

Effect of the invasive phanerophytes and associated aphids on the ant (Hymenoptera, Formicidae) assemblages

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Abstract

In Kyiv and the Kyiv region (Ukraine) during 2015-2017, 47 species of aphids (Aphididae) were found on 18 native species of plants-phanerophytes and for 9 invasive plant species, 14 aphid species were found. Native species of plants-phanerophytes were visited by 19 species of ants (Formicidae) and invasive plant species by 16 species of ants. Only one aphid species (*Aphis craccivora* Koch) found on invasive plant species was invasive. Most species of invasive phanerophytes are not very attractive for ants, since they are practically not populated by aphids (*Acer negundo*, *Amorpha fruticosa*). Some tree species are inhabited by aphids only at the beginning of their life cycle (*Padus serotina*). Only some species of invasive plants (*Quercus rubra*, *Salix fragilis*) can be infested with aphids throughout their life cycle, and accordingly, are visited by ants.

Keywords: *Aphididae*, *invasive species*, *Formicidae*, *phanerophytes*

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Introduction

Ever-increasing plant and animal invasions are a biological process that accompanies the on-going globalization. Alien species that control new areas often exert a spectacular, sometimes catastrophic impact not only on related individual native species, but also on local biodiversity, and thus they change the structure and functioning of plant and animal communities, biocoenoses and entire ecosystems. From among plant invasions and their ecological effects, the most intensely studied and best known are those of herbaceous species. Densely covering often large areas, such plants out-compete native herbs and, changing habitat conditions (soil properties, microclimate), radically and in many aspects affect local animal communities. Herb plant species, highly invasive in Europe, are e.g. goldenrods (*Solidago* spp.) and balsams (*Impatiens* spp.), and the animals tested for their impact were, among others, ants (Lenda *et al.*, 2013; Grześ *et al.*, 2018; Trigoso-Peral *et al.*, 2018).

Invasive woody plants, i.e. phanerophytes according to Raunkiaer's (1905)

classification, also play an important role in ecosystems. In the temperate zone phanerophytes are practically trees and shrubs. In the nature of things, their invasive species constitute both potential and actual threat to forestry. So the economic aspect of their impact is examined as for example in the case of the northern red oak *Quercus rubra* (Chmura, 2013) or the black cherry *Prunus serotina* (Aerts *et al.*, 2017), or the socio-economic balance of profits and losses resulting from the invasion is considered, as for the black locust *Robinia pseudoacacia* (Vitková *et al.*, 2017). Their possible effects on the animal part of biocoenosis cause far less interest.

Alien woody plants intentionally introduced into new areas for horticulture and forestry often for centuries were not considered to be dangerous invasive species. However, so far only 0.5–0.7% of the world's phanerophyte species revealed their invasive potential outside their natural range, rapidly starting spontaneous spread there, and hence gained economic and ecological importance

(Richardson and Rejmánek, 2011). Of the 622 world woody plant species recognized as invasive, 107 species occur in Europe (Richardson and Rejmánek, 2011). Seven of the latter are on a list of the '100 of the Worst' invasive species (both plants and animals) in Europe (Roy *et al.*, 2010) and 15 ones are on the similar list of the 149 invaders of Europe (Nentwig *et al.*, 2017).

The nature of vegetation significantly affecting habitat and environmental conditions determines the composition and structure of local zoocoenoses in all layers of the ecosystem – from soil to the tree crowns. In all of these layers, ants live, constituting practically in all terrestrial habitats a numerically and ecologically dominating group of the invertebrate mesofauna (Hölldobler and Wilson 1990; Wilson 1990). Relationships between plants and ants are close and multifaceted – including indirect and direct trophic connections. The vast majority of ants are pantophages: as predators they hunt for various phytophages, as melitophages they feed on plant juice, nectar, pollen and, above all, honeydew of homopterans; some also eat seeds. In the context of the present paper, the most important are the trophobiosis of ants with aphids as parasites of trees and shrubs. It can therefore be assumed that the change in vegetation associated with the presence of invasive species should trigger noticeable changes in the local myrmecofauna. The studies about the attractiveness of invasive plants for ants are single (Stukalyuk *et al.*, 2019) and most often cover the effect of invasion of single plant species on ant assemblages (Weiss *et al.*, 2005; Lenda *et al.*, 2013; Myczko *et al.*, 2018). In this study, we made an attempt to compare among themselves invasive plant species with native ones, to find out the reasons for their attractiveness or unattractiveness for ants.

The aim of the study was to verify this supposition by comparing ant assemblages in woods composed of native tree and shrub species with those more or less wooded areas with different share and composition of invasive phanerophytes. To our knowledge, research in this field has not been carried out yet.

The studied region (Kyiv region) can be a convenient model territory. Here there are all the main types of habitats characteristic of Europe - deciduous and coniferous forests and

other habitats considered in our work. Therefore, the patterns obtained by us on the model territory can be extended to vast territories with the same types of habitats. Invasive plants attractive to ants will remain so in similar habitats, and vice versa.

Materials and Methods

Study sites

The research was conducted in the years 2015–2017 in the periods from June to August in the urban greenery of Kyiv and in extra-urban environments in the Kyiv region, Ukraine. Physiographically, Kyiv is located on a border of two ecological zones: the European mixed forest zone and the forest-steppe zone (Popov *et al.*, 1968; Didukh and Aloskina, 2012). Hence, the vegetation of the region is very rich and diverse; it represents several phytosociological classes: Pulsatilla-Pinetea, Quercetea robori-petrea, Querco-Fagetea, Salicetea alba, Alnetea glutinosae (forest vegetation), Festuco-Brometea (steppes), Molinio-Arrhenatheretea, Koelerio-Corynephoretea (meadow vegetation), Phragmito-Magno-Caricetea, Lemnetae, Potametea (aquatic and bog vegetation) and others (Didukh and Aloskina, 2012). There are many urban and natural parks, gardens, botanical gardens, etc. in the city, and nature conservation areas in the city environs. Altogether, the research covered 22 study sites: 18 within the city limits and four outside the city (Fig. 1). Some sites represented more than one habitat category.

Habitat classification

Based on the classification of the European Nature Information System (see EUNIS database) the sites studied represented nine EUNIS habitat categories:

1. Category G1.A162: Mixed lime-oak-hornbeam forests (association Tilio-Carpinetum; study sites 1, 2 and 6). This forest association developed in Central and Eastern Europe (Poland, Lithuania, Belarus, Ukraine, Russia) in regions of continental climate within the range of *Carpinus betulus*, east of the range of *Fagus sylvatica*. Besides from *C. betulus* the association include *Quercus petraea*, *Quercus robur*, *Tilia cordata*, *Acer platanoides*, *Fraxinus excelsior* and some possible other tree species (for more details see Protopopova *et al.*, 2014).

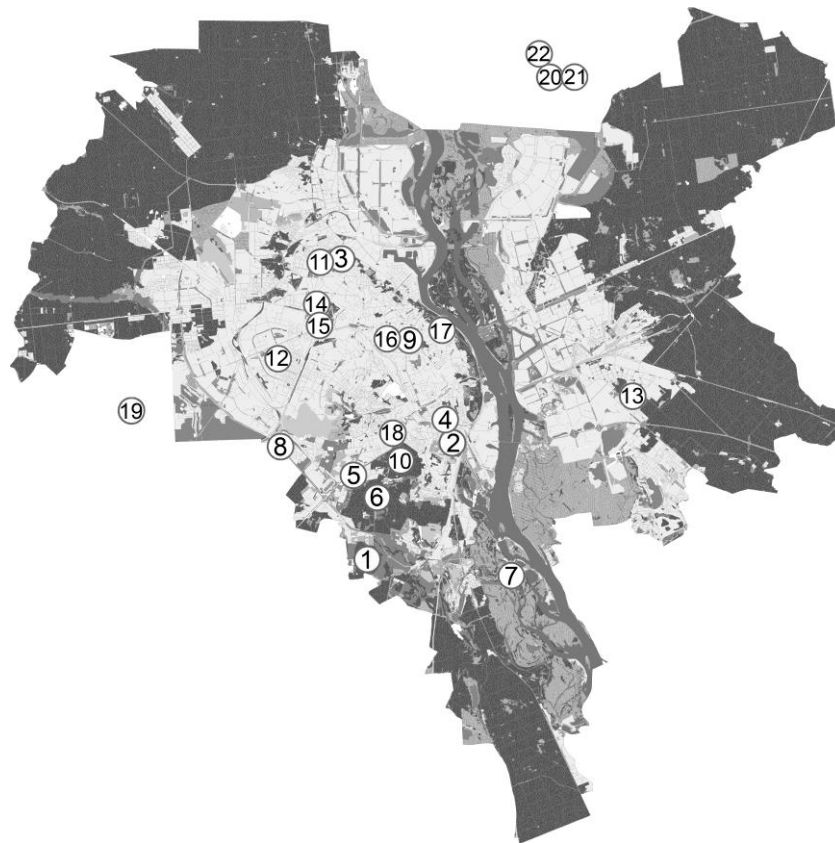


Figure 1. Kyiv in its administrative boundaries and location of study sites within and outside the city: **1.** Park of landscape garden art «Feofania»; **2.** regional landscape park «Lysa Hora» (natural park); **3.** natural landmark Kirillov Gai (natural park area); **4.** Sovskie Ponds valley (or lowland maybe better)(natural park area); **5.** Expocenter of Ukraine (a park area); **6.** Goloseyevsky Forest (a forest nature reserve); **7.** Zhukov Island (forest and meadow nature reserve); **8.** Ring Road (tree planting or lines of trees); **9.** T. G. Shevchenko Park (park area); **10.** Goloseyevsky Park (natural park area); **11.** Babi Yar Park (park area); **12.** Vidradny Park (park area); **13.** Park of Partisan Glory (park area); **14.** A. S. Pushkin Park (park area); **15.** Kyiv Polytechnic Institute (park area); **16.** A. V. Fomin Botanical Garden; **17.** Mariinsky Park (park area); **18.** street and yard greenery of the Goloseyevsky district of Kyiv (several plots close to each other); **19.** environs of the village Sofieivska Borshchagivka (Kyiv-Svyatoshinsky district); **20.** environs of the village Litky (Brovarskoy district); **21.** National natural reserve «Zalissya»; **22.** Lyubychiv island (natural territory, without park status). Gray scale: light gray – zone of high-density housing; medium gray – zone of urban and natural parks; dark gray – forest areas.

In the forests studied, the 1st layer (overstory layer) was formed by *Quercus robur* (in brackets, the numbers of trees/shrubs examined) (221), the 2nd layer (canopy layer) by *Acer platanoides* (195), *Carpinus betulus* (165) and *Fraxinus excelsior* (58), and the 3rd layer (understory) by *Euonymus verrucosus* (50), saplings of *Ulmus glabra* (90) and *A. platanoides* (210) on lighted places, and shrubs of *Sambucus nigra* (30) in shaded places. All these tree and shrub species are native; there were no phanero-phytes of foreign origin. In total, 1019 trees and shrubs

were inspected for the presence of ants on them.

2. Category X11: Large parks (study sites 9–17). Urban parks, usually >5 ha, with more or less cultivated vegetation (mown lawns, flower beds, shaped shrubberies); they may include small semi-natural or artificial woods, grasslands and water bodies. In the studied parks, we inspected especially tree and shrub clusters (up to 2 ha) and rows along avenues. A total of 1480 plants, both of native and alien origin, mainly constituting the canopy layer were examined. Native

phanerophyte species included (in brackets, the numbers of trees/shrubs examined): *Acer platanoides* (292), *Betula pendula* (173), *Tilia cordata* (167), *Quercus robur* (149), *Pinus sylvestris* (90), *Populus nigra* (58), *P. alba* (45), *Sambucus nigra* (30) and *Fraxinus excelsior* (25). The following species were alien, including four invasive ones: *Robinia pseudoacacia* (112), *Quercus rubra* (77), *Amorpha fruticosa* (60) and *Padus serotina* (30); the rest of the introduced species were *Aesculus hippocastanum* (107), *Juglans mandshurica* (40) and *Acer saccharinum* (25).

3. Category G5.1: Lines of trees (study sites 1, 5, 6, 8 and 18). More or less continuous rows of trees forming strips within a matrix of grassy or cultivated land or along communication arteries, typically planted for shelter or shading. During the research, a total of 1413 trees were examined. We considered trees, which were planted along the roads within the city borders and those creating shelterbelts in the fields. There were three sites with different types of plant associations in this habitat.

First site: Trees formed two layers – overstory layer - *Salix fragilis* (71) and canopy layer consist- *Acer negundo* species (222 trees were examined in a biotope, 157 individuals were saplings), near small groups of *Pyrus communis* trees (15), *Populus tremula* (24) and *Py. communis*, *Po. tremula* of native origin.

Second site: Alley- *Juglans mandshurica* (60, introduced species), *Salix alba* (34, native species).

Third site: Planted trees in the yards. Area up to 0.5 ha. *Robinia pseudoacacia* (194), *Acer negundo* (156) (invasive species), *Populus alba* (40), *Tilia cordata* (125), *Ulmus laevis* Pall. (31), *Betula pendula* (40), *Fraxinus excelsior* (49), *Populus nigra* (39), *Acer platanoides* (36), *Quercus robur* (76): native species; *Aesculus hippocastanum* (40), *Acer saccharinum* (137) are introduced plant species and *Quercus rubra* (24) is an invasive species.

4. Category G1.A53: East-European linden forests (study site 3). *Tilia*-dominated forests with *Quercus robur*, *Acer platanoides* and *Ulmus montana* of eastern Central Europe and the southern nemoral zone of Russia, east of the range of *Fagus sylvatica* and, for the most part, of the range of *Carpinus betulus*, and west of the Volga river. In total, 90 trees were examined, all of native species: *Quercus*

robur (30), *Tilia cordata* (30) and *Sambucus nigra* (30).

5. Category G4.F: Mixed forestry plantations (study sites 19, 20 and 21). Mixed coniferous and deciduous planted forests at the age of 70–80 years, in which at least one constituent is of foreign origin or, if composed of native species, then planted in clearly unnatural stands. In the studied pine-dominated forest, a total of 1150 trees and shrubs were examined. The native species were *Pinus sylvestris* (194), *Padus avium* (180) and *Betula pendula* (8), and the invasive ones *Padus serotina* (481), *Amorpha fruticosa* (150) and *Robinia pseudoacacia* (137).

6. Category E2.1: Permanent mesotrophic pastures (study sites 20) and grazed meadows (study site 21). Regularly grazed European mesotrophic pastures of the alliance Cynosurion. This is a classification unit of meadows vegetation based by Braun-Blanquet approach, on fertilised and well-drained soils. In total, 240 tree samplings of four species (60 of each) were inspected: *Populus nigra* and *P. alba* as native phanerophytes, and *Robinia pseudoacacia* and *Acer negundo* as invasive ones. In the studied site, they grew as single-species clumps.

