Sapienza Università Editrice

E-ISSN 2284-4880
ISSN 0429-288X

Fragmenta entomologica, 56 (2): 223–238 (2024)

Research article
Submitted: April 23rd, 2024 – *Accepted*: December 2nd, 2024 – *Published*: December 10th, 2024
DOI: 10.13133/2284-4880/1612

Effect of habitat type on the structure of ant forage areas (Hymenoptera: Formicidae)

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Abstract
The purpose of this paper is to study the structure of ant forage areas in urban habitats, semi-urban habitats and natural habitats. The study was conducted in the Ukrainian regions of Crimea (2012 to 2013) and Kyiv and its suburbs (2015 to 2018, 2021 to 2023). We examined 1321 forage trees and 849 colonies of 9 ant species in Kyiv and suburbs; and 413 trees and 141 colonies of 2 ant species in Crimea. The methods we used included transect examination of the trees with ants along a 10 m wide strip, measuring tree sizes (trunk girth) and recording ant species and numbers. Most ant species show a negative relationship between distance from the tree and the number of workers, indicating that the farther from the tree, the less is the number of ants. In natural habitats, higher numbers of ants and greater distances to forage trees are observed compared with urban or semi-urban habitats. *Quercus robur*, *Pinus sylvestris* and *Acer platanoides* were the most visited trees with a total visit frequency of 0.86 of the total number of records. In urban habitats, *Lasius niger* and *Lasius emarginatus* controlled an average of one tree each, and *Crematogaster subdentata* controlled an average of 5.8 trees. In urban habitats (Kyiv and suburbs), more common were colonies of two ant species (*L. niger*, *Formica cinerea*). There was no significant correlation between the distance from the nest to the forage tree and the tree size. Ants show different dispersal strategies in different habitat types. In urban habitats, ants settle closer to forage trees and control fewer trees due to limited food resources.

Key words: ants, dispersal, urban habitats, tree size, strategies.

Introduction

Ants (Hymenoptera; Formicidae) are a convenient object for monitoring environmental health. They are highly sensitive to environmental changes, responding to changes in soil quality, temperature, humidity, food availability and availability of places for settlement (Underwood & Fisher 2006). Ants are known to perform a number of important ecosystem functions, such as seed spreading, organic matter decomposition, soil aeration and entomophagy, and may also influence distribution of some plants (Wills & Landis 2018). Because ants respond to changes in environmental factors, their presence or absence, as well as quantitative and qualitative changes in their populations, can serve as indicators of environmental quality. In particular, a decline in the population of certain ant species may indicate soil or water pollution, climate change, or other anthropogenic impacts (Skaldina et al. 2018).

To date, ants have successfully colonized all continents except Antarctica and have mastered a wide range of terrestrial ecosystems (Wilson 1987). This range includes natural, urban and semi-urban habitats. In the latter two cases, ants live in a stressful environment, but this has not prevented some species from successfully colonizing these habitats.

Urban habitats have a number of specific characteristics that distinguish them from natural habitats. Cities are characterized by changes in the landscape to accommodate the construction of buildings, roads, parks and other infrastructure (Rebele 1994). This reduces the habitat available for many animal species, but at the same time creates new types of substrate that can be colonized by animals, including ants (Perfecto & Philpott 2023).

In cities, most areas are covered by asphalt, concrete and other artificial materials (Mohajerani et al. 2017), which can serve as nesting substrate for ants. These materials often form flat surfaces and have many small crevices and cracks that can be used by ants as habitats (e.g. under rocks, Stukalyuk & Radchenko 2022) or commuting paths. In addition, cities are rich in anthropogenic food sources

Fig. 1 – Sampling locations.

such as garbage and food waste. This may attract some ants and stimulate their activity in urban environments (Kanach 2024). At the same time, ants may lack nesting places in cities (Ślipiński et al. 2012).

Cities are densely populated and therefore characterized by intense human activity, which may influence ant behavior. Human movement can create stressful situations for ants and influence habitat selection and commuting paths (Whitford et al. 1999).

