017. Continuous lines indicate significant ( $p < 0.05$ ), dashed lines indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ ), and thin dotted lines indicate non-significant ( $p \geq 0.1$ ) effect of impervious surfaces (based on adjusted p values). In plots without lines, the number of individuals was insufficient for statistical analysis. Fitted lines are from quasi-Poisson GLMs. Note the different scales on the y-axes.

Table S2.1. List of predator species (arranged by the groups used in the NMDS analyses), their yearly and total abundance across all trees and sites, and dispersal trait values (see Figs. 20 and 21).

| Group/family                 | Species                                    | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance | Dispersal<br>ability |
|------------------------------|--|----------------------|----------------------|--------------------|----------------------|
| <b>Dermaptera</b>            |  |                      |                      |                    |                      |
| Forficulidae                 | <i>Apterygida media</i>                    | 104                  | 47                   | 151                | 0.00                 |
|                              | <i>Chelidurella acanthopygia</i>           | 5                    | 0                    | 5                  | 0.00                 |
|                              | <i>Forficula auricularia</i>               | 529                  | 146                  | 675                | 0.00                 |
| <i>Deraeocoris lutescens</i> | <i>Deraeocoris lutescens</i>               | 821                  | 629                  | 1450               | 1.00                 |
| <b>Other heteropterans</b>   |  |                      |                      |                    |                      |
| Anthocoridae                 | <i>Amphiareus obscuriceps</i>              | 1                    | 2                    | 3                  | 1.00                 |
|                              | <i>Anthocoris nemoralis</i>                | 13                   | 14                   | 27                 | 1.00                 |
|                              | <i>Cardiastethus fasciiventris</i>         | 3                    | 9                    | 12                 | 1.00                 |
|                              | <i>Orius horvathi</i>                      | 2                    | 1                    | 3                  | 1.00                 |
|                              | <i>Orius majusculus</i>                    | 1                    | 0                    | 1                  | 1.00                 |
|                              | <i>Orius minutus</i>                       | 3                    | 0                    | 3                  | 1.00                 |
|                              | <i>Orius minutus/vicinus</i>               | 32                   | 39                   | 71                 | 1.00                 |
|                              | <i>Orius niger</i>                         | 3                    | 2                    | 5                  | 1.00                 |
|                              | <i>Orius vicinus</i>                       | 7                    | 2                    | 9                  | 1.00                 |
|                              | <i>Orius</i> sp.                           | 1                    | 3                    | 4                  | 1.00                 |
| Miridae                      | <i>Agnocoris reclairei</i>                 | 8                    | 3                    | 11                 | 1.00                 |
|                              | <i>Campyloneura virgula</i>                | 16                   | 2                    | 18                 | 1.00                 |
|                              | <i>Closterotomus biclavatus</i>            | 17                   | 0                    | 17                 | 1.00                 |
|                              | <i>Closterotomus fulvomaculatus</i>        | 4                    | 1                    | 5                  | 1.00                 |
|                              | <i>Closterotomus</i> sp.                   | 2                    | 2                    | 4                  | 1.00                 |
|                              | <i>Deraeocoris flavilinea</i>              | 126                  | 1                    | 127                | 1.00                 |
|                              | <i>Deraeocoris ruber</i>                   | 12                   | 6                    | 18                 | 1.00                 |
|                              | <i>Deraeocoris</i> sp.                     | 33                   | 0                    | 33                 | 1.00                 |
|                              | <i>Deraeocoris trifasciatus</i>            | 2                    | 0                    | 2                  | 1.00                 |
|                              | <i>Dryophilocoris flavoquadrimaculatus</i> | 14                   | 2                    | 16                 | 1.00                 |
|                              | <i>Globiceps sphaegiformis</i>             | 3                    | 0                    | 3                  | 0.50                 |
|                              | <i>Grypocoris sexguttatus</i>              | 1                    | 0                    | 1                  | 1.00                 |
|                              | <i>Heterotoma planicornis</i>              | 10                   | 0                    | 10                 | 1.00                 |
|                              | <i>Malacocoris chlorizans</i>              | 21                   | 2                    | 23                 | 1.00                 |
|                              | <i>Megacoelum beckeri</i>                  | 3                    | 0                    | 3                  | 1.00                 |
|                              | <i>Mermitelocerus schmidtii</i>            | 1                    | 0                    | 1                  | 1.00                 |
|                              | <i>Miris striatus</i>                      | 15                   | 1                    | 16                 | 1.00                 |
|                              | <i>Orthotylus nassatus</i>                 | 5                    | 0                    | 5                  | 1.00                 |
|                              | <i>Phytocoris tiliae</i>                   | 76                   | 31                   | 107                | 1.00                 |
|                              | <i>Phytocoris ulmi</i>                     | 3                    | 0                    | 3                  | 0.75                 |
| <i>Phytocoris varipes</i>    | 1  | 0                    | 1                    | 0.75               |                      |
| <i>Pilophorus perplexus</i>  | 50   | 24                   | 74                   | 1.00               |                      |
| <i>Psallus assimilis</i>     | 101  | 90                   | 191                  | 1.00               |                      |



Table S2.1. continued.