7. Category G5.2: Small deciduous anthropogenic woodlands (study sites 19, 20). Plantations and small intensively-managed deciduous woods with an area smaller than 0.5 ha. A plantation of the invasive *Robinia pseudoacacia* was studied, where 217 trees of this species were examined (30-40 years old).

8. Category G1.11: Riverine *Salix* woodland (alliance Salicion albae; sites 4, 7 and 22), Floodplain forests. In total 830 plants were examined. *Populus alba* (a total of 60 trees were examined in a biotope, a native species, overstory layer), *Acer negundo* (a total of 73 trees, an invasive species, canopy layer). Other distribution of layers: *Populus alba*, *Populus nigra* (88): native species, *Salix fragilis* (65), *Acer negundo* (73, invasive species, canopy layer), *Quercus robur* (73, native species, overstory layer), *Ulmus laevis* (36, native species, canopy layer). At another point, light forest, without a clear division into layers: *Populus alba* (saplings, 80), *Populus nigra* (91), *Populus tremula* L. (25, native species), *Salix fragilis* (invasive species). In Ukraine, *S. fragilis* is an invasive species (Protopopova et al., 2009). *Amorpha fruticosa*

(239, invasive species) here forms an understory layer.

9. Category G1.C2: Exotic *Quercus* plantations (site 1). Cultivated (more or less single-species) formations of the introduced *Quercus* species (e.g. *Q. rubra*) of the age group 30-50 years, planted most often for the production of wood. A total of 313 plants were examined: 263 of the invasive *Q. rubra* and 50 of the native *Acer campestre*.

Characteristics of the invasive phanerophyte species within the study area

Among the introduced tree and shrub species, four species in Ukraine are transformer species: *A. negundo*, *Am. fruticosa*, *R. pseudoacacia*, *S. fragilis*. (Protopopova *et al.*, 2009; Burda *et al.*, 2018). All of them occur within our study area:

Acer negundo - is a kenophyte of North American origin. The range is Holarctic. The transformer species, whose influence on biotopes is manifested in the suppression of undergrowth and seedlings of other trees, and also leads to a significant depletion of the grassy layer and also changes in such ecosystems; it occurs in anthropogenic, semi-natural and natural ecotopes (Protopopova *et al.*, 2009). Due to its biological properties (high seed productivity, methods of propagation, the formation of a powerful seed bank, greater plant viability, etc.), a wide ecological amplitude contributes to the penetration and consolidation of the species in the free ecosystems of most biotopes.

Amorpha fruticosa is a kenophyte of North American origin and has a European-American (according to other data, cosmopolitan) range. It is found in anthropogenic, semi-natural and natural ecotopes. It is a robust transformer species, because it changes the soil conditions through enrichment with nitrogen, and also affects the light regime through strong shading. In addition, it plays an active coenotic role, especially in coastal cenoses, forming communities of the riverbed tree-shrub vegetation, which are considered at the level of individual syntaxa, withstands fluctuations in water levels and flooding. These features, as well as the capacity for hydrochloria, contribute to the mass dispersal of *A. fruticosa* on floodplains and other periodically flooded areas.

Robinia pseudoacacia – kenophyte, has holarctic distribution, and this species is of North American origin. The transformer species, whose influence on biotopes is manifested in the enrichment of soil with nitrogen compounds, as a result of which only nitrophilic grass species can live here. Also, the ability of rapid growth, and the emergence of a large number of shoots of root origin plus high seed productivity give them an aggressive life strategy. Due to its biological properties (high seed productivity, the formation of a powerful seed bank, a large vital ability of plants, allelopathic properties, etc.), as well as a wide ecological amplitude contribute to its penetration and fixation in the empty habitats of biotopes. The species forms spontaneous mono-species communities or settles in the undergrowth and on forest edges, changing their structure and affecting the functioning of forest ecosystems.

Salix fragilis is an archeophyte, has Euro-Mediterranean-Persian distribution and Asia Minor origin; transforming species, whose influence on biotopes is carried out through the rapid growth and capture of new territories. This is facilitated by its frost resistance and active vegetative reproduction. Occurs in anthropogenic, semi-natural and natural ecotopes (Protopopova *et al.*, 2009). Due to its biological properties (large vital ability of plants, phenotypic plasticity, etc.), as well as the ecological plasticity of the species, it easily penetrates and is fixed in free ecosystems of biotopes. The species completely changes the structure of the recipient ecosystems, which is prone to hybridization with the local species *S. alba*, hampering the natural development of native species populations (Burda *et al.*, 2018).

Fieldwork

In total, 6662 plants (trees and shrubs) of 27 species were inspected; 18 species were recognised as native, 5 species as of foreign origin but not-invasive, and 4 species were considered as invasive (or introduced plants). The inspection was aimed at determining the general presence of aphids and ants of the given species on the plant, as well as the presence of possible ant foraging trails and ant nests in the trunks, lower branches or at the base of the tree. The latter applied especially to dendrobiotic species, such as *Dolichoderus quadripunctatus* (L.), *Lasius brunneus* (Latr.),

L. emarginatus (Ol.) and *L. fuliginosus* (Latr.). As an index of the approximate ant abundance on a plant, the number of workers recorded during a two-minute observation was assumed. On large trees, ants were counted on the whole perimeter of the trunk up to a height of 2 m. On trees and shrubs lower than 2 m, ants on the entire plant were counted. The presence of ants on individual plants was checked once in the study period except that on locusts (*Robinia pseudoacacia*). For the latter, as an example of a typically invasive tree species, such observations were made twice in the season: during flowering in June, and during seeding in July. Ants, if possible, were identified to the species on the spot. When it was impossible, as in cases of the genera *Myrmica* and *Temnothorax*, individual ants were collected and identified in the laboratory based on the key given by Radchenko A. G. (2016). For each of the studied habitats, the proportion of each ant species was calculated. In total, 37870 ant individuals of 21 species were recorded.

At the same time, the presence of aphids on the plants was recorded. On shrubs and small trees their presence was found directly, while on large trees indirectly, based on ants coming down the trunk with their gasters distended with honeydew. Proportions of plants with and without aphids were determined for each plant species separately for each habitat studied. The aphids present on each plant species were sampled to 70% ethanol for subsequent identification. 61 aphid species were recorded. Species of aphids identification was carried out by V.V. Zhuravlev using the key to species of Blackman and Eastop (1994).

For plants studied, we calculated the trunk circumference at a height of 1.6 m (if applicable), life form (sapling, shrub or tree), minimum/maximum of the level of illumination in the habitat, as well as the average level of illumination under the canopy, and the projective cover of the crown (given in % from clear space). Using a Solar Power Meter CEM DT-1307 light meter, the absolute value of the illumination intensity (in lux) was measured, and then the relative value (in %) was calculated as the ratio of the intensity of illumination over plants in the study area to that in the open area.

Statistical analysis

For statistical data processing, the Origin program was used (v.8.0). The distribution of ants on plants of all species, excluding those on which ants were absent or those which were rarely visited, did not differ from the normal one (the Shapiro–Wilk Normality test; Shapiro and Wilk, 1965). This determined the choice of parametric data analysis methods (Pearson correlation between signs, t-test for the significance of differences at $p < 0.05$, cluster analysis). The cluster analysis was carried out according to two defining indicators: the species of ants on different species of plants and the plant species visited by ants. The construction of dendrograms of hierarchical cluster analysis was performed using the Ward method based on Euclidean distances. To determine the similarity of the distribution patterns of species of ants and plants in habitats, canonical correspondence analysis (Ter Braak, 1986) was used, which is one of the variants of multidimensional analysis. The calculation procedure was carried out in the ade4 package (Dray and Dufour, 2007) for the R computing environment (R Core Team, 2018).

To analyze the relationship between the abundance and frequency of species with factors, double co-inertia methods were used (the co-inertia analysis performs a double inertia analysis of two tables). For the analysis of these environmental factors, the standardized PCA method was used; for the abundance of species, centered PCA was used.

When studying the relationship of the frequency of species with factors, correspondence analysis (CoA) was applied to the data on species of ants, normalized PCA was applied to the data on the factors after deleting information related to differences in the abundance of species in locations. To exclude detection of a hidden relationship between the type of habitat and variation of the abundance of species in ant assemblages, constrained Double Principal Coordinates Analysis (cDPCoA) was used (Dray *et al.*, 2015).

Results

Species composition of ants: In total, 21 species of ants belonging to 3 subfamilies were found on native and invasive plants (See supplementary Table 2). They were: *Formica cinerea* Mayr, 1853; *F. rufibarbis* Fabricius, 1793; *F. cunicularia* Latreille, 1798; *F.*

polyctena Foerster, 1850; *F. rufa* Linnaeus, 1761; *F. fusca* Linnaeus, 1758; *Lasius niger* (Linnaeus, 1758); *L. emarginatus* (Olivier, 1792); *L. platythorax* Seifert, 1991; *L. fuliginosus* (Latreille, 1798); *L. brunneus* (Latreille, 1798); *L. umbratus* (Nylander, 1846); *Camponotus ligniperda* (Latreille, 1802); *C. vagus* (Scopoli, 1763); *C. fallax* (Nylander, 1856) (15 species, subfamily Formicinae); *Dolichoderus quadripunctatus* (Linnaeus, 1771) (1 species, subfamily Dolichoderinae); *Myrmica rubra* (Linnaeus, 1758); *M. ruginodis* Nylander, 1846; *Leptothorax muscorum* (Nylander, 1846); *Temnothorax crassispinus* (Karavaiev, 1926); *T. tuberosum* (Fabricius, 1795) (5 species, subfamily Myrmicinae). Of these, 16 species of ants were found on invasive plants (all but *L. umbratus*; *Camponotus ligniperda*, *F. cunicularia*, *F. rufa*; *F. fusca*) and all the 21 species of ants on native ones.

The distribution of ant species in habitats and associations

The most common ant species include *L. niger*, *F. cinerea*, *L. fuliginosus*, *L. emarginatus* (Table 1). These species are massively found in no less than 6-8 habitats. The first two species can comprise from 5.0 % to 48.0 % of all ants in each of the habitats.

Other ant species are either found in one habitat (*F. rufa*, *F. polyctena*, *F. rufibarbis*, *C. ligniperda*), or make up a small fraction of all ants in several habitats (*D. quadripunctatus*, *L. brunneus*, *Myrmica spp.*, *C. fallax*, *C. vagus*, *L. platythorax*). The total number of ant species in habitats differs by almost four times: the maximum is recorded for habitats G1.A162 and X11 (14 and 13 species), the minimum is in E2.1 (3 species). The numbers of ants for *C. vagus*, *C. ligniperda*, which forages mainly in the evening, when other dominants are less active, are underestimated in our studies, since during the surveys there was a minimum of their foragers at the forage area.

The most common ant species can make up more than a third of all the ants found in a habitat (*L. niger*, *F. cinerea*, habitats X11, G5.1, E2.1) and occupy a dominant position in the multi-species ant assemblages. Other ant species that are obligate dominants in ant associations (*L. fuliginosus*, *F. rufa*, *F. polyctena*, *F. cinerea*, in: Zakharov classification, 1991) or facultative (*L.*

emarginatus, *C. vagus*, *C. ligniperda*, *L. niger*) dominants significantly influence the structure of ant assemblages in forest and forest park habitats. In addition to dominants, associations include subordinate species: subdominants (*L. brunneus*, *D. quadripunctatus*, *C. fallax*), as well as influents (other species of ants).

Among the species of ants (Table 1), the differences relate to the share of each of them in the association. The largest total number of ants was observed in habitats G1.A162, X11, G5.1 (Table 1), the smallest - in habitats E2.1, G5.2, G1.C2. The average number of ants per plant is maximum in G1.A162, X11, G1.A5 habitats (Table 1), 1.4 times less in G5.1 habitat, 2.6 times less in G5.2, G1.C2, G1.11, 5.9 times - in habitats G4.F and E2.1 ($p < 0.05$).

The maximum number of individuals per plant and the total number of ant species is noted for habitats G1.A162, X11, in which either native species of plants (G1.A162) are present or invasive species make up less than half of the total. In the deciduous forest (G1.A162), species of ants are represented more evenly, without the overwhelming numerical dominance of one of them. The habitat G1.A5 has a similar structure, where we surveyed a small number of plants. In the X11 habitat, two species of ants, *L. niger*, *F. cinerea*, already dominate.

The same ratio of ant species, but with less attendance, is preserved in the planting of red oak in the G1.C2 habitat, which forms mono-species communities or dominates in the first layer. The participation of forest ant species (*L. fuliginosus*, *L. emarginatus*, *L. brunneus*, *D. quadripunctatus*) is preserved in the habitat G5.1, but their proportion is less significant than in *L. niger*, *F. cinerea* (Table 1). In other habitats, low attendance by ants was noted with a large number of invasive plant species or the participation of these species in the community (for example, *P. serotina* in the pine forests, the habitat G4.F, or *Am. fruticosa* in the floodplain forest, the habitat G1.11), including unattractive for ants (*Ac. negundo*, *Am. fruticosa*, *Ae. hippocastanum* and others). Among the ant species in such habitats, *L. niger* prevails as a rule.

In the hierarchical structure of ant species compiled by the distribution of species in habitats, 4 clusters can be distinguished (Fig. 2).

Effect of the invasive phanerophytes and associated aphids on the ant assemblages

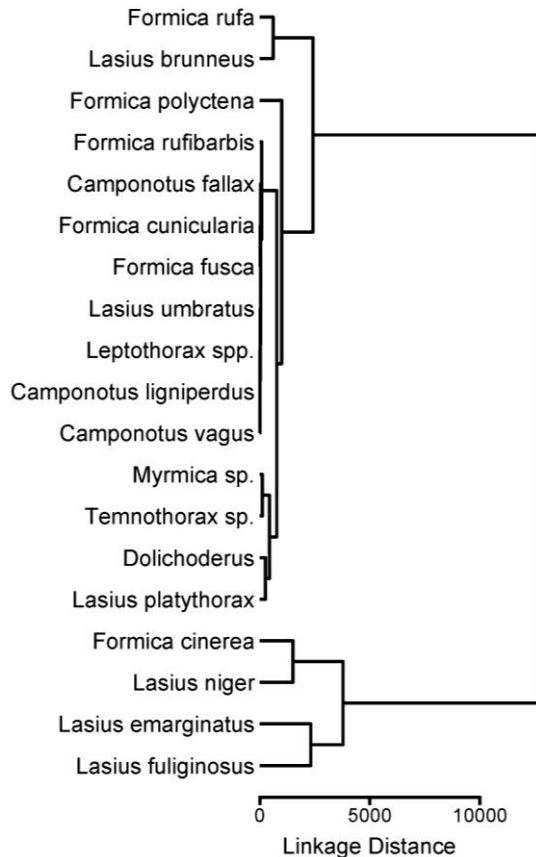


Figure 2: Dendrogram of the species composition of ants in biotopes by association (see also Fig. 5a)

The first cluster includes widespread dominants-dendrobionts in deciduous forests: *L. fuliginosus*, *L. emarginatus*. In addition to forests, they are often found in parks, yards and squares on trees (in G5.1), that is, in habitats, where forest vegetation is still preserved. These species form the core of forest ant assemblages. In the absence of these dominants, two species of ants are widely represented - *L. niger*, *F. cinerea* (in X11, G5.1), included in the second cluster. These are the most common species of ants in habitats of varying degrees of disturbance as a result of human activity.