Urban habitats differ from natural habitats in basic parameters such as temperature, humidity, pollution levels and presence of chemicals. Temperatures in cities are several degrees higher than in surrounding natural habitats, a phenomenon known as heat islands, which can also influence ant behaviour and activity. In addition, street lighting at night (artificial light) can alter ant activity cycles (Trigos-Peral et al. 2024). Noise, vibration and other types of pollution such as chemicals can also have influence on ants by altering their habitat conditions (Cammaerts & Cammaerts 2018).

Therefore, urban habitats represent unique environments that can have specific effects on ants and other animal species.

Semi-urban habitats are ecosystems that lie between fully urban and natural environments. Like urban habitats, they are characterized by modified landscapes associated with anthropogenic activities. These include houses and roads in population centers (villages), agricultural land (fields), irrigation systems (canals), tree lines along highways, and man-made parks and gardens (Hisamatsu & Yamane 2006).

These habitats include elements of urban ecosystems as well as natural elements such as forest belts. In contrast to urban ecosystems, most trees are planted by humans. All of the above components of semi-urban habitats can serve as the main source of food and shelter for animals, including ants. At the same time, human activities in these areas can also alter the living conditions for ants, although to a lesser extent than in urban areas (Stukalyuk & Akhmedov 2022).

Semi-urban habitats are therefore mixed environments that combine both natural and anthropogenic elements. This makes them unique for studying interactions between animals and human activities. As for natural habitats, they are represented by undisturbed or slightly disturbed areas of human activity, whose vegetation characteristics are linked to a specific climatic zone and a set of abiotic factors (Chytrý et al. 2020).

Each type of habitat therefore has specific characteristics that are unique to it. Studies of how ants adapt to urban and semi-urban habitats are of great practical interest, as they can provide insight into the strategies utilized by ant species that have successfully colonized these habitats.

Papers on the structure of ant communities in urban areas cover a fairly wide geographical area. Ant communities have been studied in cities such as Detroit (Uno et al. 2010), New York (Pećarević et al. 2010), Cleveland, Cincinnati and

Colombo (Perez & Diamond 2019), Tucson (Miguelena & Baker 2019), Sao Paulo (Angilletta et al. 2007; Perfecto & Philpott 2023), Rio de Janeiro (Santos et al. 2019), Buenos Aires (Josens et al. 2017), Macau (Leong et al. 2017), Tokyo (Yamaguchi 2004), New Zealand cities (Stringer et al. 2009) and other cities around the world. For Europe, the cities studied include Helsinki (Vepsäläinen et al. 2008), Warsaw (Ślipiński et al. 2012; Trigos-Peral et al. 2020), Kyiv (Radchenko et al. 2019; Stukalyuk et al. 2020; 2022), Lviv (Doroshenko & Nazaruk 2022), Lyon (Gippet et al. 2017), Brussels (Dijon et al. 2023), Sofia (Lapeva-Gjonova et al. 2004; Antonova & Penev 2008; Penev et al. 2008), Basel (Melliger et al. 2018), Milan (Castracani et al. 2020), Parma (Lucky et al. 2014), Cagliari (Bazzato et al. 2022) and some cities in Spain (Carpintero & Reyes-López 2014).

Despite the large number of publications on ants in cities, most of them are dedicated to invasive ant species, methods of their control, and ants as vectors of infectious disease spread. Themes such as the influence of air pollution on ant communities in cities, as well as recommendations for the conservation of natural ant species in urban environments, remain relevant and poorly studied (Santos 2016). Some papers provide comparative data on the size of ant colonies in different types of habitats, including urban ones (Stukalyuk et al. 2021, 2022), as well as characteristics of ant communities depending on the level of anthropogenic pressure (Antonov 2008). Ports are pointed to play the role of potential gateways for the spread of invasive ant species (Kouakou et al. 2018).

In the present paper, we present detailed characteristics of the 10 most common ant species living in urban habitats (Kyiv, Sudak, Yevvpatoriya, Ukraine), semi-urban habitats and natural habitats (Kyiv Oblast and Crimea, Ukraine). We used two different geographical locations — Central Ukraine (Kyiv Oblast) and Southern Ukraine (Crimea) — to test for possible general trends in ant adaptations to urban environments. We estimated the distances from ant nests to food sources (trees). Trees can be visited by the same ant colony for many years (Zakharov 1991), thus providing a perennial source of resources. In urban environments, where grass cover is often absent and vegetation is represented by tree lines, the latter may be the only source of resources, such as honeydew from aphid colonies or invertebrates living on trees. Therefore, we used the distance from trees to ant nests as a key parameter. Other studies have reported a limited number of ant nesting sites in urban environments (Ślipiński et al. 2012). In our paper, we present detailed data on the most common species, with an explanation of possible reasons for changes in the parameters of distance from nests to trees in different types of habitat.