| Group/family                    | Species                              | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance | Dispersal<br>ability |
|---------------------------------|--------------------------------------|----------------------|----------------------|--------------------|----------------------|
| Miridae                         | <i>Psallus perrisi</i>               | 1                    | 0                    | 1                  | 1.00                 |
|                                 | <i>Psallus perrisi/wagneri</i>       | 4                    | 0                    | 4                  | 1.00                 |
|                                 | <i>Psallus</i> sp.                   | 62                   | 16                   | 78                 | 1.00                 |
|                                 | <i>Psallus wagneri</i>               | 3                    | 0                    | 3                  | 1.00                 |
|                                 | <i>Reuteria marqueti</i>             | 47                   | 10                   | 57                 | 1.00                 |
|                                 | <i>Rhabdomiris striatellus</i>       | 22                   | 0                    | 22                 | 1.00                 |
| Nabidae                         | <i>Himacerus apterus</i>             | 18                   | 7                    | 25                 | 0.25                 |
|                                 | <i>Himacerus mirmicoides</i>         | 14                   | 7                    | 21                 | 0.25                 |
|                                 | <i>Himacerus</i> sp.                 | 1                    | 0                    | 1                  | 0.25                 |
|                                 | <i>Nabis pseudoferus</i>             | 1                    | 0                    | 1                  | 1.00                 |
|                                 | <i>Nabis rugosus</i>                 | 1                    | 0                    | 1                  | 0.75                 |
|                                 | <i>Nabis</i> sp.                     | 1                    | 0                    | 1                  | 0.88                 |
| Reduviidae                      | <i>Nagusta goedelii</i>              | 43                   | 18                   | 61                 | 1.00                 |
| <b>Harmonia axyridis adults</b> |                                      |                      |                      |                    |                      |
| Coccinellidae                   | <i>Harmonia axyridis</i> adults      | 936                  | 248                  | 1184               | 1.00                 |
| <b>Harmonia axyridis larvae</b> |                                      |                      |                      |                    |                      |
| Coccinellidae                   | <i>Harmonia axyridis</i> larvae      | 236                  | 19                   | 255                | 1.00                 |
| <b>Other coccinellids</b>       |                                      |                      |                      |                    |                      |
| Coccinellidae                   | <i>Adalia bipunctata</i>             | 23                   | 23                   | 46                 | 1.00                 |
|                                 | <i>Adalia decempunctata</i>          | 29                   | 20                   | 49                 | 1.00                 |
|                                 | <i>Anatis ocellata</i>               | 0                    | 1                    | 1                  | 1.00                 |
|                                 | <i>Calvia quatuordecimguttata</i>    | 11                   | 7                    | 18                 | 1.00                 |
|                                 | <i>Chilocorus bipustulatus</i>       | 1                    | 2                    | 3                  | 1.00                 |
|                                 | <i>Chilocorus renipustulatus</i>     | 7                    | 3                    | 10                 | 1.00                 |
|                                 | <i>Coccinella septempunctata</i>     | 151                  | 31                   | 182                | 1.00                 |
|                                 | <i>Exochomus quadripustulatus</i>    | 262                  | 119                  | 381                | 1.00                 |
|                                 | <i>Hippodamia variegata</i>          | 3                    | 0                    | 3                  | 1.00                 |
|                                 | <i>Hyperaspis</i> sp.                | 1                    | 0                    | 1                  | 1.00                 |
|                                 | <i>Nephus quadrimaculatus</i>        | 8                    | 8                    | 16                 | 1.00                 |
|                                 | <i>Oenopia conglobata</i>            | 132                  | 72                   | 204                | 1.00                 |
|                                 | <i>Oenopia lyncea</i>                | 4                    | 1                    | 5                  | 1.00                 |
|                                 | <i>Propylea quatuordecimpunctata</i> | 20                   | 34                   | 54                 | 1.00                 |
|                                 | <i>Scymniscus horioni</i>            | 0                    | 1                    | 1                  | 1.00                 |
|                                 | <i>Scymnus abietis</i>               | 1                    | 0                    | 1                  | 1.00                 |
|                                 | <i>Scymnus frontalis</i>             | 5                    | 5                    | 10                 | 1.00                 |
|                                 | <i>Scymnus interruptus</i>           | 32                   | 18                   | 50                 | 1.00                 |
| <i>Scymnus rubromaculatus</i>   | 18                                   | 6                    | 24                   | 1.00               |                      |
| <i>Scymnus subvillosus</i>      | 16                                   | 7                    | 23                   | 1.00               |                      |
| <b>Neuroptera</b>               |                                      |                      |                      |                    |                      |
| Chrysopidae                     | <i>Chrysopa phyllochroma</i>         | 1                    | 0                    | 1                  | 1.00                 |

Table S2.1. continued.