Separate cluster form *F. rufa* and *L. brunneus*, often found together. Despite the fact that *F. rufa* is an obligate high territorial dominant, *L. brunneus* is able to coexist with it, foraging on drying out oaks in closed tunnels, inaccessible to red wood ants.

The fourth cluster includes ant species represented in native plant communities — forests (pine and broadleaved, habitats G1.A162, G4.F, G1.A5), and also in meadows (*F. rufibarbis* in E2.1). These associations also

include red wood ants (*F. polycтена*), but they are much less common than other dominants (like the second species, *F. rufa*) and only in two habitats. The ratio between the most widespread species in all types of forests — broadleaf, coniferous, floodplain, as well as in forest parks and artificial habitats with areas of forest vegetation (Table 1) is changing.

The ant species which visit the maximum number of plant species in all habitats: *L. niger* - 22 species of 27, *F. cinerea*, *L. emarginatus* - 20 species, *L. fuliginosus*, *L. brunneus* - 15 species each, 18 species - *D. quadripunctatus*; *Myrmica* spp., *C. fallax* - 14 species each. 12 species - *Temnothorax* spp., 11 - *L. platythorax*. Other ant species visited 1-7 plant species.

By species, plant species in habitats belong to one cluster (Fig. 3). Outside the cluster are native species (*Q. robur* and *Ac. platanoides*). Pedunculate oak (*Q. robur*), the most attractive tree for ants. It was visited by 17 species of ants.

The rest of the plants are less attractive to ants. So, *Ac. platanoides* is visited by 13 species, *R. pseudoacacia* and *Pi. sylvestris* - 12 species each, *Q. rubra* - 10 species, *C. betulus* - 9 species of ants. 8 species were marked on *F. excelsior*, *Po. alba*, *T. cordata*, *B. pendula*, *Po. nigra*, *Ac. saccharinum*. On the remaining plants 3-7 species of ants were found. Of the invasive species the lowest number of species of ants was observed on *Ac. negundo* (5), *Am. fruticosa* (4). Thus, invasive species of phanerophytes can have different effects on the species richness of ants, entering both the groups with a high number of species and with a minimum. At the same time, the mass attendance of trees by ants better reflects the attractiveness of plants for ants.

General analysis of the influence of factors on the distribution of ants in assemblages

The relationship of abundance (species abundance) and relative frequency of species is expressed with environmental factors (illumination, canopy cover, the presence of aphids, the species of plants, their shape or age status (shrub, tree, saplings), the stem perimeter, as well as their origin and invasiveness (species origin 'nativeness'), as well as their behaviour and impacts ('invasiveness')).

Table 1. Distribution and mass character of ant species in habitats (in %)

Habitat	G1.A162	X11	G5.1	G1.A5	G4.F	E2.1	G5.2	G1.C2	G1.11
Ant species									
<i>Lasius niger</i>	0	43.0	45.0	0	0	36.0	5.0	20.0	40.0
<i>Formica cinerea</i>	2.0	32.0	16.0	0	48.0	36.0	0	0	5.0
<i>Myrmica</i> spp.	4.0	< 0.1	0	3.0	< 0.1	0	0	13.0	1.0
<i>Formica rufa</i>	16.0	0	0	0	0	0	0	0	0
<i>Lasius fuliginosus</i>	29.0	5.0	21.0	27.0	15.0	0	27.0	36.0	39.0
<i>Lasius brunneus</i>	4.0	4.0	5.0	11.0	< 0.1	0	17.0	4.0	6.0
<i>Lasius platythorax</i>	3.0	0	0	< 0.1	7.0	0	0	0	0
<i>Temnothorax</i> spp.	5.0	< 0.1	< 0.1	6.0	< 0.1	0	< 0.1	4.0	0
<i>Formica fusca</i>	< 0.1	0	0	0	< 0.1	0	0	0	0
<i>Camponotus fallax</i>	< 0.1	< 0.1	< 0.1	0	0	0	3.0	< 0.1	< 0.1
<i>Camponotus vagus</i>	0	< 0.1	0	0	< 0.1	0	0	0	0
<i>Camponotus ligniperda</i>	< 0.1	< 0.1	0	0	0	0	0	0	0
<i>Dolichoderus quadripunctatus</i>	2.0	2.0	1.0	8.0	0	0	1.0	4.0	2.0
<i>Leptothorax muscorum</i>	0	< 0.1	0	0	< 0.1	0	0	0	0
<i>Lasius emarginatus</i>	35.0	14.0	12.0	45.0	0	0	47.0	19.0	6.0
<i>Formica rufibarbis</i>	0	< 0.1	< 0.1	0	0	28.0	0	0	< 0.1
<i>Formica cunicularia</i>	< 0.1	0	0	0	0	0	0	0	0
<i>Formica polyctena</i>	0	0	0	0	28.0	0	0	0	0
<i>Lasius umbratus</i>	0	0	0	0	0	0	0	0	1.0
Total number of ant species in a habitat	14	13	9	8	10	3	7	10	10
Total number of worker ants counted in a habitat N + (%)	7821 (20.6)	14448 (38.1)	8361 (22.0)	603 (1.5)	2169 (5.8)	257 (0.7)	809 (2.2)	810 (2.2)	2592 (6.9)
Total number of plant specimens recorded in a habitat N + (%)	929 (14.0)	1480 (22.2)	1413 (21.2)	90 (1.3)	1150 (17.3)	240 (3.6)	217 (3.3)	313 (4.7)	830 (12.4)
Average number of recorded ants / 1 plant / 2 min in a habitat	8.34± 0.90	9.76 ±1.22	5.91± 0.40	6.70 ±1.51	1.88 ±0.34	1.07± 0.19	3.72 ±1.06	2.67 ±0.36	3.13 ±0.47

Note. Vertically - 100% - the total number of all ants recorded in a habitat, horizontally - 100% - the total number of ants and plant individuals in all habitats.

Effect of the invasive phanerophytes and associated aphids on the ant assemblages

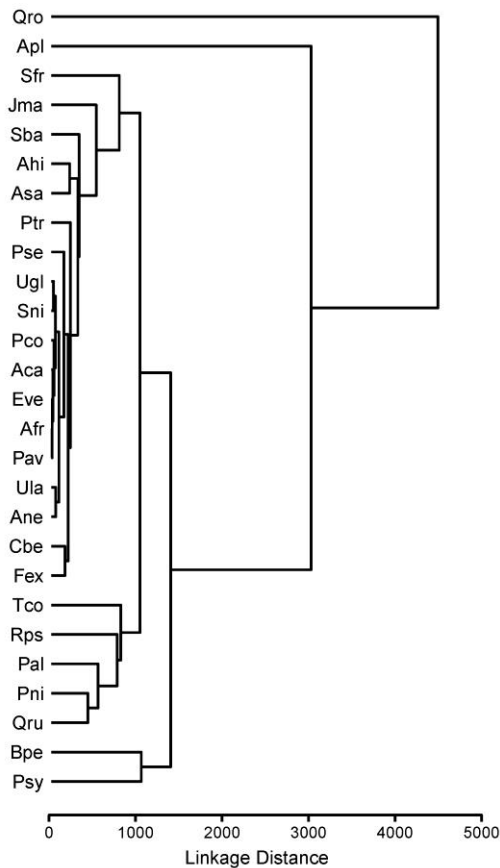


Figure 3: Dendrogram of ant's attendance of plant species in biotopes.

The analysis of co-inertia showed a low correlation between the abundance of species in individual locations and a complex of environmental factors, RV coefficient is less than 0.06, although it is clearly visible for some species of ants and individual factors (Fig. 4 a and b). Some environmental variables have a similar effect on the abundance of ant species (aphid presence and lifeform; stem perimeter, canopy cover and tree species) or the opposite, for example, canopy cover and illumination, aphid presence and plant origin (nativeness). The connection of the abundance of a species with environmental factors is more pronounced than in others in *L. niger*, *L. fuliginosus*, *L. emarginatus*, *F. cinerea*, *F. rufa* (Fig. 4a). The main drivers of an abundance of ant species are: the presence of colonies of aphids, the size of the tree trunk, the luminance (or crowns density) (Fig. 4b). Aphids on trees to be the most important for *L. niger* and *F. cinerea*, which form a separate cluster, *L. fuliginosus* and *L. emarginatus*, *L. brunneus* and *F. rufa* (see the dendrogram on the right in Figure 5a). The size of the trunk

has a similar effect and is combined with the previous factor in the cluster (left dendrogram Fig. 5a). The high abundance of *F. cinerea* is also associated with the woody life form of plants. The association of the abundance of other species with environmental variables is not obvious or disguised.

The influence of a complex of factors on the relative frequency of species is more pronounced than on abundance, RV coefficient - 0.11. The similarity of the effect of environmental variables is preserved, for example, the correlation of cover-origin-tree and circum-ap, but their meaning (loadings) differs from the previous analysis (Fig. 4d-e, Fig. 5b). So, the main factor is the life form / age state (form), which also reflects the layer. The effect of this factor is maximum and correlates with the size of the trunk, the presence of aphids and the type of tree according to the first component. For the second component, the second most loaded factor after the form is canopy cover (or illumination). The relationship of the relative frequency of a species with environmental variables, primarily the life form — the age state — is most pronounced for *Myrmica* sp., *Temnothorax* sp., forming a separate cluster according to the similarity of the response to factors (Fig. 5b). In *F. rufibarbis*, the relative frequency is also higher in the lower layer, but in low light there is a negative correlation with il (relative illuminance). A separate cluster (Fig. 5b) forms *Leptothorax* spp., *C. vagus*, and *F. fusca*, the relative frequency of which is higher in trees of the native flora fraction - a positive correlation with an origin, and for *F. rufa* the size of the tree is crucial (circum). The influence of the origin and invasiveness of the tree species (origin) on the relative frequency of ant species is not obvious. Habitats are poorly separated by variations in the relative frequency of species, but their ellipses of variation are oriented along form or circum factors, which isolates the E2.1 habitat, in which the presence of plants of low-layer and high illumination create favorable conditions for *F. rufibarbis* (Fig. 4e).

Although the classical analysis of covariance does not allow separating the assemblages of ants in separate habitats (Fig. 4d), removing variations related to plant size by the cDPCoA method, the difference in the assemblages of ants in habitats has become more apparent.

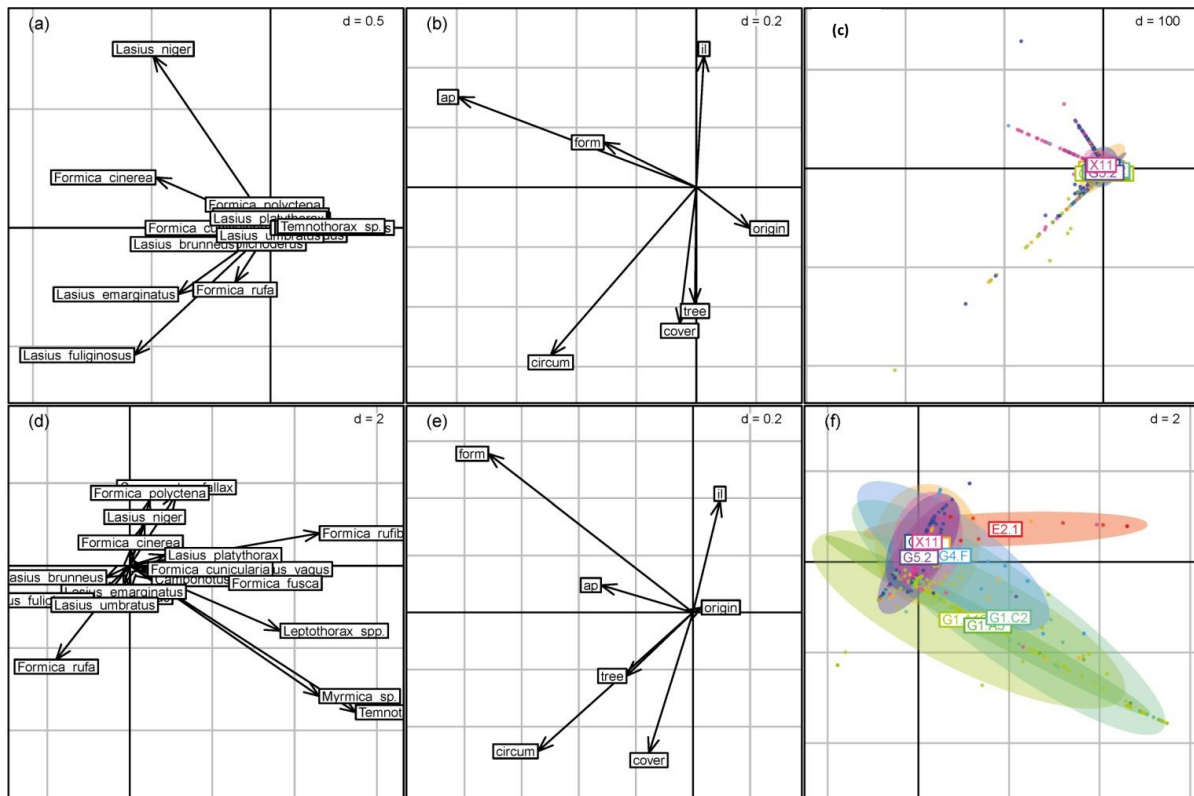


Figure 4: The co-inertia analysis of two data sets (ant species and environmental variables). **Panels a-d:** PCA-PCA COIA based on absolute ant's species composition. **Panel a:** factor map of the ant species abundance. **Panel b:** the factor map of environmental variables. **Panel c:** species-constrained locality scores grouped by habitats. The ellipsoids represent species association variability within habitats. **Panels d-f:** Same as in panels a-d, but for PCA-CA COIA based on ant species' relative frequency. Code for environmental variables: ap – aphids' colonies presence on trees; circum – trees stem perimeter, cover – canopy cover; form – life form and life history stage of woody plants, il – relative illuminance; origin – woody plant origin ('nativeness') and 'invasiveness', tree – woody plant species