The aim of this paper is to study ants' adaptive settlement strategies in urban habitats, semi-urban habitats and natural habitats. Research task: a) analyze distances from nests to forage trees in ant species in three types of biotopes (urban, semi-urban, natural); b) determine dependence of the number of ants, going along the trail from the nest to the tree, on the distance; c) analyze the rate of ant visits to different types of forage trees (deciduous, fruit, coniferous, introduced); d) determine sizes of trees (trunk girth, m) of different species visited by ants.

Materials and Methods

Table 1 – List of the surveyed tree species and the number of their individuals.

Tree_species	**Count**
Quercus robur	**349**
Pinus sylvestris	**325**
Acer platanoides	**264**
Tilia cordata	**155**
Larix decidua	**102**
Robinia pseudoacacia	**90**
Pinus pallasiana	**72**
Populus alba	**64**
Salix fragilis	**43**
Morus nigra	**42**
Ulmus laevis	**32**
Cedrus libani	**29**
Fraxinus excelsior	**23**
Juglans regia	**15**
Pinus brutia	**15**
Albizia julibrissin	**14**
Prunus armeniaca	**12**
Prunus cerasifera	**12**
Cupressus sempervirens	**11**
Populus nigra	**10**
Prunus domestica	**10**
Ailanthus altissima	**8**
Betula pendula	**8**
Populus tremula	**8**
Acer negundo	**3**
Thuja occidentalis	**3**
Gleditsia triacanthos	**2**
Malus domestica	**2**
Prunus dulcis	**2**
Pyrus communis	**2**
Acer campestre	**1**
Aesculus hippocastanum	**1**
Cotinus coggygria	**1**
Elaeagnus commutata	**1**
Pistacia mutica	**1**
Platanus orientalis	**1**
Ulmus glabra	**1**

Research Areas

The research was conducted in 2012 and 2013 in Crimea (Yevvpatoriya, Sudak, Mykhailivka Village), from 2015 to 2018 and from 2021 to 2023 in Kyiv and Oblast (outskirts of Litky, Bucha, Boyarka, Nizhyn in Chernihiv Oblast, Fig. 1).

Some of the data have been published previously (Stukalyuk 2015; Stukalyuk & Radchenko 2018; Stukalyuk et al. 2020, 2023), but in this paper we use the previously unpublished data on distances from nests to forage trees. In Crimea, we studied urban habitats (cities of Yevvpatoriya and Sudak) and semi-urban habitats (Mykhailivka Village, Saky Rayon), while in Kyiv Oblast we studied all three types of habitats [cities of Kyiv, Boyarka and Bucha (urban habitats), Kyiv Oblast [semi-urban habitats and natural habitat)]. In natural habitats, we studied deciduous and coniferous forests [oak (*Quercus robur*), maple (*Acer platanoides*), hornbeam (*Carpinus betulus*) are the dominant tree species in deciduous forests, and pine (*Pinus sylvestris*) in coniferous forests]. In semi-urban habitats areas [tree plantations (willow (*Salix fragilis*), black poplar (*Populus nigra*)], in urban habitats areas [tree alleys (linden (*Tilia cordata*), black locust (*Robinia pseudoacacia*), introduced species, white poplar (*Populus alba*), black poplar, and fruit trees]. A complete list of the 37 tree species is given in Table 1.

Table 2 – Distribution of surveyed trees by location, habitat type and between ant species.

By Location	Count
Boyarka	**92**
Bucha	**14**
Crimea	**413**
Kyiv	**700**
Kyiv Oblast	**500**
Nyzhyn	**15**
By Biotope	**Count**
Natural	**698**
Semi-urban	**54**
Urban	**982**
By Ant species	**Count**
Camponotus vagus	**121**
Crematogaster subdentata	**113**
Formica cinerea	**234**
Formica polyctena	**220**
Formica rufa	**228**
Lasius brunneus	**20**
Lasius emarginatus	**176**
Lasius fuliginosus	**74**
Lasius neglectus	**322**
Lasius niger	**226**

Sample

In total, 1321 forage trees and 849 colonies of ants of 9 species were examined in Kyiv Oblast and the city of Kyiv. In Crimea, 413 trees and 141 colonies of 2 invasive ant species were examined. The number of trees and ant species examined is detailed in Table 2.