| Group/family                | Species                         | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance | Dispersal<br>Ability |
|-----------------------------|---------------------------------|----------------------|----------------------|--------------------|----------------------|
| Chrysopidae                 | <i>Chrysopa</i> sp.             | 6                    | 1                    | 7                  | 1.00                 |
|                             | <i>Chrysoperla carnea</i>       | 41                   | 10                   | 51                 | 1.00                 |
|                             | <i>Chrysoperla lucasina</i>     | 6                    | 0                    | 6                  | 1.00                 |
|                             | <i>Chrysoperla mediterranea</i> | 1                    | 0                    | 1                  | 1.00                 |
|                             | <i>Chrysoperla pallida</i>      | 31                   | 10                   | 41                 | 1.00                 |
|                             | <i>Hypochrysa elegans</i>       | 3                    | 0                    | 3                  | 1.00                 |
|                             | <i>Peyerimhoffina gracilis</i>  | 1                    | 0                    | 1                  | 1.00                 |
|                             | <i>Pseudomallada prasinus</i>   | 2                    | 1                    | 3                  | 1.00                 |
|                             | <i>Pseudomallada</i> sp.        | 2                    | 1                    | 3                  | 1.00                 |
| Hemerobiidae                | <i>Hemerobius humulinus</i>     | 3                    | 1                    | 4                  | 1.00                 |
|                             | <i>Hemerobius perelegans</i>    | 1                    | 0                    | 1                  | 1.00                 |
|                             | <i>Hemerobius pini</i>          | 0                    | 1                    | 1                  | 1.00                 |
|                             | <i>Hemerobius</i> sp.           | 1                    | 0                    | 1                  | 1.00                 |
|                             | <i>Micromus angulatus</i>       | 3                    | 1                    | 4                  | 1.00                 |
|                             | <i>Symphherobius elegans</i>    | 5                    | 8                    | 13                 | 1.00                 |
| <b>Web building spiders</b> |                                 |                      |                      |                    |                      |
| Agelenidae                  | <i>Allagelena gracilens</i>     | 1                    | 0                    | 1                  | 0.25                 |
| Araneidae                   | Araneidae sp.                   | 3                    | 0                    | 3                  | NA                   |
|                             | <i>Araneus</i> sp.              | 5                    | 2                    | 7                  | NA                   |
|                             | <i>Araniella cucurbitina</i>    | 12                   | 0                    | 12                 | 1.00                 |
|                             | <i>Araniella opisthographa</i>  | 3                    | 7                    | 10                 | 0.75                 |
|                             | <i>Araniella</i> sp.            | 74                   | 67                   | 141                | 0.89                 |
|                             | <i>Cyclosa conica</i>           | 1                    | 0                    | 1                  | 0.75                 |
|                             | <i>Gibbaranea gibbosa</i>       | 6                    | 0                    | 6                  | 0.00                 |
|                             | <i>Gibbaranea</i> sp.           | 1                    | 1                    | 2                  | 0.00                 |
|                             | <i>Nuctenea umbratica</i>       | 0                    | 1                    | 1                  | 1.00                 |
|                             | <i>Zilla diodia</i>             | 1                    | 3                    | 4                  | 0.25                 |
|                             | Dictynidae                      | <i>Brigittea</i> sp. | 0                    | 11                 | 11                   |
| <i>Brigittea vicina</i>     |                                 | 6                    | 2                    | 8                  | 0.25                 |
| <i>Dictyna arundinacea</i>  |                                 | 1                    | 0                    | 1                  | 0.50                 |
| <i>Dictyna</i> sp.          |                                 | 2                    | 0                    | 2                  | 0.50                 |
| Dictynidae sp.              |                                 | 2                    | 2                    | 4                  | NA                   |
| <i>Lathys humilis</i>       |                                 | 7                    | 11                   | 18                 | 0.50                 |
| <i>Nigma flavescens</i>     |                                 | 2                    | 3                    | 5                  | 0.75                 |
| <i>Nigma</i> sp.            |                                 | 7                    | 5                    | 12                 | 0.75                 |
| <i>Nigma walckenaeri</i>    |                                 | 1                    | 1                    | 2                  | 0.75                 |
| Hahniidae                   | <i>Hahnia nava</i>              | 0                    | 1                    | 1                  | 0.00                 |
| Linyphiidae                 | <i>Agyneta rurestris</i>        | 1                    | 2                    | 3                  | 1.00                 |
|                             | <i>Frontinellina frutetorum</i> | 0                    | 2                    | 2                  | 0.25                 |
|                             | Linyphiidae sp.                 | 1                    | 1                    | 2                  | NA                   |
|                             | <i>Porrhomma microphthalmum</i> | 1                    | 0                    | 1                  | 1.00                 |
|                             | <i>Tenuiphantes flavipes</i>    | 1                    | 0                    | 1                  | 0.75                 |

Table S2.1. continued.

| Group/family                        | Species                                | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance | Dispersal<br>ability |
|-------------------------------------|--|----------------------|----------------------|--------------------|----------------------|
| Linyphiidae                         | <i>Tenuiphantes tenuis</i>             | 1                    | 0                    | 1                  | 1.00                 |
| Tetragnathidae                      | <i>Pachygnatha</i> sp.                 | 0                    | 1                    | 1                  | NA                   |
|                                     | <i>Tetragnatha obtusa</i>              | 0                    | 1                    | 1                  | 0.75                 |
|                                     | <i>Tetragnatha</i> sp.                 | 1                    | 5                    | 6                  | 0.75                 |
|                                     | Tetragnathidae sp.                     | 0                    | 1                    | 1                  | NA                   |
| Theridiidae                         | <i>Anelosimus vittatus</i>             | 30                   | 91                   | 121                | 0.50                 |
|                                     | <i>Asagena phalerata</i>               | 0                    | 1                    | 1                  | 0.75                 |
|                                     | <i>Dipoena melanogaster</i>            | 12                   | 9                    | 21                 | 0.25                 |
|                                     | <i>Enoplognatha latimana</i>           | 1                    | 1                    | 2                  | 0.50                 |
|                                     | <i>Heterotheridion nigrovariegatum</i> | 31                   | 7                    | 38                 | 0.25                 |
|                                     | <i>Neottiura bimaculata</i>            | 1                    | 4                    | 5                  | 1.00                 |
|                                     | <i>Paidiscura pallens</i>              | 6                    | 37                   | 43                 | 0.75                 |
|                                     | <i>Parasteatoda tepidariorum</i>       | 3                    | 0                    | 3                  | 0.50                 |
|                                     | <i>Platnickina tincta</i>              | 4                    | 22                   | 26                 | 0.75                 |
|                                     | <i>Phylloneta impressa</i>             | 2                    | 1                    | 3                  | 0.75                 |
|                                     | <i>Phylloneta</i> sp.                  | 14                   | 27                   | 41                 | 0.75                 |
|                                     | <i>Simitidion simile</i>               | 0                    | 1                    | 1                  | 0.50                 |
|                                     | <i>Steatoda bipunctata</i>             | 1                    | 0                    | 1                  | 0.50                 |
|                                     | <i>Theridion mystaceum</i>             | 1                    | 1                    | 2                  | 0.50                 |
|                                     | <i>Theridion pinastris</i>             | 16                   | 4                    | 20                 | 0.75                 |
|                                     | <i>Theridion varians</i>               | 2                    | 0                    | 2                  | 0.75                 |
|                                     | <i>Theridion</i> sp.                   | 27                   | 39                   | 66                 | 0.73                 |
|                                     | Theridiidae sp.                        | 2                    | 10                   | 12                 | NA                   |
|                                     | <b><i>Philodromus aureolus</i> gr.</b> |                      |                      |                    |                      |
| Philodromidae                       | <i>Philodromus collinus</i>            | 1                    | 0                    | 1                  | 0.75                 |
|                                     | <i>Philodromus longipalpis</i>         | 1                    | 0                    | 1                  | 0.75                 |
|                                     | <i>Philodromus praedatus</i>           | 9                    | 0                    | 9                  | 0.50                 |
|                                     | <i>Philodromus</i> sp.                 | 327                  | 414                  | 741                | 0.55                 |
| <b><i>Philodromus rufus</i> gr.</b> |  |                      |                      |                    |                      |
| Philodromidae                       | <i>Philodromus albidus</i>             | 8                    | 0                    | 8                  | 0.75                 |
|                                     | <i>Philodromus rufus</i>               | 28                   | 17                   | 45                 | 0.75                 |
|                                     | <i>Philodromus</i> sp.                 | 296                  | 343                  | 639                | 0.75                 |
| <b>Other hunting spiders</b>        |  |                      |                      |                    |                      |
| Anyphaenidae                        | <i>Anyphaena accentuata</i>            | 87                   | 82                   | 169                | 1.00                 |
| Clubionidae                         | <i>Clubiona brevipes</i>               | 1                    | 0                    | 1                  | 0.50                 |
|                                     | <i>Clubiona comta</i>                  | 0                    | 1                    | 1                  | 0.50                 |
|                                     | <i>Clubiona</i> sp.                    | 11                   | 19                   | 30                 | 0.50                 |
| Cheiracanthidae                     | <i>Cheiracanthium mildei</i>           | 13                   | 7                    | 20                 | 0.50                 |
|                                     | <i>Cheiracanthium virescens</i>        | 2                    | 0                    | 2                  | 0.50                 |
|                                     | <i>Cheiracanthium</i> sp.              | 109                  | 79                   | 188                | 0.50                 |
| Lycosidae                           | Lycosidae sp.                          | 1                    | 0                    | 1                  | NA                   |