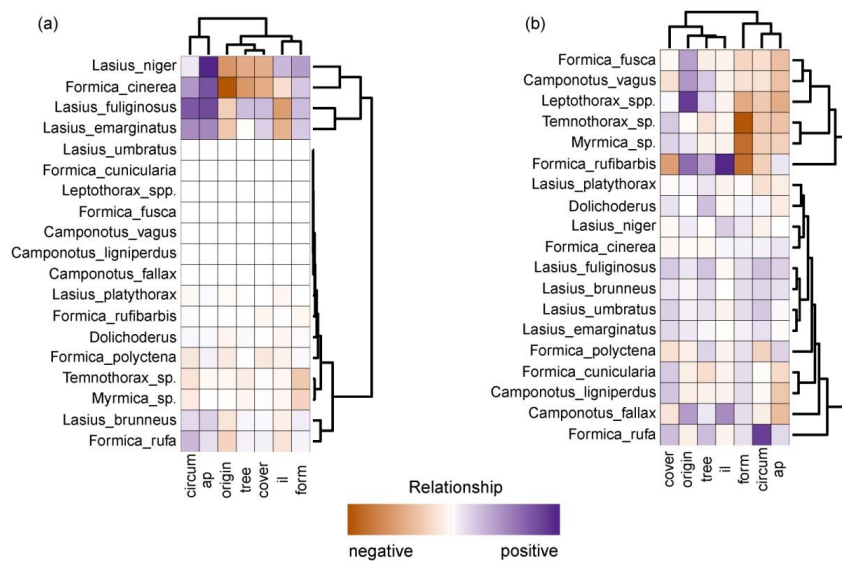


Figure 5: The crossed table coefficients resulted from COIA. **Panel a:** relationships between ant species abundance and environmental variables. **Panel b:** same as in panel a, but for species relative frequency. The dendrograms are the results of crossed table coefficients running through the Average hierarchical clustering algorithm. (see Fig. 4 for environmental variables cod)

Effect of the invasive phanerophytes and associated aphids on the ant assemblages

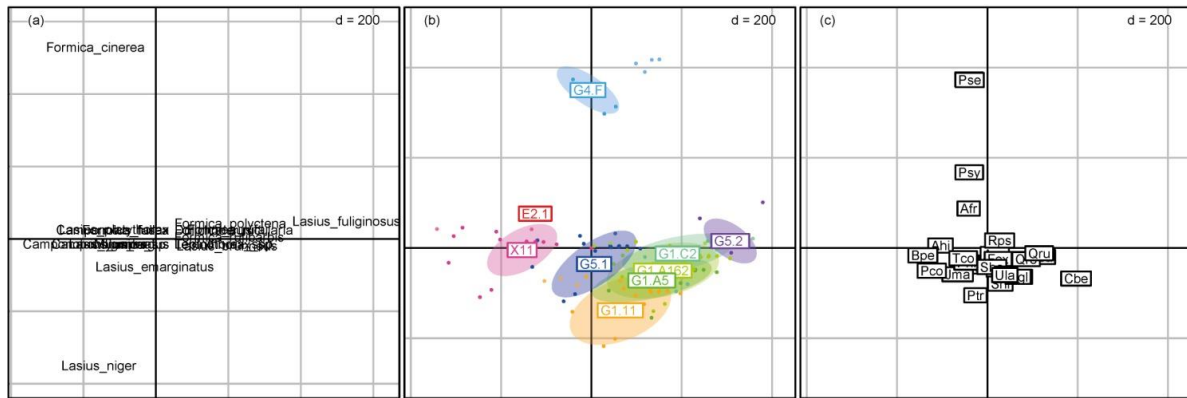


Figure 6: Panel a: The effect of each ant species in association variability. Panel b: Decomposition of the ants' association according to habitat type resulting from between-class analysis (cDPCoA), in which the effect of plant size has been removed. Panel c: The effect of plant species on ant community variation (see Fig. 4 for environmental variables cod)

The percentage variation in species abundance unrelated to plant size was 12% ($p < 0.001$). The differences in habitats in ant assemblages are associated with the dominance of *F. cinerea*, *L. niger*, *L. fuliginosus*, and *L. emarginatus* in habitats, where there are high incidence of invasive species in the studied areas (Fig. 6 a-c). Thus, workers of *F. cinerea* were found in large numbers in G4.F (67% of invasive woody plants), including the invasive species *Padus serotina*. In E2.1. (50% of invasive species) *F. cinerea* with co-dominant *L. niger* are found on invasive *Robinia pseudoacacia*. *L. niger* has a high abundance in X11 (~ 20% of invasive trees), where besides native species it is abundant on *Quercus rubra* and *Robinia pseudoacacia*. In G5.1, invasive plants (~ 50%) showed a high abundance of not only *L. niger* and *F. cinerea*, but also other species of ants. *L. fuliginosus*, and *L. emarginatus* influence the variation of associations due to the high abundance of introduction of invasive plants in G1.C2 (~ 80% of invasive trees) and G5.2 (~ 100% of invasive woody plants).

The attractiveness of different species of plants for ants in different habitats

The plant species most widely visited by ants is the pedunculate oak (Supplementary Table 1). From 7 to 23 ants / 2 min were found on oak trunks. Oak is followed by maple (*Ac. platanoides*) and white poplar (*Po. alba*), on which from 6 to 16 ants / 2 min in different habitats. The well-visited plants by ants also include linden (*T. cordata*), birch (*B. pendula*), pine (*Pi. sylvestris*), red oak (*Q. rubra*),

Manchurian walnut (*J. mandshurica*) and, to a lesser extent, *Robinia (Ro. pseudoacacia)*. The following species are practically not visited by ants: *Ac. negundo* (0.006 to 0.5 / 2 min), *Pa. serotina* (from 0 to 0.45), *Am. fruticosa* (from 0 to 0.4), hornbeam (*C. betulus*, 1.8), Euonymus (*E. verrucosus*, 0.2). The remaining species of plants are visited by ants to a greater extent, but not as actively as plants with maximum attendance.

According to the average ants attendance of phanerophyte for all habitats, we can distinguish several groups in descending order. The first group includes oak (*Q. robur*), maple (*Ac. platanoides*), as well as weeping willow (*S. alba*), all native species widely visited by ants (12-16 ants / 2 min). The second group includes plants that are 1.5-2.0 times ($p < 0.05$) less visited by ants - *Po. alba*, *T. cordata*, *B. pendula*, *Pi. sylvestris*, *Q. rubra*, *S. fragilis*, *J. mandshurica*, *Po. tremula*, *Po. nigra* (6-8 ants / 2 min). Of these, 1 species is invasive (*S. fragilis*), 2 are introducents (*Q. rubra*, *J. mandshurica*). The remaining 6 species are native. The third group consists of species with attendance of 6-8 times less than that of plants of group 1 (1-3 ant / 2 min, with $p < 0.05$). These include the following species of phanerophytes: *Ae. hippocastanum*, *Ac. saccharinum*, *Py. communis*, *R. pseudoacacia*, *S. nigra*, *U. laevis*, *F. excelsior*, *C. betulus*, undergrowth of *Ac. platanoides*. Of these, 2 species (*Ae. hippocastanum*, *Ac. saccharinum*) are introduced species, 1 is invasive (*R. pseudoacacia*), and the remaining 6 are native. Finally, the last group is formed by plant species that are practically not visited by ants

(attendance on average 0.3 ant / 2 min, 40-50 times less than that of plants of group 1, with $p < 0.05$). These include the following species: *Ac. campestre*, *Ac. negundo*, *Pa. avium*, *Pa. serotina*, *Am. fruticosa*, *U. glabra*, *E. verrucosus*. Almost half of them are invasive plant species and introducents (*Ac. negundo*, *Pa. serotina*, *Am. fruticosa*). All these species belong to shrubs (*Pa. avium*, *Pa. serotina*, *Am. fruticosa*, *E. verrucosus*) or young trees (*U. glabra*, *Ac. campestre*, *Ac. negundo*). The exception is *Ac. negundo*, unattractive to ants in the form of undergrowth, and in the form of trees. The same features are preserved in plants and in each of the habitats. So, *Ac. negundo* in habitat G5.1 is 27 times less than *S. fragilis* in attendance, as many as in G1.11 habitat in white poplar trees (*Po. alba*) and 83 times in oak (*Q. robur*) right there ($p < 0.05$). For *Am. fruticosa* in the G4.F habitat is 190 times lower in attendance than in pine (*Pi. sylvestris*) and 9 times less than in *Pa. serotina*. The same applies to other plants. In some plants, depending on the conditions of the habitat, attendance may vary. For *R. pseudoacacia* in the X11 habitat, attendance is 3 times less than that of *Po. alba*, and in the habitat G5.1 - almost the same. Some species differ in attendance at different phases of the life cycle. At the undergrowth stage of *Ac. negundo* attendance is 100 times lower than that of mature trees in the habitat G5.1, and in *Ac. platanoides* in the habitat G1.A162 is only 1.8 times less ($p < 0.05$). For *Po. alba* in habitat G1.11 similar data were obtained - 3 times lower attendance of seedlings ($p < 0.05$). For *Q. rubra* in the habitat G1.C2, saplings and undergrowth are 4 times less intensively visited by ants ($p < 0.05$).

Invasive and introduced species are included in all groups, except for those most visited by ants. The attendance rates (maximum or minimum) for different species are preserved in all habitats where these plants are present. In the transition from plants with a maximum to those with a minimum attendance of ants, the number of invasive and introduced species increases. The total attendance of ants prevails on native plant species.

A smaller total number of ants were recorded on introduced species of plants, and a minimum total number of ants were recorded on plants of invasive species. Thus, due to invasive species of plants that are unattractive to ants, abundantly represented in a number of

habitats (*Am. fruticosa*, *Ac. negundo*), their overall impact on the ants' mass visits is negative. For introduced species, the effect is generally neutral.

Trophobiosis of ants with aphids

Ants nest and have food trails on phanerophytes. One of the reasons for the attractiveness of plants for ants is the presence of aphid colonies producing sugary excreta (Fig. 7). Excreta of aphids are the main source of carbohydrate for the ant colony.

On *Am. fruticosa* plants we observed colonies of aphids visited by ants only in isolated cases (Fig. 7A). In some cases (for example, on the red oak trees), there are colonies of aphids numbering hundreds of individuals (Fig. 7B). Colonies of aphids feeding on *Robinia* may not be visited directly by ants. In this case, food was observed in sugary excreta, which fell on the leaves on the lower branches (Fig. 7D). In other cases, the ants visited the aphids (Fig. 7C). On *P. serotina* plants, ants visiting colonies of aphids, were observed only in spring, in April (Fig. 7 E). For white poplar, which is an invasive species north of Moscow, and in Ukraine - a native one, an active visit by ants to colonies of aphids on leaves and young shoots was also observed (Fig. 7E).

Plants whose life forms are perennial (trees, shrubs) have been a resource for ants for many years. Therefore, control over them is a priority for dominant ants with large colonies. The food trails of most dominant species always end in trees, where the aphid colonies are located. According to our data, the average attendance by ants of phanerophytic plants with aphid colonies in all habitats is 10 times higher compared to plants without aphids ($3.3 \pm 0.05 / 2$ min for plants without aphid colonies and $31.7 \pm 1.12 / 2$ min for plants with aphid colonies, $p < 0.01$). However, different plant species have different ants attendance rates due to different susceptibility by aphids (Table 2).

The most common colonies of aphids are found on pedunculate oak, white poplar, linden, birch, red oak, black poplar, pine, and brittle and weeping willows, sugar maple and platanol maple (from 17 to 40% of the plants examined). Of these, 2 species are introduced species (*Q. rubra*, *Ac. saccharinum*) and 1 - invasive (*S. fragilis*). In this case, pedunculate oak prevails over the rest species of the plants

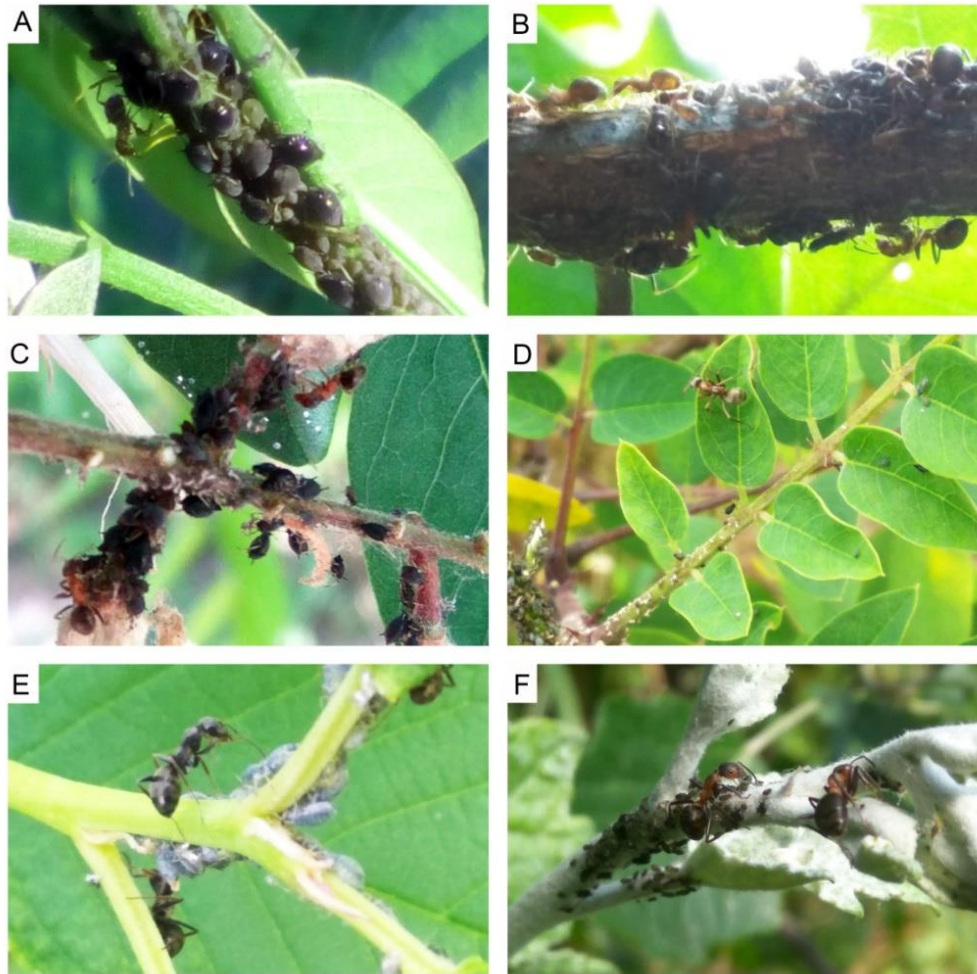


Figure 7: Ants attendance of aphid colonies on native, introduced and invasive species of phanerophytes. **A.** *Amorpha fruticosa*, ants *Formica cinerea* and aphids *Aphis craccivora*; **B.** *Quercus rubra*, ants *F. polycтена* and aphids *Lachnus roboris*; **C.** *Robinia pseudoacacia*, ants *Lasius emarginatus* and aphids *Aphis craccivora*; **D.** *R. pseudoacacia*, ants *F. cinerea* and aphids *Aphis craccivora*; **E.** *Padus serotina*, ants *Camponotus vagus* and aphids *Rhopalosiphum padi*; **F.** *Populus alba*, *F. rufa* ants and aphids *Chaitophorus populeti*.