Research Methods

We used the transect method described in Stukalyuk & Maak (2023). The observer recorded all trees with ants along a 10 m wide transect (5 m in each direction). We determined the species of the trees and their size (trunk girth, m). The trunk girth was measured with a tape measure. The species of ants that formed clearly visible trails were included were identified. The taxonomic keys of Radchenko (2016) and Seifert (2018) were used to determine ant species. The number of ants passing through the trail in either direction was counted during a 2-minute continuous sampling of the trail leading from the tree to the nest. The count was made on the ground on a section of the trail leading to the forage tree (in the shade). All measurements at all sites were taken between 10:00 and 13:00. This is the time when most ant species have a peak of morning activity according to our previous data (Stukalyuk 2013, 2015, 2018; Stukalyuk & Ivanov 2013; Stukalyuk & Radchenko 2018; Stukalyuk & Maak 2023). The second peak of activity occurs in the evening, but we did not take measurements at this time because ant activity in the evening may differ from that in the morning. Also, according to our observations, ant trails are usually in the shade, which reduces the negative effects of illumination and high (soil and air) temperatures.

For each counting, we determined the location of the nest from which the ants moved to the forage tree. If the anthill was clearly visible, as is typical in red wood ants, this was not difficult. If the nest was not clearly visible, the ants were followed along the trail from the tree to the nest. If ants were moving through tunnels (i.e., underground), their presence and direction was determined by excavation. The distance from the nest to the forage tree was measured in meters. In cases where a colony foraged on multiple trees, these trees were often connected by foraging trails. This is true for polydomous colonies living in several nests, some of which are forage (auxiliary), as well as for supercolonies (red wood ants and *Crematogaster subdentata*). The different colonies were not connected by trails and were spatially separated. The choice of species with clearly visible trails was made to ensure accurate determination of the distance from the tree to the nest and to minimize errors. However, it should be noted that this approach excludes species that do not forage through permanent trails, which represents a limitation of this study.

Statistical Analysis

To characterize the ant colonies in the different biotope types, the number of workers passing along foraging trails during a 2-minute observation period was recorded, and the distance from nests to forage trees was measured for each ant colony. In addition, trunk circumference (or girth) of the forage trees at breast height was measured as an indicator of their age. These data were further analyzed, taking into account classification of biotopes into three types (natural, semi-urban and urban). These data were further analyzed using analysis of variance (ANOVA) to compare differences between the three biotope types (natural, semi-urban, and urban). Post-hoc Tukey tests were applied to identify significant pairwise differences. For relationships between the number of workers and distance to forage trees, regression analyses were performed, and results were assessed using R^2 values and regression coefficients to characterize species-specific responses."

Basic descriptive statistics, namely mean and standard error and deviation, number of workers and distance to forage trees were determined for each habitat type and each ant species. They characterize the structure of foraging areas, and varied according to ant species and biotope transformation degree/type.

Regression analysis was used to study the relationship between the number of workers and the distance to forage trees. All computations and graphs were performed using the R environment (https://cran.r-project.org, ver. 3.5.6). Parameters of the regression models were computed separately for each ant species to characterize the species-specific response. Due to the high variation and large values of the number of workers, the latter indicator was used in log-transformed form to reduce the range of values. The models were analyzed using the value of determination coefficient R^2 and values of the regression coefficient (sign and absolute value). The first indicator characterizes quality of the linear model fit, the second shows how quickly the number of workers changes with distance from food trees.

To compare the structure of foraging areas in different biotope types, graphs of the range of numbers of workers and distances to food trees were constructed. The hypothesis of no significant differences (H0) was tested using analysis of variance (ANOVA). The test significance level was taken as p-value<0.05. In addition, Tukey's test was used to verify the significance of differences between pairs of compared biotopes.