Table S2.1. continued.

| Group/family                  | Species                         | Abundance<br>in 2016            | Abundance<br>in 2017 | Total<br>abundance | Dispersal<br>ability |      |
|-------------------------------|---------------------------------|---------------------------------|----------------------|--------------------|----------------------|------|
| Mimetidae                     | <i>Ero aphana</i>               | 0                               | 1                    | 1                  | 0.50                 |      |
| Oxyopidae                     | <i>Oxyopes lineatus</i>         | 1                               | 7                    | 8                  | 0.50                 |      |
| Philodromidae                 | <i>Philodromus dispar</i>       | 3                               | 2                    | 5                  | 0.75                 |      |
|                               | <i>Philodromus emarginatus</i>  | 6                               | 5                    | 11                 | 0.75                 |      |
|                               | <i>Philodromus margaritatus</i> | 5                               | 0                    | 5                  | 0.75                 |      |
|                               | <i>Philodromus</i> sp.          | 48                              | 21                   | 96                 | 0.75                 |      |
|                               | <i>Tibellus oblongus</i>        | 1                               | 0                    | 1                  | 0.75                 |      |
|                               | Salticidae                      | <i>Ballus chalybeius</i>        | 3                    | 4                  | 7                    | 0.75 |
| <i>Carrhotus xanthogramma</i> |                                 | 0                               | 1                    | 1                  | 0.50                 |      |
| <i>Heliophanus cupreus</i>    |                                 | 0                               | 2                    | 2                  | 0.75                 |      |
| <i>Heliophanus</i> sp.        |                                 | 1                               | 2                    | 3                  | 0.75                 |      |
| <i>Icius subinermis</i>       |                                 | 1                               | 0                    | 1                  | 0.50                 |      |
| <i>Macaroeris nidicolens</i>  |                                 | 17                              | 23                   | 40                 | 0.50                 |      |
| <i>Pseudeuophrys lanigera</i> |                                 | 1                               | 0                    | 1                  | 0.75                 |      |
| <i>Pseudicius encarpatus</i>  |                                 | 0                               | 1                    | 1                  | 0.50                 |      |
| <i>Salticus</i> sp.           |                                 | 0                               | 8                    | 8                  | 0.75                 |      |
| <i>Salticus zebraneus</i>     |                                 | 5                               | 0                    | 5                  | 0.75                 |      |
| <i>Talavera</i> sp.           |                                 | 0                               | 1                    | 1                  | NA                   |      |
| Thomisidae                    |                                 | <i>Diaea livens</i>             | 8                    | 14                 | 22                   | 0.75 |
|                               |                                 | <i>Diaea</i> sp.                | 2                    | 0                  | 2                    | 0.75 |
|                               |                                 | <i>Ebrechtella tricuspidata</i> | 3                    | 8                  | 11                   | 0.75 |
|                               | <i>Misumena vatia</i>           | 33                              | 2                    | 35                 | 0.75                 |      |
|                               | <i>Pistius truncatus</i>        | 10                              | 14                   | 24                 | 0.50                 |      |
|                               | <i>Synema globosum</i>          | 4                               | 13                   | 17                 | 0.50                 |      |
|                               | <i>Thomisus onustus</i>         | 3                               | 0                    | 3                  | 0.50                 |      |
|                               | <i>Tmarus stellio</i>           | 2                               | 0                    | 2                  | 0.50                 |      |
|                               | <i>Tmarus</i> sp.               | 5                               | 1                    | 6                  | 0.50                 |      |
|                               | <i>Xysticus kochi</i>           | 0                               | 1                    | 1                  | 1.00                 |      |
|                               | <i>Xysticus lanio</i>           | 0                               | 1                    | 1                  | 0.75                 |      |
| <i>Xysticus</i> sp.           | 24                              | 53                              | 77                   | 0.88               |                      |      |

Table S2.2. Study sites with percentage of landscape variables within 500 m radius around the site center.