- aphids, visited by ants here on almost every second tree. The second group includes species of phanerophytes with 0.5 - 2.0 times less susceptibility by aphids - aspen, robinia, hornbeam, ash, elder, elm (*U. laevis*), manchurian nut (from 3 to 14%). Of these, 1 species is introduced (*J. mandshurica*) and 1 is invasive (*R. pseudoacacia*). Finally, the third group consists of plants that are practically not populated by aphids, at least those species that are not associated with ants by trophobiosis. Part of the species we studied (*Euonymus* and some others), due to the small sample size, fell into the third group, although there are aphids on them (see below). These include *Amorpha*, both species of bird cherry trees, ash-leaved maple, pear, chestnut, spindle tree and elm (*U.*

glabra), as well as *Acer campestre*. 2 of them are invasive (*Am. fruticosa*, *Ac. negundo*), 2 - introducents (*A. hippocastanum*, *Pa. serotina*). Invasive species of phanerophytes, as well as introducents, in terms of susceptibility by aphids (and, as a result, attractiveness for ants) can be included in all three groups of plants, having both positive, neutral and negative effects.

In the wood of still living plants not all species of ants can nest, but only dendrobionts (see. Material and methods). This is associated with less attractiveness of phanerophytes as habitats for ants (Table 2). The first group consists of pedunculate oak, willow brittle and weeping, as well as white poplar. Only one of the species is invasive (*S. fragilis*). The ants

nesting in these plants in the range of 11-22%. In the plants of the second group, ants are nesting 2-5 times less often (from 2 to 8% of all trees of this species, $p < 0.05$). These are: *C. betulus*, *F. excelsior*, *R. pseudoacacia*, *Po. nigra*, *Po. tremula*, *Ac. saccharinum*, *A. hippocastanum*, *U. laevis*, *J. mandshurica*, *Q. rubra*, *Pi. sylvestris*, *B. pendula*, *T. cordata*, *Ac. platanoides*. Of these, 1 species is invasive, 4 are introduced species. Finally, the third group consists of species in which ants do not build nests in the wood, or these cases are rare: *Pa. serotina*, *Am. fruticosa*, *Ac. negundo*, *Acer campestre*, *Pyrus communis*, *Padus avium*, *S. nigra*, *U. glabra*, *E. verrucosus*. It should be noted that most of them belong to the shrubs and dominant ants in them are not inhabited. On the other hand, ants such as *Temnothorax* spp., *Leptothorax* spp. can even nest on shrubs (in thin stalks or trunks) but they were not included in our records. Ants did not inhabit in *Ac. negundo* trees and in rare cases marked on trees *Pa. serotina*.

As for the food trails of ants, their presence is directly connected with colonies of aphids or with a nest in the trunk of a given tree. The relationship between aphid colonies and food trails is more clearly seen (0.92). This is due to the fact that not all species of ants arrange nests in the trunks of trees (0.44). However, not all trees with nests have colonies of aphids (0.41). Thus, the attendance of ants of trees is primarily associated with the presence of aphid colonies, and only the second with nesting.

The attendance by ants on mature trees, undergrowth and seedlings

Different life forms of the same plant species may have unequal attractiveness for aphids, and therefore for visiting ants. For example, *Robinia* undergrowth is inhabited by aphids 2.0 times more often ($p < 0.05$, Table 2) than mature trees. If maple (*Ac. platanoides*) and white poplar saplings are affected by aphids almost as often as mature trees, then brittle willow and red oak have the opposite effect ($p < 0.05$, Table 2). In general, meristemophilous species of aphids live on the undergrowth, phyllobionts can settle equally often on the undergrowth and on adult plants, while the inhabitants of the bark of branches and trunks will be on adult plants.

Undergrowth and trees of *Ac. negundo* are not attractive to ants and aphids. Nevertheless in isolated cases, trees are inhabited by dendrobiontic ants and are visited by individual foragers (Supplementary Table 1). Species of phanerophytes belonging to shrubs, as a rule, are less attractive for ants (*Am. fruticosa*, etc.). For different species of phanerophytes (including invasive ones), mutually opposite tendencies can be observed in visiting undergrowth and mature trees. Some species are unattractive to ants, both in the form of undergrowth and trees.

47 species of aphids (Aphididae) were found on 18 native species of plants-phanerophytes (Supplementary Table 2). For 9 invasive plant species, 14 aphid species were found. Only one aphid species (*Aphis craccivora* Koch) found on invasive plant species is invasive.

The effect of illumination on the attendance of ants on invasive plant species

Among habitats, the maximum average illumination is fixed for G5.2 (Supplementary Table 3), followed by habitats with illumination 1.3 times less (E2.1) and 3.8 times (X11, G5.1, G1.A5, G4.F, G1.11, G1.C2). The minimum illumination in the habitat of G1.A16 is 12 times less. Depending on the species composition of plants, the average light intensity in a habitat will vary. Different species of plants will make a different contribution. For example, *Ac. negundo* enhances shading, as does *Ac. platanoides* (Supplementary Table 3). Under oak trees, which make up 1st layer, the illumination on average in habitats is 1.4–1.5 times higher than that under *Ac. platanoides*. Thus, in the habitat G1.A16, in the second layer, composed of hornbeam and maple trees, the illumination is already worse. In the 3rd layer, composed of bushes, the illumination varies - from 1.4 times smaller under the *Euonymus* (than under the *A. platanoides*, Supplementary Table 3) to 7 times smaller under the *S. nigra* (than under the *A. platanoides*, Supplementary Table 3).

R. pseudoacacia has no significant effect on shading. *Amorpha fruticosa* grows in more illuminated places, but, it is practically not visited by ants. *Padus serotina* at the undergrowth also does not have a significant effect on shading, but when it becomes a tree, it can strengthen it. Overlaying layers on each

Effect of the invasive phanerophytes and associated aphids on the ant assemblages

other will enhance shading, especially if they include species that contribute to it.

The average number of ants per plant / 2 min in areas with high illumination (from 5% of illumination in open areas) and in areas with low does not differ significantly (up to 5%): In the first case, the average number of ants for 2 min was 11.64 ± 0.70 , in the second 13.68 ± 0.55 . We found no significant correlations between the total number of ants and the level of shading in all habitats.

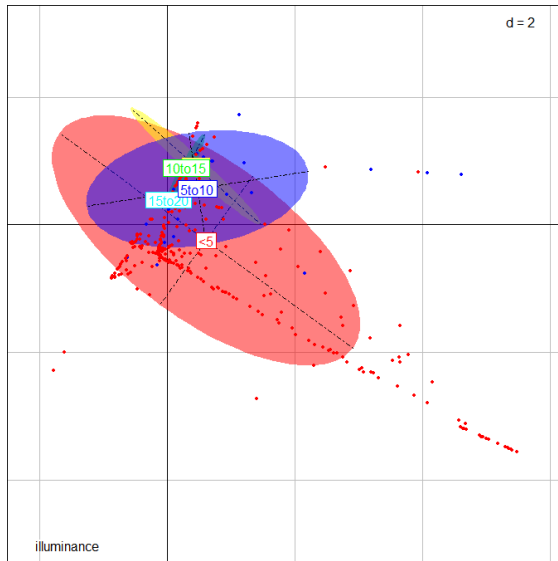


Figure 8: The total number of ants, depending on the level of illumination (up to 5, 5-10, 10 or more% of the coefficient in open areas).

Different species of ants can make the main contribution to the attendance of plants due to their stationary preferences. For example, *F. cinerea* prevails in habitats with a high level of illumination, while *L. fuliginosus*, *L. brunneus*, on the contrary, prefer shaded areas.

With a more detailed comparison of the total number of ants in areas with different illumination, it was found that most of all ants live in habitats with a low level of illumination (Fig. 8).

Approximately 1.5 times less ants were recorded in areas with illumination from 5 to 10%, and at least in well-illuminated areas (from 10%). Thus, the total number of ants in all the studied habitats is inversely proportional to the illumination level.

Ant's attendance on *Robinia pseudoacacia* during the flowering and fruiting phase

Robinia pseudoacacia is one of the two invasive plants we studied, which is a honey plant. The second one is *Pa. serotina*, but for it species we did not conduct studies. We found no difference in attendance by ants between flowering *Robinia* trees and the same trees during the fruiting (an average of 3.58 ± 0.71 ants per 2 min in flowering and 4.85 ± 1.65 in fruiting ones). At the same time, the number of species of ants on flowering plants is 2.0 times greater ($p < 0.05$): 0.6 ± 0.08 against 0.31 ± 0.06 .

Table 2. The occurrence of colonies of aphids, the number of nests and food trails of ants on plants-phanerophytes

Species of plants	The occurrence of aphids colonies, %*	The number of ants nests, %*	The number of forage trails, %*
<i>Quercus robur</i>	40.36	22.90	40.36
<i>Acer platanoides</i>	29.06 + 10.47 (\$)	6.69	29.06 + 3.80 (\$)
<i>Salix alba</i>	20.58	17.60	20.58
<i>Populus alba</i>	32.41 + 29.28 (\$)	11.72	33.10 + 6.42 (\$)
<i>Tilia cordata</i>	31.98	8.07	31.98
<i>Betula pendula</i>	34.38	2.26	34.38
<i>Pinus sylvestris</i>	20.07	2.81	20.07
<i>Quercus rubra</i>	18.03 + 0 (\$)	5.34	17.69 + 0 (\$)
<i>Salix fragilis</i>	24.26 + 0 (\$)	11.76	24.26 + 0 (\$)
<i>Juglans mandshurica</i>	14.0	6.00	14.0
<i>Euonymus verrucosus</i>	0	0	0
<i>Ulmus glabra</i>	0	0	0
<i>Ulmus laevis</i>	4.47	7.46	7.46
<i>Salix nigra</i>	11.11	0	0
<i>Aesculus hippocastanum</i>	0	2.72	10.88
<i>Acer saccharinum</i>	17.92	5.66	17.92

<i>Padus avium</i>	0	0	0
<i>Pyrus communis</i>	0	0	0
<i>Populus tremula</i>	14.28	4.08	14.28
<i>Acer campestre</i>	0	0	0
<i>Populus nigra</i>	22.7 + 0 (\$)	1.86	22.2 + 0 (\$)
<i>Robinia pseudoacacia</i>	11.06 + 26.6 (\$)	4.39	11.06 + 3.33 (\$)
<i>Fraxinus excelsior</i>	0	7.22	7.22
<i>Carpinus betulus</i>	3.12	6.66	3.03
<i>Acer negundo</i>	0 + 0 (\$)	0.33	0 + 0 (\$)
<i>Padus serotina</i>	0.40	0	0.39
<i>Amorpha fruticosa</i>	0.95	0	0

Note. * - 100% of all trees of this species are taken in all habitats. (\$- saplings)

We did not observe direct visits by ants on flowers. In addition to the dominants of *L. emarginatus*, *L. niger*, the subdominants *L. brunneus*, *C. fallax* were also noted during flowering. Perhaps it is these species of ants that are attracted not only to the excreta of aphids, but also to the nectar of flowers. In addition, it is possible for ants to collect nectar from fallen flowers on the earth's surface, but we did not conduct any special studies on this subject.

Discussion

The attractiveness of invasive phanerophyte for ants

North American species in the flora of Kyiv have the largest proportion (share) among those introduced in the 20th century (Mosyakin and Yavorska, 2002). According to literary data, among invasive plant species, both a positive (or neutral) effect on the species richness of ants and a negative one are manifested. *Robinia* has a positive effect on the cover of nitrophilic and ruderal plant species (Dzwonko and Loster, 1997). Among the 18 studied arthropod taxa in Berlin, Germany, *Robinia* has a negative effect on the abundance of five (Chilopoda, Formicidae, Diptera, Heteroptera, Hymenoptera, according to (Buchholz *et al.*, 2015)). For example, in forest areas dominated by *Robinia*, ant species are 2.5 times less than in areas with birch (6 vs. 14 species, (Weiss *et al.*, 2005)). This is also shown by our data, in the mapping of ants' attendance rates of trees and the undergrowth of *Robinia*, nesting and the occurrence of aphid colonies.

In the EU countries, Poland and Germany, red oak (as well as *P. serotina*, according to (Tokarska-Guzik, 2005)) is one of the most economically significant invasive phanerophytes. Red oak contributes to the

reduction of biodiversity in forest communities, both in the form of seedlings and mature trees. Mature trees have a negative effect on the cover of seedlings of other species, as well as on the shrub layer. Seedlings have a negative effect on seedlings of other tree species (Chmura, 2013). Coating of another invasive species - *P. serotina* negatively correlates with the number of grassy plant species (Godefroid *et al.*, 2005). For red oak, according to our data, in the conditions of Kyiv and the region, ants attendance rates can be attributed to the average among all plants. This plant does not have a clear negative effect on the ant assemblages, which may be a consequence of the development of colonies of myrmecophilous aphids on it.

Nesting: In addition to trunks or branches of trees, ants can be populated on their fruits. The acorns of red oak are intensively populated by ants *Leptothorax ambiguus* Emery in North America (Alloway and Hodgson, 1990). On the territory of the secondary range of *Q. rubra*, in Europe, another species of ants, *Temnothorax crassispinus*, populates acorns of red oak in large quantities, and significantly more than natural oak species (Myczko *et al.*, 2018). For *Ac. negundo* attendance and nesting of ants were not recorded, not only according to our data, but also on the previously obtained data for the parks of Warsaw, Poland (Czechowski *et al.*, 1990). At the same time, other species of invasive phanerophytes were visited and colonized by ants - chestnut (ants: *L. brunneus*, *L. niger*), *Robinia* (*L. brunneus*, *M. laevinodis*). Ants are fixed on red oak trees. As in our case, the most populated and visited trees by ants belonged to natural species - maple (*Ac. platanoides*) and pedunculate oak.

Relationship between invasive phanerophytes and aphids

For aphids, plants from the *Salix*, *Quercus*, and *Betula* genera are most attractive, based on data from Hungary (Csóka, 1998; Csóka, and Hirka, 2002). It is also noted that specialized phytophages almost never colonize red oak plants (Csóka and Hirka 2002; Holman, 2009). Later data showed that red oak in Europe (the Czech Republic and other countries), in addition to natural ones, is colonized by the North American species of aphids *Myzocallis walshii*, which feeds only on this plant (Havelka and Stary, 2007).