The analysis of the rate of visits to food trees was based on counting the frequency of ant species for each species of forage trees. The top 10 most visited tree species were further analyzed. Tree species were conventionally divided into introduced species, and native species. The classification of the 10 most frequently visited tree species into types [fruit (e.g., mulberry), coniferous (e.g., pine), or deciduous (e.g., oak, maple, linden)] was used to count the number of trees visited within each category. These counts were summarized descriptively to show the distribution of ant visitation among different tree types. For the 10 trees most visited by ants, we computed the mean and variation indicators of trunk girth at breast height as a relative indicator of tree age. The choice of the 10 most frequently visited tree species was made to focus the analysis on those species that accounted for most of the ant activity, representing 86% of all visitation records. This approach allowed us to identify key patterns in ant-tree interactions while maintaining a manageable dataset for detailed analysis.

Results

Number of workers and distance to forage trees in different habitats

ANOVA test results indicate significant differences in the number of workers among the different biotope types, with higher values recorded for natural habitats (ANOVA p-value = 7.03e-29 < 0.05, Fig. 2A). Similarly, the distances to forage trees also vary significantly, with greater distances observed in natural habitats compared to semi-urban and urban biotopes (ANOVA p-value = 1.36e-49, Fig. 2B). However, in pairwise comparisons, the differences in number of workers and distance to forage trees are not significantly different in semi-urban habitats and urban biotopes. In natural biotopes, the number of workers is higher

Table 3 – Basic statistical estimates of the number (N) of workers and the distance to forage trees in different biotope types. W is for number of workers, Wr is for range (min-max) of values of number of workers, L is for distances to forage trees, Lr is for range of distances to forage trees, D is for girth of forage trees, Dr is for range of values of diameter of forage trees.

Biotope	N	W	Wr	L	Lr	D	Dr
Natural	698	107.4±114.6	2–600	5.99±5.87	0.05–51	0.85±0.74	0.05–4.5
Semi-urban	54	52.2±51.6	1–191	3.6±3.45	0.05–15	1.61±0.55	0.4–2.9
Urban	982	58.9±59.9	1–320	2.54±3.25	0.05–17	0.86±0.55	0.05–3.3

(2-fold, Table 2, Fig. 2A) and the distance to forage trees is greater (1.5-fold, Fig. 2B, Table 3).

In semi-urban biotopes, tree girth is on average 2 times larger. This is since the basis of the tree groves surveyed are old specimens of willow and poplar with trunks of more than 1 m in girth. Such trees are well suited for ants, especially when they are alone in the meadows next to the roads.

Distribution of distances to forage trees for different ant species

The regression coefficient is negative for almost all ant species, which means that the number of workers decreases with distance from the tree (Table 4).

The only exception was *Camponotus vagus*, which was observed to build busy trails to trees located far from the nest. This dependence is most pronounced for *Lasius neglectus*, which means that this species settles very close to forage trees. For red wood ants, as well as 4 other species of the genus *Lasius*, the number of ants decreases more slowly with distance from the nest, which means that their nests can be located at some distance from the tree (Table 4). For the arboreal species (i.e., dendrobionts: *Lasius brunneus*, *L. fuliginosus*, *Crematogaster subdentata*), Table 4 provides data on distances to forage trees in the vicinity of the main nest.
Fig. 3 shows examples of the dependence of the number of workers in two species (*L. neglectus*, *C. subdentata*) on the distance to the tree.

While for *Lasius neglectus* this distance is up to 2 m (Fig. 3A), for *Crematogaster subdentata* this distance is much greater, up to 15 m (Fig. 3B). The majotity of the nests is concentrated at distances of up to 0.4 m for *L. neglectus* and up to 4 m for *C. subdentata*, i.e. their nests are most often located at these distances. For *C. subdentata*, the distance given is the average distance from the central nest to the nearest forage tree.