| Site                | Coordinates          | Impervious surfaces* | Roads | Buildings | Forests | Meadows | Gardens | Parks |
|---------------------|----------------------|----------------------|-------|-----------|---------|---------|---------|-------|
| Normafa             | 47.506997, 18.961790 | 2.37                 | 1.47  | 0.90      | 87.91   | 8.95    | 0.77    | 0     |
| Csillebérc          | 47.490103, 18.961085 | 6.77                 | 2.41  | 4.36      | 83.68   | 0.81    | 5.42    | 3.32  |
| Széchenyi-hegy      | 47.495394, 18.975084 | 7.41                 | 4.04  | 3.37      | 59.29   | 13.82   | 19.42   | 0.06  |
| Farkasvölgy         | 47.484851, 18.985957 | 12.26                | 4.62  | 7.64      | 40.91   | 0.62    | 44.95   | 1.26  |
| Törökbálint         | 47.432365, 18.927832 | 12.91                | 5.83  | 7.08      | 17.71   | 40.63   | 21.88   | 6.87  |
| Diósd               | 47.413386, 18.939710 | 13.56                | 8.64  | 4.92      | 8.09    | 50.92   | 20.78   | 6.65  |
| Hűvösvölgy          | 47.542103, 18.963670 | 14.28                | 7.95  | 6.33      | 65.21   | 0       | 14.15   | 6.36  |
| Gellért-hegy        | 47.485994, 19.047549 | 20.47                | 13.59 | 6.88      | 21.47   | 1.76    | 24.78   | 19.17 |
| Rácz Aladár út      | 47.482858, 18.996020 | 20.06                | 10.1  | 9.96      | 4.54    | 0       | 45.96   | 29.44 |
| Hegyalja út         | 47.485419, 19.017079 | 21.96                | 7.01  | 14.95     | 8.10    | 12.69   | 54.48   | 2.77  |
| Zugligeti út        | 47.517792, 18.985779 | 22.31                | 6.21  | 16.1      | 8.53    | 0.17    | 66.08   | 2.91  |
| Városmajor          | 47.508537, 19.016546 | 32.81                | 11.52 | 21.29     | 0       | 0       | 45.24   | 21.95 |
| Alkotás utca        | 47.489611, 19.024278 | 51.99                | 27.32 | 24.67     | 0       | 0       | 17.10   | 30.91 |
| Karolina út         | 47.479345, 19.031602 | 51.12                | 25.12 | 26        | 0       | 0       | 32.46   | 16.42 |
| Róbert Károly körút | 47.535794, 19.062975 | 51.26                | 37.79 | 13.47     | 0       | 0       | 0.88    | 47.86 |
| Szent István park   | 47.518891, 19.051179 | 52.58                | 29.59 | 22.99     | 0       | 0       | 0       | 18.50 |
| Ludovika tér        | 47.481188, 19.084699 | 57.55                | 27.74 | 29.81     | 0       | 0       | 0.08    | 42.37 |
| Haller park         | 47.474293, 19.080415 | 62.01                | 36.98 | 25.03     | 0       | 0       | 1.91    | 36.08 |
| Vérmező             | 47.501132, 19.025539 | 71.63                | 44.26 | 27.37     | 0       | 0       | 0       | 28.37 |
| Mátyás tér          | 47.492129, 19.079237 | 87.72                | 44.9  | 42.82     | 0       | 0       | 0.37    | 11.91 |
| Hunyadi tér         | 47.505785, 19.067037 | 94.69                | 30.29 | 64.40     | 0       | 0       | 0       | 5.31  |
| Rákóczi tér         | 47.492746, 19.071719 | 94.88                | 38.35 | 56.53     | 0       | 0       | 0       | 5.12  |

\* Pooled proportion of roads and buildings.

Table S2.3. Kendall rank correlation coefficients between landscape variables (proportion of landscape elements within 500 m-radius buffer around the site centers). Numbers in bold indicate significant ( $p < 0.05$ ) correlations.

| Landscape variables | Buildings    | Roads        | Forests      | Meadows      | Gardens      | Parks        |
|---------------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Impervious surfaces | 0.827        | 0.810        | -0.754       | -0.569       | -0.338       | 0.351        |
| <i>p</i> value      | <b>0.000</b> | <b>0.000</b> | <b>0.000</b> | <b>0.001</b> | <b>0.029</b> | <b>0.023</b> |
| Buildings           |              | 0.636        | -0.724       | -0.580       | -0.224       | 0.316        |
| <i>p</i> value      |              | <b>0.000</b> | <b>0.000</b> | <b>0.001</b> | 0.150        | <b>0.041</b> |
| Roads               |              |              | -0.764       | -0.560       | -0.390       | 0.490        |
| <i>p</i> value      |              |              | <b>0.000</b> | <b>0.001</b> | <b>0.012</b> | <b>0.001</b> |
| Forests             |              |              |              | 0.579        | 0.241        | -0.536       |
| <i>p</i> value      |              |              |              | <b>0.001</b> | 0.145        | <b>0.001</b> |
| Meadows             |              |              |              |              | 0.296        | -0.473       |
| <i>p</i> value      |              |              |              |              | 0.079        | <b>0.005</b> |
| Gardens             |              |              |              |              |              | -0.092       |
| <i>p</i> value      |              |              |              |              |              | 0.552        |

Table S2.4. List of predatory groups and genera which were involved in the quasi-GLM analyses with the yearly and total abundance of species belonging to them across all trees and sites (see Table 5).