Thus, in some cases, red oak can be populated with both invasive and natural aphids and be attractive to ants. This is shown by our observations. For *Pa. serotina* in the Netherlands indicates 13 species of aphids, 5 of which were encountered in the autumn (Lambers, 1971). In the absence of their main primary food plants, these species of aphids can over-winter on the bird cherry and in the spring produce several generations, i.e. the bird cherry contributes to the preservation of these species even in the absence of their main food plants. However, this phenomenon is rather extreme, not massive. This can hardly be considered as a potential attractiveness for ants as a whole, although the number of species far exceeds that found by us. Perhaps the effect of bird cherry on the association of ants is neutral.

Some species of invasive phanerophytes are intensively colonized by aphids. For example, for *Robinia* in Iran, the cosmopolitan species *Aphis craccivora* Koch, 1856 is indicated, visited by the ants *Crematogaster inermis* Mayr, 1862 (Mortazavi *et al.*, 2015). This species of aphids is indicated as an effective agent against the spread of *Robinia* (Jalalipour *et al.*, 2017).

Acer saccharinum can also be inhabited by aphids (*Stomaphis graffi*) and, accordingly, can be visited by ants (*Myrmica rugulosa*, (Depa, 2012)), although the findings of these aphids are rare for Ukraine. Based on our data, *Acer saccharinum* is attractive to aphids and ants. The species of phanerophytes that are not populated by aphids (*Ac. negundo* and others) are unattractive for ants.

Species of aphids and their life cycles on native and invasive phanerophytes

In the greenery of Kyiv on *Acer negundo* in May - early June, small colonies of the European species (1) *Periphyllus testudinaceus* (Ferne, 1852) can be observed. They arise from the dispersal of aphids from native species of maples (*Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *A. tataricum*) and the introduced species *A. saccharinum*, on which eggs hibernate. In early spring (with warm weather in the third week of March) founders develop from eggs. These colonies are visited by ants, in the spring. But in the beginning of June aphid colonies completely disappear, because *P. testudinaceus* develops with an obligate summer larval diapause and in summer only diapausing larvae (dimorphs) remain on the plants. Sexual generation (morphs) and fundatrices of *P. testudinaceus* on *Acer negundo* were not found and the holocyclic life cycle of aphids was not revealed. *Acer negundo* is probably not suitable for feeding the fundatrices of *P. testudinaceus*.

Robinia pseudoacacia is massively affected by the North American species of aphids, *Aphis craccivora* Koch, 1854. This aphid species was introduced, along with some food plant (probably *R. pseudoacacia*), to Europe, presumably in the 17th century, now cosmopolitan. In most of the range, anholocyclic development occurs, the larvae of *A. craccivora* overwinter on the root parts of herbaceous plants. Data on the development of aphids with a full cycle were also observed, there were reports of hibernating eggs found on the basal parts of alfalfa (*Medicago sativa*), but the sexual generation and founders were not described (Mamontova, 1957). Regardless of the type of life cycle, in May there is active resettlement of plants mainly to plants of the Leguminosae family (2).

At this time, white (*R. pseudoacacia*) and yellow acacia (*Caragana arborescens*) are massively affected by aphids. Aphids are localized on young shoots, inflorescences are colonized during the flowering period, and they are transferred to active growth of young plants.

(1) *Periphyllus testudinaceus* imported to N. America, Australia and New Zealand.

(2) *Aphis craccivora* can colonize plants of other families, most often during a hot period, on the basis of this fact, the species is considered as a polyphage.

Colonies of aphids are massively visited by ants, they can stay on plants until September. According to literary data, *R. pseudoacacia* can also be settled by *Aphis fabae* Scopoli, 1763 (Blackman and Eastop, 1994; Holman, 2009).

The colonies of *A. craccivora* were marked on several plants of *Amorpha fruticosa*, the aphids colonized young shoots; during the flowering period they were localized in inflorescences and passed on to the fruits during their formation and maturation. According to literary data, *A. fruticosa* can also be populated by *Aphis cytisorum* Hartig, 1841 and *A. fabae* Scopoli. (Blackman and Eastop, 1994; Holman, 2009).

Archaeophyte *Salix fragilis* is well populated by native species of aphids. So in the area of our research on this plant, 12 species of aphids were identified, of which 9 are myrmecophilous. *Chaitophorus mordvilkoii* Mamontova and Szelegiewicz, 1961 and *Ch. truncatus* (Hausmann, 1802) are not visited by ants (Pintera, 1987), and in the colonies of *Ch. niger* Mordvilko, 1929, ants are found sporadically. Aphids of the genus *Cavariella* delGuercio, 1911 (*C. aegopodii* (Scopoli, 1763), *C. archangelicae* (Scopoli, 1763), *C. pastinacae* (Linnaeus, 1758), *C. theobaldi* (Gillette & Bragg, 1918)) develop with heteroecious cycle at the end of May-June migrating to the plants of the family Umbelliferae (Mamontova, 1961). On willows, colonies of aphids along with ants are localized on the lower surface of leaves. The remaining species of aphids are monoecious. *Tuberolachnus salignus* (J.F. Gmelin, 1790) development is anholocyclic, aphids are localized on old shoots, the maximum number is reached in the second half of summer, always visited by ants en masse. Due to an anholocyclic development, the number of aphids in different years strongly depends on the conditions of the winter period and the number of surviving hibernating larvae. In the case of a warm winter, mass outbreaks can be recorded, and in case of strong winter frosts, aphids are practically absent as in the summer. Aphids of the genus *Pterocomma* Buckton, 1879 (*P. pilosum* Buckton, 1879, *P. salicis* (Linnaeus, 1758)) are localized on old shoots, at the base and in cracks in the bark on trunks, often in shelters created by ants, develop strongly throughout the season, but they can greatly influence the number parasites and

predators. *Ch. vitellinae* (Schrank, 1801) inhabits young branches and leaf petioles, develops from spring to autumn, although the number during the season may vary depending on weather conditions and pressure from predators and parasites. *Aphis farinosa* J.F. Gmelin, 1790 forms dense colonies on the bark of young shoots, always with ants. The maximum number is observed in May-June, a facultative shortened life cycle is a characteristic (bisexual generations appear in the beginning of July, at the same time parthenogenetic generation can develop until September). In this regard, the number of aphids drops significantly in the second half of summer, and the species is heavily affected by parasites at this time of the year. The number of species of introduced plants in the green spaces of Kyiv is difficult to estimate, many species are represented by single specimens in botanical gardens and some parks. A number of species are widely introduced into green building and are found everywhere. Of these species, in places where our studies were conducted, *Aesculus hippocastanum*, *Juglans manshurica*, *Padus serotina*, *Acer sacharinum*, *Quercus rubra* are massively represented.

Species of aphids that are trophically confined to the *Aesculus hippocastanum* are not known. However, sometimes during the flowering period, polyphages *A. fabae* and *A. craccivora*, visited by ants, can be observed in the inflorescences. After flowering, aphids completely disappear. According to literary data, maple species of *P. testudinaceus* and *Drepanosiphum platanoidis* (Schrank, 1801) were observed on horse chestnut, which was probably the result of accidental colonization (Blackman and Eastop, 1994; Holman, 2009). In the greenery of Kyiv, these species of aphids on *Aesculus hippocastanum* were never found. *Juglans manshurica* marked adventive colonies of aphids of the species *Panaphis juglandis* (Goeze, 1778), which had long since penetrated, following their forage plant *Juglans regia* probably from initially Asia Minor and Middle Asia into the territory of Ukraine. As a rule, aphids *Panaphis juglandis* live on walnuts; there are few reports of their colonization of manzhur walnut (Holman, 2009). The basis of the food for ants on the Manchurian nut and some other plants not inhabited by aphids can be other sucking insects - coccides and Diaspididae. Aphids are located on the upper surface of the leaves

along the large veins, develop throughout the season, and are actively visited by ants.

The colonies of *Rhopalosiphum padi* (Linnaeus, 1758) are found on *Padus serotina*. This species is currently almost cosmopolitan, in Europe it is usually inhabited by *Padus avium*, in North America it is common on *P. virginiana*, but it is also known on *P. serotina* (Blackman and Eastop, 1994). The species is obligatory heteroecious, host-alternating between bird cherry and many cereals. It starts to develop quite early, the fundatrices can sometimes be found already at the end of March, by the end of April they can reach a considerable number by localizing on young shoots and leaves, after twisting them. They are actively visited by ants. By mid-May, most aphids leave the bird cherry flying onto cereals. By the end of May they migrate completely.

Acer sacharinum is well mastered by native species of aphids. The plant is colonized by European species of aphids: oligophage *P. testudinaceus* which feed on many species of maples, and trophic related with *Acer pseudoplatanus* include aphids like *Periphyllus acericola* (Walker, 1848) and *Drepanosiphum platanoidis* (Schrank, 1801), as well as *Periphyllus lyropictus* (Kessler, 1886). *P. lyropictus* is widespread in Europe on *Acer platanoides*. Aphids, *P. acericola*, as well as *P. testudinaceus*, are characterized by a life cycle with an obligate summer larval diapause. Therefore, from the beginning of June only diapausing larvae (dimorphs) remain on plants. Thus, *P. testudinaceus* and *P. acericola* may affect the attractiveness of *Acer sacharinum* for ants only in spring. Unlike these species, *P. lyropictus* develops without summer diapause and can be observed on the leaves of *Acer sacharinum* throughout the seasons, however, the mass reproduction of aphids occurs usually in June; aphids secrete a lot of honeydew and heavily pollute the plants. *D. platanoidis* reaches numbers at the end of May-June, however, with a cool summer, the peak of numbers may shift by July-August (with a hot summer there is a summer diapause). All species are localized on the lower surface of the leaves, and *P. testudinaceus* is also seen on young shoots (the fundatrices appearing before the leaves bloom are localized on the bark of the shoots of previous year, which indicates the holocyclic development of this species of aphids on *Acer*

sacharinum, unlike *Acer negundo*), *P. lyropictus* can transfer on to young fruits. All species of aphids myrmecophylic.

Until recently, aphids were not recorded on *Quercus rubra* in the study area, but we found significant colonies of *Lachnus roboris* (Linnaeus, 1758), which may indicate a gradual acquisition of red oak by this species of aphids. The literary data on the findings of *L. roboris* on *Quercus rubra* are single (Holman, 2009; Havelka and Stary, 2007), however this species of aphids populates not only *Q. robur*, but also a number of other species of oaks, in particular, previously recorded on the American species *Q. palustris*. Aphids form colonies on the bark of the branches, are massively visited by ants (see below).

Of the native species, *Q. robur* was the most visited by ants, which, not least of all, is associated with a high percentage of aphids-colonized plants. In the region of the study, 8 species of aphids were recorded on this species. Of these, the most attractive to the ants was *L. roboris*. Aphids *Thelaxes dryophila* (Schrank, 1801), *Tuberculatus annulatus* (Hartig, 1841) and to a lesser extent, *Myzocallis castanicola* Baker, 1917 were also regularly visited by ants. Fundatrices of *L. roboris* appeared in April, aphids are placed on the bark of the branches, summer colony number may reach 200 individuals, develop until late autumn. *Th. dryophila* is localized on the shoots of the current year, the underside of the leaves, and later on the pluses of young acorns. The species is characterized by an optional short life cycle, i.e. some of the colonies are ending their development by the beginning of the July and in the second half of the summer the number of aphids is much lower. *T. annulatus* is found on the underside of the leaves; aphids do not form dense colonies, however, during mass reproduction, the larval density (adults are only winged) is very high. From the end of June, the number of aphids can fall significantly due to the possible summer imaginal diapause. *M. castanicola* also lives on the lower surface of leaves (adults are only winged). The species does not form dense colonies, the larvae are located singly near the veins, their numbers and density are usually lower than those of *T. annulatus*, and therefore this species is less attractive to ants. A number of species of aphids are noted only on individual plants, but

in this case their attractiveness for ants contributed. In old parks, a relict species *Stomaphis quercus* (Linnaeus, 1758) was recorded on aged oaks. Aphids inhabit cracks in the bark at the bottom of the trunks in the shelters created by ants. The species is closely related to ants, without which it cannot exist at all, but it is rarely found. *Lachnus pallipes* (Hartig, 1841) is well visited by ants, however it was found only once in the study area. *Tuberculatus borealis* (Krzywicz, 1971) is found on only one plant in small numbers with isolated individuals of ants. *Tuberculatus querceus* (Kaltenbach, 1843) is not attractive for ants because of its small size and solitary lifestyle.

A high percentage of plants inhabited by aphids have been identified for native species *Populus alba*, *P. nigra*, *Salix alba*, *Tilia cordata*, *Acer platanoides*, *Betula pendula*, *Pinus sylvestris*. In the region of the study, *Populus alba* has 3 species of aphids that inhabit it. The most widespread species of aphids is *Chaitophorus populeti* (Panzer, 1801), this meristemophilous species in addition to adult poplar plants, affects their young undergrowth. The phylobiont *Chaitophorus populialbae* (Boyerde Fonscolombe, 1841) was recorded on a smaller number of plants; however, in some poplars (especially young ones) it inhabits at least 2/3 of the total number of leaves on each of the plants. The inhabitant of the bark of the branches *Pterocomma populeum* (Kaltenbach, 1843) occurs sporadically. All species of monoecious, develop throughout the season. There are 4 species of aphids on *P. nigra* (not counting halophores that are inaccessible to ants). The meristophilous species *Chaitophorus nassonowi* Mordvilko, 1894, the philobiont *Chaitophorus leucomelas* Koch, 1854 (except for the fundatrices of last year's bark-living shoots), above mentioned *P. populeum*, and the relict *Stomaphis longirostris* (Fabricius, 1787), are found only in one location on the trunks of several plants. All species are monoecious, develop throughout the season, are actively visited by ants, and *Stomaphis longirostris* will live in the shelters created by ants.

13 species of aphids were found on *Salix alba*. The complex is similar to *Salix fragilis*, except for the absence of the myrmecophilous *Chaitophorus mordvilkoii* and *Ch. truncatus* on *Salix alba* and the presence

of *Pterocomma rufipes* (Hartig, 1841), *Cavariella cicutae* (Koch, 1854) and found on *Salix alba* plants (in the same habitat as *P. nigra*) a rare species of aphid *Stomaphis longirostris*. All, with the exception of *Ch. niger*, myrmecophylic, their characteristic is given above.

Tilia cordata is populated with one species of aphids – *Eucallipterus tiliae* (Linnaeus, 1758), however, this species inhabits many plants, and allocates a lot of honeydew, strongly polluting the leaves. The largest numbers are in June, later both larval and imaginal summer diapause are possible.

Acer platanoides inhabits 5 species of aphids, *P. testudinaceus* is noted on many plants, *Periphyllus aceris* (Linnaeus, 1761) is common, the species with an obligatory summer diapause, occurs until the first decade of June. *P. lyropictus* develops without a summer diapause; it can produce massive outbreaks in some locations populating 100% of maples; *Periphyllus viridulus* Mamontova, 1955 also develops without summer larvaceous diapause, occurs sporadically. All these species are visited by ants. *Drepanosiphum aceris* Koch, 1855 does not affect the attendance of plants by ants because of its small number.