| Taxon                                      | Species                                | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance |
|--|--|----------------------|----------------------|--------------------|
| <b>Araneae</b>                             |  |                      |                      |                    |
| <i>Araniella</i> spp.                      | <i>Araniella cucurbitina</i>           | 12                   | 0                    | 12                 |
|  | <i>Araniella opisthographa</i>         | 3                    | 7                    | 10                 |
|  | <i>Araniella</i> sp.                   | 74                   | 67                   | 141                |
| <i>Cheiracanthium</i> spp.                 | <i>Cheiracanthium mildei</i>           | 13                   | 7                    | 20                 |
|  | <i>Cheiracanthium virescens</i>        | 2                    | 0                    | 2                  |
|  | <i>Cheiracanthium</i> sp.              | 109                  | 79                   | 188                |
| <i>Philodromus aureolus</i><br>species gr. | <i>Philodromus collinus</i>            | 1                    | 0                    | 1                  |
|  | <i>Philodromus longipalpis</i>         | 1                    | 0                    | 1                  |
|  | <i>Philodromus praedatus</i>           | 9                    | 0                    | 9                  |
|  | <i>Philodromus</i> sp.                 | 327                  | 414                  | 741                |
| <i>Philodromus rufus</i><br>species gr.    | <i>Philodromus albidus</i>             | 8                    | 0                    | 8                  |
|  | <i>Philodromus rufus</i>               | 28                   | 17                   | 45                 |
|  | <i>Philodromus</i> sp.                 | 296                  | 343                  | 639                |
| 'other Theridiidae'                        | <i>Asagena phalerata</i>               | 0                    | 1                    | 1                  |
|  | <i>Dipoena melanogaster</i>            | 12                   | 9                    | 21                 |
|  | <i>Enoplognatha latimana</i>           | 1                    | 1                    | 2                  |
|  | <i>Heterotheridion nigrovariegatum</i> | 31                   | 7                    | 38                 |
|  | <i>Neottiura bimaculata</i>            | 1                    | 4                    | 5                  |
|  | <i>Paidiscura pallens</i>              | 6                    | 37                   | 43                 |
|  | <i>Parasteatoda tepidariorum</i>       | 3                    | 0                    | 3                  |
|  | <i>Platnickina tincta</i>              | 4                    | 22                   | 26                 |
|  | <i>Phylloneta impressa</i>             | 2                    | 1                    | 3                  |
|  | <i>Phylloneta</i> sp.                  | 14                   | 27                   | 41                 |
|  | <i>Simitidion simile</i>               | 0                    | 1                    | 1                  |
|  | <i>Steatoda bipunctata</i>             | 1                    | 0                    | 1                  |
|  | <i>Theridion mystaceum</i>             | 1                    | 1                    | 2                  |
|  | <i>Theridion pinastri</i>              | 16                   | 4                    | 20                 |
|  | <i>Theridion varians</i>               | 2                    | 0                    | 2                  |
|  | <i>Theridion</i> sp.                   | 27                   | 39                   | 66                 |
|  | <i>Theridiidae</i> sp.                 | 2                    | 10                   | 12                 |
| <i>Xysticus</i> spp.                       | <i>Xysticus kochi</i>                  | 0                    | 1                    | 1                  |
|  | <i>Xysticus lanio</i>                  | 0                    | 1                    | 1                  |
|  | <i>Xysticus</i> sp.                    | 24                   | 53                   | 77                 |
| 'other Thomisidae'                         | <i>Diaea livens</i>                    | 8                    | 14                   | 22                 |
|  | <i>Diaea</i> sp.                       | 2                    | 0                    | 2                  |
|  | <i>Ebrechtella tricuspadata</i>        | 3                    | 8                    | 11                 |
|  | <i>Misumena vatia</i>                  | 33                   | 2                    | 35                 |
|  | <i>Pistius truncatus</i>               | 10                   | 14                   | 24                 |
|  | <i>Synema globosum</i>                 | 4                    | 13                   | 17                 |
|  | <i>Thomisus onustus</i>                | 3                    | 0                    | 3                  |

Table S2.4. continued.

| Taxon                   | Species                         | Abundance<br>in 2016 | Abundance<br>in 2017 | Total<br>abundance |
|-------------------------|---------------------------------|----------------------|----------------------|--------------------|
| <b>Araneae</b>          |                                 |                      |                      |                    |
| 'other Thomisidae'      | <i>Tmarus stellio</i>           | 2                    | 0                    | 2                  |
|                         | <i>Tmarus</i> sp.               | 5                    | 1                    | 6                  |
| <b>Coleoptera</b>       |                                 |                      |                      |                    |
| <i>Scymnus</i> spp.     | <i>Scymnus abietis</i>          | 1                    | 0                    | 1                  |
|                         | <i>Scymnus frontalis</i>        | 5                    | 5                    | 10                 |
|                         | <i>Scymnus interruptus</i>      | 32                   | 18                   | 50                 |
|                         | <i>Scymnus rubromaculatus</i>   | 18                   | 6                    | 24                 |
|                         | <i>Scymnus subvillosus</i>      | 16                   | 7                    | 23                 |
| <b>Heteroptera</b>      |                                 |                      |                      |                    |
| <i>Orius</i> spp.       | <i>Orius horvathi</i>           | 2                    | 1                    | 3                  |
|                         | <i>Orius majusculus</i>         | 1                    | 0                    | 1                  |
|                         | <i>Orius minutus</i>            | 3                    | 0                    | 3                  |
|                         | <i>Orius minutus/vicinus</i>    | 32                   | 39                   | 71                 |
|                         | <i>Orius niger</i>              | 3                    | 2                    | 5                  |
|                         | <i>Orius vicinus</i>            | 7                    | 2                    | 9                  |
|                         | <i>Orius</i> sp.                | 2                    | 3                    | 4                  |
| <b>Neuroptera</b>       |                                 |                      |                      |                    |
| <i>Chrysoperla</i> spp. | <i>Chrysoperla carnea</i>       | 41                   | 10                   | 51                 |
|                         | <i>Chrysoperla lucasina</i>     | 6                    | 0                    | 6                  |
|                         | <i>Chrysoperla mediterranea</i> | 1                    | 0                    | 1                  |
|                         | <i>Chrysoperla pallida</i>      | 31                   | 10                   | 41                 |



Table S2.5. Results of the quasi-GLMs for the monthly abundance of aphids, predators and ants (response variable) depending on the percentage of impervious surfaces (explanatory variable). Numbers in bold indicate significant ( $< 0.05$ ) and numbers in italic indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ )  $p$  values.

| Response variable | Month     | Estimate | SE    | Exp. Estimate | Adj. $p$     | Unadj. $p$   | Pseudo- $R^2$ |
|-------------------|-----------|----------|-------|---------------|--------------|--------------|---------------|
| <b>2016</b>       |           |          |       |               |              |              |               |
| Aphids            | April     | 0.020    | 0.004 | 1.020         | <b>0.001</b> | <b>0.000</b> | 51.3          |
| Predators         | April     | 0.007    | 0.004 | 1.007         | 0.113        | <i>0.081</i> | 15.6          |
| Ants              | April     | -0.024   | 0.014 | 0.976         | 0.162        | <i>0.092</i> | 19.5          |
| Aphids            | May       | -0.036   | 0.018 | 0.965         | <i>0.054</i> | <i>0.054</i> | 35.9          |
| Predators         | May       | 0.004    | 0.002 | 1.004         | 0.106        | <i>0.061</i> | 15.9          |
| Ants              | May       | -0.024   | 0.011 | 0.976         | 0.116        | <b>0.046</b> | 23.0          |
| Predators         | June      | -0.005   | 0.004 | 0.996         | 0.258        | 0.221        | 7.5           |
| Ants              | June      | -0.029   | 0.010 | 0.972         | <i>0.079</i> | <b>0.011</b> | 38.7          |
| Predators         | July      | -0.004   | 0.004 | 0.996         | 0.277        | 0.277        | 6.1           |
| Ants              | July      | -0.028   | 0.013 | 0.973         | 0.116        | <i>0.050</i> | 27.7          |
| Predators         | August    | -0.008   | 0.003 | 0.992         | <b>0.030</b> | <b>0.005</b> | 33.6          |
| Ants              | August    | 0.000    | 0.011 | 1.000         | 0.992        | 0.992        | 0.0           |
| Predators         | September | -0.007   | 0.003 | 0.994         | <i>0.089</i> | <b>0.038</b> | 20.1          |
| Ants              | September | -0.009   | 0.013 | 0.991         | 0.574        | 0.492        | 3.6           |
| Aphids            | October   | 0.014    | 0.005 | 1.014         | <b>0.030</b> | <b>0.020</b> | 25.5          |
| Predators         | October   | -0.011   | 0.004 | 0.989         | <b>0.030</b> | <b>0.009</b> | 32.1          |
| Ants              | October   | -0.018   | 0.014 | 0.982         | 0.296        | 0.211        | 10.5          |
| <b>2017</b>       |           |          |       |               |              |              |               |
| Aphids            | May       | 0.017    | 0.006 | 1.017         | <b>0.007</b> | <b>0.007</b> | 33.5          |
| Predators         | May       | 0.004    | 0.004 | 1.004         | 0.449        | 0.380        | 4.5           |
| Ants              | May       | -0.010   | 0.013 | 0.991         | 0.452        | 0.452        | 4.8           |
| Predators         | July      | -0.004   | 0.006 | 0.996         | 0.449        | 0.449        | 3.7           |
| Ants              | July      | -0.020   | 0.009 | 0.980         | 0.116        | <b>0.039</b> | 23.2          |
| Aphids            | September | 0.035    | 0.006 | 1.035         | <b>0.000</b> | <b>0.000</b> | 67.2          |
| Predators         | September | -0.006   | 0.006 | 0.994         | 0.449        | 0.330        | 5.8           |
| Ants              | September | -0.023   | 0.014 | 0.977         | 0.173        | 0.115        | 18.1          |

Table S2.6. Results of the quasi-GLMs for the total abundance of aphids (response variable) depending on the total abundance of predators and ants (explanatory variables) in 2016 and 2017. Numbers in bold indicate significant ( $< 0.05$ )  $p$  values.

| Explanatory variable | Model      | Estimate | SE    | Exp. Estimate | $p$          | Pseudo- $R^2$ |
|----------------------|------------|----------|-------|---------------|--------------|---------------|
| <b>2016</b>          |            |          |       |               |              |               |
| Sum predator         | Full model | -0.004   | 0.002 | 0.996         | <b>0.017</b> | 27.6          |
| Sum ant              | Full model | 0.000    | 0.001 | 1.000         | 0.960        | 27.6          |
| Sum predator         | Best model | -0.004   | 0.002 | 0.996         | <b>0.013</b> | 27.6          |
| Sum ant              | Best model | NA       | NA    | NA            | NA           | NA            |
| <b>2017</b>          |            |          |       |               |              |               |
| Sum predator         | Full model | 0.000    | 0.002 | 1.000         | 0.938        | 12.7          |
| Sum ant              | Full model | -0.006   | 0.004 | 0.994         | 0.184        | 12.7          |
| Sum predator         | Best model | NA       | NA    | NA            | NA           | NA            |
| Sum ant              | Best model | -0.006   | 0.004 | 0.994         | 0.162        | 12.7          |

Table S2.7. Results of the quasi-GLMs for the annual abundance of aphids (response variable) depending on the monthly abundance of predators and ants (explanatory variables). Numbers in bold indicate significant ( $<0.05$ ) and numbers in italic indicate marginally significant ( $\geq 0.05$  and  $< 0.1$ )  $p$  values.