On *Betula pendula* 11 species of aphids were found, 8 of them affect the attractiveness of birch for ants. These are the species that live on the surface of bark *Symydobius oblongus* (vonHeyden, 1837), and meristemophilous species *Glyphina betulae* (Linnaeus, 1758), phylobionts *Betulaphis brevipilosa* Börner, 1940, *Betulaphis quadrituberculata* (Kaltenbach, 1843), *Calaphis flava* Mordvilko, 1928, *Callipterinella calliptera* (Hartig, 1841), *Callipterinella tuberculata* (vonHeyden, 1837), *Euceraphis punctipennis* (Zetterstedt, 1828). On one plant there can be 5-6 different species of aphids, which ensures their high attractiveness for ants. It should be noted that the population of plants with aphids is the highest in late May-June. Such species as *E. punctipennis*, *C. flava* Mordvilko, *B. brevipilosa*, *B. quadrituberculata* disappear in the second half of June due to imaginal or larval summer diapause. The aphid species *Glyphina betulae*, actively visited by ants is characterized by a shortened life cycle and many colonies of this aphid complete their development by mid-end of June, although in

some plants aphids can be observed until August. Thus, by the middle of summer, the attractiveness of silver birch for ants is provided by *S. oblongus* aphids developing throughout the season (a common species, always with ants), and to a lesser extent, *Call. calliptera*, *Call. tuberculata* (the number of these aphids decreases by the middle of summer). *Clethrobium comes* (Walker, 1848) in its biology is similar to *S. oblongus*, it is visited by ants, however it is found in the study area only once and does not play a large role in the attractiveness of plants for ants. The larvae of *Monaphis antennata* (Kaltenbach, 1843) are single on the leaves of birch trees and are not attractive to ants. In the colonies of *Hamamelistes betulinus* (Horvath, 1896), ants are not marked.

Five species of aphids have been identified on *Pinus sylvestris*. The attractiveness of Scots pine for ants is provided by the common species of aphids *Cinara pinea* (Mordvilko, 1895), *C. pini* (Linnaeus, 1758) and *Schizolachnus pineti* (Fabricius, 1781). The first species lives on the shoots of the current and previous years between the needles, it affects the growth on young pines, the second species is localized on the bark of the older branches, the third one lives on the needles. All species are monoecious, developing throughout the seasons. *Cinara pilosa* (Zetterstedt, 1840) is close to *C. pinea*, but it was found only once in the study region, *Eulachnus agilis* (Kaltenbach, 1843) is not very attractive for ants.

For a number of native species, a noticeably smaller number of plants infested with aphids has been recorded. Thus, *Populus tremula* most commonly affects the attendance of ants by the plants already discussed above; *Ch. populeti*, *Pterocomma tremulae* Börner is much less frequently observed, and *Chaitophorus tremulae* Koch, 1854 does not belong to the myrmophilous species. One species of *Myzocallis carpini* aphids (Koch, 1855) is known on *Carpinus betulus*, this species is often found on plants in ornamental curbs, where it can reach a considerable number. However, on many plants, aphids, if present, are in low numbers. It should also be noted that the adults of this species are only winged, the larvae settle alone near the veins on the underside of the leaves (sometimes with high density), the number of aphids drops from

the second half of June (summer diapause is possible). *Fraxinus excelsior* in green areas of Kyiv has registered *Prociphilus bumeliae* (Schrank, 1801) the species inhabits the shoots of the current and last year, knocking the lower side of the leaves into the nests. The species of aphids is obligate dioecious, migrates to the roots of fir (*Abies*) no later than the first ten days of June, and sometimes occurs in parks where there are fir trees. In recent years, a monoecious adventive species of North American origin *Prociphilus fraxinifolii* (Riley, 1879) has been observed in green plantations, introduced together with *Fraxinus pennsylvanica* used in green building. At the same time, in ash trees with high aphid colonies were noticed. *Sambucus nigra* is populated by one species of aphids *Aphis sambuci* Linnaeus, 1758, the species is found sporadically, but forms powerful colonies of a large number of individuals, it is massively visited by ants. The species is facultative dioecious, migrates to the roots of *Rumex* spp., *Lychnis* spp., However, part of the colonies may be placed on young elderberry.

On *Ulmus laevis* (except gall formers, inaccessible to ants), *Tinocallis platani* (Kaltenbach, 1843) is noted, the species populates the lower surface of the leaves, sometimes young shoots. On some young plants they can reach a significant number, highly polluting the plants.

On some natural plants, aphids were not found at the collection points of this study, which may be due to the small number of plants we examined. But in the study area, aphids on these plants were reported (Zhuravlev, 2005). So on *Padus avium* notes *Rhopalosiphum padi* described above, on *Ulmus glabra* – *Tinocallis platani*, on *Acer campestre* – *P. testudinaceus*, developing without summer diapause, *Periphyllus obscurus* Mamontova, 1955, and a rather rare obligate, dioecious species migrating to elm roots, *Mimeuria ulmiphila* (delGuercio, 1917). *Euonymus verrucosus* is one of the primary food plants of the aphids of the *Aphis fabae* group (*Aphis fabae* Scopoli, 1763; *Aphis euonymi* Fabricius, 1775; *Aphis cirsiiacanthoidis* Scopoli, 1763; *Aphis solanella* Theobald, 1914), however, we note that these species are more often populated with *Euonymus europaeus*. On *Pyrus communis* we observed 5 species (*Melanaphis pyraria* (Passerini, 1861); *Rhopalosiphum*

insertum (Walker, 1849); *Anuraphis farfarae* (Koch, 1854); *Anuraphis subterranea* (Walker, 1852); *Dysaphis pyri* (Boyerde Fonscolombe, 1841)). All these species of aphids are rare and have an obligate dioecious life cycle; therefore they can be observed on a *Pyrus communis* only until mid-June.

Conclusions

For Kyiv, 59 species of ants are known, belonging to 22 genera and 4 subfamilies (Radchenko *et al.*, 2019). Of these, for forests and parks, the authors cite 27 species of ants. This practically corresponds to the number of ant species we found in the studied habitats (21 species, 3 subfamilies). Consequently, arboreal and shrubby vegetation is fairly well visited by most ant species (in the region under study). The reasons for such a visit were established by us - these are nesting places and the presence of colonies of myrmecophilous aphids. Among the myrmecofauna of Kyiv, invasive ant species are also known - 4 of them were found (Radchenko *et al.*, 2019). These species were not included in our study, since 3 of them live in heated premises (greenhouses etc.). An exception was one species, *Lasius neglectus* Van Loon *et al.*, 1990, found on the territory of public gardens in the central part of Kyiv (Radchenko *et al.*, 2019).

The fauna of dendrophilous aphids in the green spaces of Kyiv numbers 176 species (Zhuravlev, 2005). Of the species found here on the examined plants, only *Aphis crassivora* and *Panaphis juglandis* can be considered as adventive species. Among the dendrophilous aphid species common in Kyiv and its environs at the moment, at least 35 (19.8% of the total number of aphid species in Kyiv) are adventive. Moreover, 17 of them are trophically related to gymnosperms, which were introduced for green building. The origin of a number of aphid species is unknown. Of the aphids inhabiting invasive and introduced plant species, 2/3 of the species are native species, and 1/3 are adventive. Usually, introduced plants are assimilated by native species of oligophagous aphids, trophically associated with representatives of the same or phylogenetically close genera of plants of the native flora. For example, the North American maple species *Acer sacharinum* is inhabited by aphids trophically related to the European maple species *A. platanoides* (species of

aphids *Periphyllus lyropictus* (Kessler, 1886), *P. testudinaceus* (Fernie, 1852)) and *A. pseudoplatanus* (species of aphids *Drepanosiphum platanoides* (Schrank, 1801), *Periphyllus acericola* (Walker, 1848), *P. testudinaceus*). This example demonstrates the possibility of colonization by aphids of introduced plants originating from outside their original range, if they belong to the same genus as the original food plants of the aphids. Apparently, this possibility depends on the biochemical composition of the plant sap and the presence of enzymes in aphids that can assimilate it. This article also provides a case of colonization of the North American oak species *Quercus rubra* L. by the European species of the aphid *Lachnus roboris* (Linnaeus, 1758). However, the range of dendrophilic oligophagous aphid species is often very wide and in different parts of the range they can feed on various plant species of the same genus. Thus, the Far Eastern populations of the Trans-Palaeartic aphid species *Callipterinella calliptera* (Hartig, 1841) inhabit *Betula mandshurica* (Regel) Nakai and *B. dahurica* Pall., and the European populations on *Betula pendula*, therefore, when Far Eastern birch species are introduced to Ukraine, the aboriginal populations of *C. calliptera* successfully master them. This may also be associated with a significant diversity of aphid species on *Salix fragilis*. At least some of this aphid species inhabiting the willow have wide ranges (Holarctic, Trans-Palaeartic, or Euro-Siberian). This wide range of aphid species apparently including the original range of *S. fragilis*. Possibly, that the *S. fragilis* was invaded by many aphids species, because the *Salix fragilis* is an archeophyte in Ukraine. This also may be the reason for the large species diversity of aphids on the *S. fragilis* and, as a consequence, its attractiveness for ants.

On the other hand, the invasive North American maple *Acer negundo* in the study region is inhabited by only one species of aphid *P. testudinaceus*. Colonies of aphids on this plant are not large and not persistent, probably still, in terms of its biochemical characteristics; this maple is not quite suitable for this type of aphid. In the fauna of Ukraine there are no species of aphids living on maples with Holarctic ranges (some species of aphids were brought to North America), including the original range of *Acer negundo*. In addition,

this species of maple belongs to the kenophytes i.e. its invasion occurred relatively recently. Therefore, *Acer negundo* is partially mastered by only one species of aphids, which possesses the widest range of food plants of all European species of aphids living on maples. Hence, the attractiveness of *Acer negundo* to ants remains extremely low.

Thus, the possibility of developing a new ecological niche provided by introduced and invasive plant species to native species of ants and aphids exists and depends on a) the biochemical correspondence of the plant sap and aphid enzymes, b) the correspondence of the aphid range with the initial range of the introduced plant, c) the time of plant species invasion. Probably, depending on the age of the plant invasion, its gradual colonization by local aphid species is observed, and, further, the increasing attractiveness of this plant species for visiting by ants.

Due to the narrow trophic specialization of aphids, introduced plants that do not have phylogenetic closely related forms in the flora of Ukraine are practically not inhabited by aboriginal aphids (except for the polyphage *Aphis fabae* Scopoli). However, they can be damaged by trophically specialized adventive species that penetrate into new territories following their food plant. For example, plant species *Catalpa bignonioides* Walt. inhabited by aphid species *Aphis catalpae* Mamontova, plant *Juglans regia* L. – by aphids *Chromaphis juglandicola* Kaltenbach and *Panaphis juglandis* Goeze. Among herbaceous plants on the territory of Kyiv, such an example is plant species *Impatiens parviflora* DC. and the related aphid species *Impatiens asiaticum* Nevsky (Stukalyuk, 2016). If, along with such a plant, the invasion of trophically related aphid species does not occur, then in new territories these plants remain unattractive for aphids and, as a consequence, for ants.

At the moment, most of the invasive phanerophyte plant species are not attractive to ants and aphids (in the studied Kyiv region). However, native species of aphids and ants are able to form stable trophic relations with certain invasive species of both phanerophytes and herbaceous plants, for example, *Heracleum mantegazzianum* Manden, *Onopordum acanthium* L., *Asclepias syriaca* L., *Oenothera biennis* L. (Stukalyuk *et al.*, 2019) from the same area. It is noteworthy that

of these herbaceous plant species, the archeophyte species (*Onopordum acanthium*) was the most visited by ants and was also affected by aphids, which, in this case, may be due to the age of invasion of the plant species, which predetermined the population of aphids and the attractiveness of the plant for ants.

More than 1600 plant species are known from the territory of Kyiv city and the region, of which no more than 95 species are invasive, 5.9% of all plant species) (Yavorska, 2002; Protopopova *et al.*, 2009; Grechyshkina, 2010). Among the total number of plant species in the territory of Kyiv, 182 species are phanerophytes, which is 11.3% of their total number (Pikhalo, 2011). Of the 1647 plant species in Moscow, about 10% are invasive (Shcherbakov and Lyubeznova, 2018). There are 146 known phanerophytes, or 8.8% of the total number of vascular plant species in Moscow (Yakushina, 1969; Shcherbakov and Lyubeznova, 2018).

The flora of the Czech Republic numbers 4360 species and subspecies of vascular plants, of which 1454 are adventive. Among them, 61 (4.2%) are invasive species (Pyšek *et al.*, 2012). The flora of Zagreb (Croatia) includes 351 species of vascular plants, among which 22 species or 6.26% are invasive (Hudina *et al.*, 2012). Flora of Rome has 1649 species, 186 of which are neophytes. Unfortunately, in the list of species submitted in the article, the authors do not indicate the number of invasive ones, and they are not marked in the list itself, but based on materials from other cities, they should not exceed 5-10% of the total number of species (Celestigrapow *et al.*, 2013).

Thus, large cities are places of primary appearance of new invasive plant species in the secondary range. Further, these plant species can very successfully spread to neighboring territories. This spread leads to the gradual displacement of native plant species or to a decrease in their number. Then there is their gradual replacement in native phytocenoses. And this leads to a decrease in the natural coenotic diversity, which can subsequently lead to the impoverishment of communities, their uniformity, deterioration of the structure of the herbage, and a decrease in tiering.

Currently, in the green spaces of cities, and especially in botanical gardens, there are a greater number of invasive plant species that

could potentially be assimilated by local species of aphids and ants. At the same time, invasive plant species are more often colonized by native aphid species and visited by native ant species. Thus, in urban conditions, invasive plant species can more quickly, in comparison with natural habitats, be assimilated by local aphid species and become attractive to local ant species.