| Explanatory variable | Month     | Model      | Estimate | SE    | Exp. Estimate | Adj. $p$     | Unadj. $p$   | Pseudo- $R^2$ |
|----------------------|-----------|------------|----------|-------|---------------|--------------|--------------|---------------|
| <b>2016</b>          |           |            |          |       |               |              |              |               |
| Predators            | April     | Full model | -0.016   | 0.016 | 0.985         | 0.392        | 0.333        | 6.8           |
| Ants                 | April     | Full model | -0.003   | 0.003 | 0.997         | 0.846        | 0.390        | 6.8           |
| Predators            | April     | Best model | -0.009   | 0.014 | 0.991         | 0.514        | 0.514        | 2.4           |
| Ants                 | April     | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Predators            | May       | Full model | 0.007    | 0.017 | 1.007         | 0.677        | 0.677        | 2.3           |
| Ants                 | May       | Full model | -0.004   | 0.008 | 0.996         | 0.846        | 0.604        | 2.3           |
| Predators            | May       | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Ants                 | May       | Best model | -0.004   | 0.008 | 0.996         | 0.626        | 0.626        | 1.3           |
| Predators            | June      | Full model | -0.011   | 0.008 | 0.989         | 0.364        | 0.163        | 17.1          |
| Ants                 | June      | Full model | -0.004   | 0.007 | 0.996         | 0.846        | 0.526        | 17.1          |
| Predators            | June      | Best model | -0.013   | 0.007 | 0.987         | 0.148        | <i>0.089</i> | 14.9          |
| Ants                 | June      | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Predators            | July      | Full model | -0.011   | 0.008 | 0.989         | 0.364        | 0.208        | 11            |
| Ants                 | July      | Full model | 0.009    | 0.007 | 1.009         | 0.837        | 0.239        | 11            |
| Predators            | July      | Best model | -0.007   | 0.007 | 0.993         | 0.468        | 0.374        | 4.3           |
| Ants                 | July      | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Predators            | August    | Full model | -0.011   | 0.011 | 0.989         | 0.392        | 0.336        | 13.3          |
| Ants                 | August    | Full model | 0.015    | 0.011 | 1.016         | 0.837        | 0.167        | 13.3          |
| Predators            | August    | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Ants                 | August    | Best model | 0.015    | 0.011 | 1.015         | 0.388        | 0.194        | 8.4           |
| Predators            | September | Full model | -0.024   | 0.008 | 0.976         | <i>0.056</i> | <b>0.008</b> | 34.4          |
| Ants                 | September | Full model | 0.001    | 0.01  | 1.001         | 0.948        | 0.948        | 34.4          |
| Predators            | September | Best model | -0.024   | 0.008 | 0.976         | <b>0.030</b> | <b>0.006</b> | 34.4          |
| Ants                 | September | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| Predators            | October   | Full model | -0.010   | 0.004 | 0.99          | <i>0.060</i> | <b>0.017</b> | 27.7          |
| Ants                 | October   | Full model | -0.001   | 0.005 | 0.999         | 0.919        | 0.788        | 27.7          |
| Predators            | October   | Best model | -0.010   | 0.004 | 0.990         | <b>0.035</b> | <b>0.014</b> | 27.5          |
| Ants                 | October   | Best model | NA       | NA    | NA            | NA           | NA           | NA            |
| <b>2017</b>          |           |            |          |       |               |              |              |               |
| Predators            | May       | Full model | 0.006    | 0.010 | 1.006         | 0.951        | 0.563        | 2.7           |
| Ants                 | May       | Full model | -0.003   | 0.008 | 0.997         | 0.720        | 0.720        | 2.7           |
| Predators            | May       | Best model | 0.006    | 0.009 | 1.006         | 0.536        | 0.536        | 2.0           |
| Ants                 | May       | Best model | NA       | NA    | NA            | NA           | NA           | NA            |

Table S2.7. continued.

| Explanatory variable | Month     | Model      | Estimate | SE    | Exp. Estimate | Adj. $p$ | Unadj. $p$ | Pseudo- $R^2$ |
|----------------------|-----------|------------|----------|-------|---------------|----------|------------|---------------|
| Predators            | July      | Full model | -0.002   | 0.006 | 0.998         | 0.951    | 0.787      | 12.4          |
| Ants                 | July      | Full model | -0.021   | 0.015 | 0.980         | 0.258    | 0.172      | 12.4          |
| Predators            | July      | Best model | NA       | NA    | NA            | NA       | NA         | NA            |
| Ants                 | July      | Best model | -0.020   | 0.014 | 0.980         | 0.172    | 0.172      | 12.0          |
| Predators            | September | Full model | 0.000    | 0.003 | 1.000         | 0.951    | 0.951      | 17.1          |
| Ants                 | September | Full model | -0.016   | 0.011 | 0.984         | 0.258    | 0.158      | 17.1          |
| Predators            | September | Best model | NA       | NA    | NA            | NA       | NA         | NA            |
| Ants                 | September | Best model | -0.016   | 0.010 | 0.984         | 0.172    | 0.137      | 17.1          |

Table S2.8. Results of GLMMPQL (penalized quasi-likelihood GLMM) analyses with quasi-Poisson errors for the abundance of predators and ants (response variables) depending on the abundance of aphids, season, and year (explanatory variables). In the models, only the months of peak aphid activity were considered. A random variable = (1|site) was added to the intercept of all models, but only fixed effects are reported here. Number in bold indicate significant ( $< 0.05$ )  $p$  value.

| Response variable | Explanatory variable | Estimate | SE    | $t$    | $p$          |
|-------------------|----------------------|----------|-------|--------|--------------|
| Predators         | Aphids               | 0.000    | 0.001 | -0.705 | 0.483        |
|                   | Season               | -0.827   | 0.100 | -8.279 | <b>0.000</b> |
|                   | Year                 | 0.150    | 0.097 | 1.553  | 0.124        |
| Ants              | Aphids               | 0.001    | 0.001 | 0.832  | 0.408        |
|                   | Season               | 0.141    | 0.208 | 0.681  | 0.498        |
|                   | Year                 | 0.043    | 0.195 | 0.223  | 0.824        |