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Supplementary Tables

Table 1. Average number of ants / 2 min in habitats on different tree species

Habitat/ Species of plants	G1.A162	X11	G5.1	G1.A5	G4.F	E2.1	G5.2	G1.11	G1.C2	X
<i>Quercus robur</i>	23.61 ± 3.47	17.45 ± 2.26	7.43 ± 1.43	13.93 ± 4.05	0	0	0	20.08 ± 4.61	0	16.4
<i>Acer platanoides</i>	6.77 ± 0.95	14.35 ± 1.56	15.11 ± 2.73	0	0	0	0	0	0	12.0
<i>Acer platanoides</i> saplings	3.59 ± 0.43	0	0	0	0	0	0	0	0	3.6
<i>Carpinus betulus</i>	1.86 ± 0.40	0	0	0	0	0	0	0	0	1.8
<i>Fraxinus excelsior</i>	1.93 ± 0.81	5.32 ± 2.64	2.42 ± 1.14	0	0	0	0	0	0	3.2
<i>Euonymus verrucosus</i>	0.22 ± 0.07	0	0	0	0	0	0	0	0	0.2
<i>Ulmus glabra</i>	0.62 ± 0.10	0	0	0	0	0	0	0	0	0.6
<i>Ulmus laevis</i>	0	0	2.64 ± 0.82	0	0	0	0	2.36 ± 1.32	0	2.6
<i>Salix nigra</i>	1.00 ± 0.17	0.1 ± 0.1	0	2.03 ± 0.26	0	0	0	0	0	1
<i>Robinia pseudoacacia</i>	0	5.07 ± 0.94	5.47 ± 0.82	0	0.48 ± 0.11	1.40 ± 0.46	3.72 ± 1.06	0	0	3.2
<i>Populus alba</i>	0	16.08 ± 2.53	8.52 ± 1.90	0	0	2.85 ± 0.54	0	6.61 ± 1.32 2.02 ± 0.67 (\$)	0	7.2
<i>Tilia cordata</i>	0	5.95 ± 0.59	12.72 ± 1.22	4.13 ± 1.35	0	0	0	0	0	7.6
<i>Betula pendula</i>	0	15.5 ± 2.16	8.17 ± 0.77	0	2.50 ± 2.36	0	0	0	0	8.7
<i>Populus nigra</i>	0	12.24 ± 1.42	3.94 ± 0.41	0	0	0.03 ± 0.02 (\$)	0	1.98 ± 0.55	0	6.0
<i>Juglans mandshurica</i>	0	3.42 ± 1.47	14.5 ± 4.64	0	0	0	0	0	0	8.9
<i>Aesculus hippocastanum</i>	0	3.17 ± 0.76	2.9 ± 1.84	0	0	0	0	0	0	3.0
<i>Acer saccharinum</i>	0	2.64 ± 0.73	4.3 ± 0.37	0	0	0	0	0	0	3.4
<i>Quercus rubra</i>	0	7.62 ± 1.25	10.95 ± 1.4	0	0	0	0	0	4.67 ± 0.74 1.00 ± 0.11 (\$) 1.70 ± 0.29 (\$)	7.7
<i>Pinus sylvestris</i>	0	7.88 ± 1.12	0	0	9.54 ± 1.96	0	0	0	0	8.7
<i>Amorpha fruticosa</i>	0	0	0	0	0.04 ± 0.01	0	0	0.02 ± 0.01	0	0.02

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<i>Padus serotina</i>	0	0	0	0	0.45 ± 0.07	0	0	0	0	0.22
<i>Padus avium</i>	0	0	0	0	0.03 ± 0.01	0	0	0	0	0.03
<i>Salix fragilis</i>	0	0	13.63 ± 2.23	0	0	0	0	2.71 ± 0.78 0 ± 0(\$)	0	8.1
<i>Acer negundo</i>	0	0	0.50 ± 0.15	0	0	0	0	0.24 ± 0.10	0	0.25
<i>Acer negundo</i> saplings	0	0	0.006 ± 0.006	0	0	0	0	0	0	0.006
<i>Pyrus communis</i>	0	0	2.06 ± 0.72	0	0	0	0	0	0	2.1
<i>Populus tremula</i>	0	0	7.12 ± 3.13	0	0	0	0	4.60 ± 1.69	0	5.8
<i>Salix alba</i>	0	0	13.41 ± 7.61	0	0	0	0	0	0	13.4
<i>Acer campestre</i>	0	0	0	0	0	0	0	0	0.56 ± 0.20	0.6

(Note: \$- saplings)

Table 2. List of aphid and ant species on invasive and native plants

Invasive plant species	Aphid species	Ant species
<i>Acer negundo</i>	<i>Periphyllus testudinaceus</i> (Ferne, 1852)	<i>Formica cinerea</i> , <i>Lasius emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>L. umbratus</i>
<i>Robinia pseudoacacia</i>	<i>Aphis craccivora</i> Koch, 1854	<i>Camponotus fallax</i> , <i>C. vagus</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. polyctena</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>Temnothorax</i> sp.
<i>Amorpha fruticosa</i>	<i>Aphis craccivora</i> Koch, 1854	<i>Formica cinerea</i> , <i>Lasius niger</i> , <i>L. platythorax</i>
<i>Salix fragilis</i>	<i>Aphis farinosa</i> J. F. Gmelin, 1790, <i>Tuberolachnus salignus</i> (J. F. Gmelin, 1790), <i>Cavariella aegopodii</i> (Scopoli, 1763)	<i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius fuliginosus</i> , <i>L. niger</i>
<i>Juglans mandshurica</i>	<i>Panaphis juglandis</i> (Goeze, 1778)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. niger</i> , <i>Temnothorax</i> sp.
<i>Padus serotina</i>	<i>Rhopalosiphum padi</i> (Linnaeus, 1758)	<i>Camponotus vagus</i> , <i>Formica cinerea</i> , <i>F. fusca</i> , <i>Lasius platythorax</i> , <i>Leptothorax</i> sp., <i>Myrmica</i> sp., <i>Temnothorax</i> sp.
<i>Acer sacharinum</i>	<i>Periphyllus testudinaceus</i> (Ferne, 1852), <i>Periphyllus acericola</i> (Walker, 1848), <i>Periphyllus lyropictus</i> (Kessler, 1886), <i>Drepanosiphum platanoidis</i> (Schränk, 1801)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>Myrmica</i> sp.

<i>Quercus rubra</i>	<i>Lachnus roboris</i> (Linnaeus, 1758)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>Myrmica</i> sp., <i>Temnothorax</i> sp.
<i>Aesculus hippocastanum</i>	<i>Aphis fabae</i> Scopoli, 1763	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. niger</i> , <i>Temnothorax</i> sp.
Native plant species	Aphid species	Ant species
<i>Quercus robur</i>	<i>Lachnus roboris</i> (Linnaeus, 1758), <i>Lachnus pallipes</i> (Hartig, 1841), <i>Thelaxes dryophila</i> (Schrank, 1801), <i>Tuberculatus annulatus</i> (Hartig, 1841), <i>Myzocallis castanicola</i> Baker, 1917, <i>Stomaphis quercus</i> (Linnaeus, 1758)	<i>Camponotus fallax</i> , <i>C. ligniperdus</i> , <i>C. vagus</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. cunicularia</i> , <i>F. fusca</i> , <i>F. rufa</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>L. umbratus</i> , <i>Myrmica</i> sp., <i>Temnothorax</i> sp.
<i>Populus alba</i>	<i>Chaitophorus populeti</i> (Panzer, 1801), <i>Chaitophorus populialbae</i> (Boyer de Fonscolombe, 1841), <i>Pterocomma populeum</i> (Kaltenbach, 1843)	<i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>Myrmica</i> sp.
<i>Salix babylonica</i>	<i>Aphis farinosa</i> J. F. Gmelin, 1790, <i>Chaitophorus vitellinae</i> (Schrank, 1801), <i>Pterocomma. Pilosum</i> Buckton, 1879, <i>Pterocomma salicis</i> (Linnaeus, 1758), <i>Pterocomma rufipes</i> (Hartig, 1841), <i>Cavariella. aegopodii</i> (Scopoli, 1763), <i>Cavariella archangelicae</i> (Scopoli, 1763), <i>Cavariella pastinacae</i> (Linnaeus, 1758), <i>Cavariella theobaldi</i> (Gillette & Bragg, 1918), <i>Stomaphis longirostris</i> (Fabricius, 1787)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Lasius brunneus</i> , <i>L. fuliginosus</i> , <i>L. niger</i>
<i>Populus nigra</i> (not counting inaccessible for ant halophores)	<i>Chaitophorus nassonowi</i> Mordvilko, 1894, <i>Chaitophorus leucomelas</i> Koch, 1854, <i>Pterocomma populeum</i> (Kaltenbach, 1843), <i>Stomaphis longirostris</i> (Fabricius, 1787)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i>
<i>Tilia cordata</i>	<i>Eucallipterus tiliae</i> (Linnaeus, 1758)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. rufibarbis</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. niger</i> , <i>Myrmica</i> sp.
<i>Acer platanoides</i>	<i>Periphyllus testudinaceus</i> (Ferne, 1852), <i>Periphyllus aceris</i> (Linnaeus, 1761),	<i>Camponotus fallax</i> , <i>C. ligniperdus</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. cunicularia</i> , <i>F. fusca</i> , <i>F. rufa</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L.</i>

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	<i>Periphyllus lyropictus</i> (Kessler, 1886), <i>Periphyllus coracinus</i> (Koch, C.L., 1854)(= <i>Periphyllus viridulus</i> Mamontova, 1955)	<i>fuliginosus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>Myrmica</i> sp., <i>Temnothorax</i> sp.
<i>Betula pendula</i>	<i>Symydobius oblongus</i> (von Heyden, 1837), <i>Glyphina betulae</i> (Linnaeus, 1758), <i>Callipterinella calliptera</i> (Hartig, 1841), <i>Callipterinella tuberculata</i> (von Heyden, 1837), <i>Euceraphis punctipennis</i> (Zetterstedt, 1828), <i>Betulaphis brevipilosa</i> Börner, 1940, <i>Betulaphis quadrituberculata</i> (Kaltenbach, 1843), <i>Calaphis flava</i> Mordvilko, 1928, <i>Clethrobius comes</i> (Walker, 1848)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>Temnothorax</i> sp.
<i>Populus tremula</i>	<i>Chaitophorus populeti</i> (Panzer, 1801), <i>Pterocomma tremulae</i> Börner, 1940	<i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>L. fuliginosus</i> , <i>L. niger</i>
<i>Carpinus betulus</i>	<i>Myzocallis carpini</i> (Koch, 1855)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica fusca</i> , <i>F. rufa</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. platythorax</i> , <i>Myrmica</i> sp.
<i>Sambucus nigra</i>	<i>Aphis sambuci</i> Linnaeus, 1758	<i>Lasius emarginatus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>Leptothorax</i> sp., <i>Myrmica</i> sp., <i>Temnothorax</i> sp.
<i>Fraxinus excelsior</i>	<i>Prociphilus bumeliae</i> (Schrank, 1801)	<i>Camponotus fallax</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>Myrmica</i> sp.
<i>Pinus sylvestris</i>	<i>Cinara pinea</i> (Mordvilko, 1895), <i>Cinara pilosa</i> (Zetterstedt, 1840), <i>Cinara pini</i> (Linnaeus, 1758), <i>Schizolachnus pineti</i> (Fabricius, 1781)	<i>Camponotus fallax</i> , <i>C. vagus</i> , <i>Dolichoderus quadripunctatus</i> , <i>Formica cinerea</i> , <i>F. polycтена</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> , <i>L. platythorax</i> , <i>Leptothorax</i> sp., <i>Myrmica</i> sp.
<i>Ulmus laevis</i> (except for halophores, inaccessible to ants)	<i>Tinocallis platani</i> (Kaltenbach, 1843)	<i>Formica cinerea</i> , <i>Lasius brunneus</i> , <i>L. emarginatus</i> , <i>L. fuliginosus</i> , <i>L. niger</i> ,

Table 3. The effect of illumination on the attendance of phanerophytes by ants in different habitats

Species of plants	Habitats									X
	G1.A16	X11	G5.1	G1.A5	G4.F	E2.1	G5.2	G1.11	G1.C2	
<i>Quercus robur</i>	1.43± 0.05	2.78± 0.07	1.79±0.01	2.35± 0				1.35 ± 0.09		1.94 ± 0.27
<i>Acer platanoides</i>	1.0 ± 0.02	1.85± 0.07	1.49± 0.35							1.45 ± 0.24
<i>Acer platanoides</i> <i>undergrowth</i>	0.8 ± 0.02									0.83 ± 0.02
<i>Fraxinus excelsior</i>	1.8 ± 0.15	2.24± 0.26	4.53± 0.34							2.86 ± 0.84
<i>Carpinus betulus</i>	1.24 ± 0.07									1.24 ± 0.07
<i>Euonymus verrucosus</i>	1.02 ± 0									1.02 ± 0
<i>Ulmus glabra</i>	1.02 ± 0							0.51 ± 0.01		0.76 ± 0.25
<i>Ulmus laevis</i>			1.31± 0.18							1.31 ± 0.18
<i>Sambucus nigra</i>	0.18 ± 0	1.87± 0		2.35± 0						1.46 ± 0.65
<i>Robinia pseudoacacia</i>		3.06± 0.10	5.85± 0.26		4.98± 0.23	10.8±0 (\$)	13.18±0.26			7.57 ± 1.89
<i>Populus alba</i>		1.82± 0.12	1.45± 0.12			10.8 ± 0 (\$)		3.46 ± 0.28 (trees) 20.0 ± 0 (\$)		7.50 ± 3.55
<i>Tilia cordata</i>		1.21± 0.04	4.01± 0.18	2.35 ± 0						2.52 ± 0.81
<i>Betula pendula</i>		5.16± 0.33	4.88± 0.42		2.25 ± 0					4.09 ± 0.92
<i>Populus nigra</i>		4.36± 0.36	2.22± 0.28			10.8 ± 0 (\$)		7.47 ± 0.50		6.21 ± 1.87
<i>Juglans mandshurica</i>		3.10± 0.19	4.93± 0.35							4.01 ± 0.91
<i>Aesculus hippocastanum</i>		1.45± 0.09	2.05± 0.41							1.75 ± 0.30
<i>Acer saccharinum</i>		2.34± 0.38	2.59± 0.23							2.46 ± 0.12
<i>Quercus rubra</i>		3.10± 0.16	1.98± 0.08						3.0±0 (trees) 3.0 ± 0 (\$)	2.77 ± 0.26
<i>Pinus sylvestris</i>		4.77			5.15± 0.17					4.96 ± 0.19
<i>Amorpha fruticosa</i>		5.35± 0			2.26 ± 0			6.80 ± 0.19		4.80 ± 1.34
<i>Padus serotina</i>		0.55± 0			3.57± 0.11					2.06 ± 1.51
<i>Padus avium</i>					4.68± 0.20					4.68 ± 0.20
<i>Salix fragilis</i>			1.26± 0.12					6.47 ± 0.43 15.7 ± 0 (\$)		7.81 ± 4.22

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<i>Acer negundo</i>			2.02± 0.08					0.63 ± 0.01		1.32 ± 0.69
<i>Acer negundo</i> saplings			36.6± 2.39			6.65±0				21.62± 14.97
<i>Pyrus communis</i>			4.62 ± 0							4.62 ± 0
<i>Populus tremula</i>			2.00 ± 0					1.78 ± 0.11		1.89 ± 0.11
<i>Salix alba</i>			1.98± 0.17							1.98 ± 0.17
<i>Acer campestre</i>									3.0 ± 0	3.0 ± 0
X	1.06± 0.16	2.93± 0.43	4.60± 1.80	2.35± 0	3.81± 0.54	9.76± 1.03	13.18±0.26	6.41 ± 2.09	3.0 ± 0	

(Note: \$- saplings)