Table 4 – Regression model parameters for dependence of the number of workers on the distance to forage trees for different ant species.

ant_species	Estimate	std.error	Statistic	p.value
Camponotus vagus	**1.54**	**0.76**	**2.04**	**4.39E-02**
Formica polyctena	**-6.34**	**0.89**	**-7.08**	**1.92E-11**
Formica rufa	**-9.51**	**1.43**	**-6.67**	**1.93E-10**
Lasius neglectus	**-117.97**	**8.12**	**-14.53**	**4.37E-37**
Formica cinerea	**-7.80**	**0.73**	**-10.66**	**7.43E-22**
Lasius niger	**-11.13**	**0.79**	**-14.09**	**1.03E-32**
Lasius fuliginosus	**-5.52**	**0.96**	**-5.78**	**1.80E-07**
Lasius brunneus	**-5.88**	**1.45**	**-4.07**	**7.23E-04**
Lasius emarginatus	**-1.40**	**0.46**	**-3.04**	**2.73E-03**
Crematogaster subdentata	**-12.91**	**1.23**	**-10.52**	**2.29E-18**

Statistical indicators of the structure of foraging areas of different ant species

In urban habitat biotopes, *Lasius brunneus* was observed to forage on fewer forage trees, despite the greater average distance to trees compared to other biotope types (Table 5). The same dependence is observed for other species (*Lasius fuliginosus*, *Camponotus vagus*) as well as for *Formica cinerea* when comparing natural and semi-urban habitats. We attribute this to the fact that these species in urban habitats were mainly recorded in parks, where trees are, on average, farther apart (separated by areas of grass) than in natural conditions. At the same time, the maximum

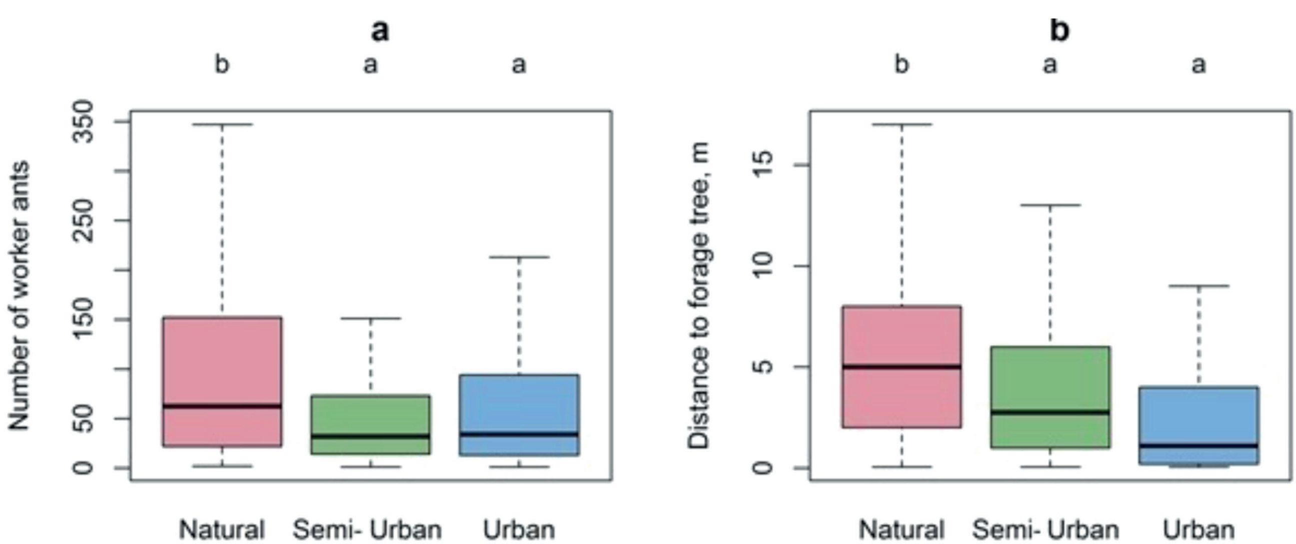

Fig. 2 – Distribution of the number of workers **(a)** and distance to forage trees (m) **(b)** in different biotopes. The figures show box plots of the distributions of the number of worker ants in natural, semi-urban and urban biotopes. The letters above each figure indicate results of testing pairwise comparisons with the Tukey test for significance of differences in values for different pairs of biotopes.

Table 5 – Mean distances to forage trees and abundance of different ant species in different biotope types. **D** is for dendrobiont (i.e., arboreal ant species), **H** is for herpetobiont (i.e., ground-dwelling ant species) [see Dlussky (1981) and Zryanin (2011) for additional information on this terminology]. Basic statistical estimates of the number (**N**) of worker ants and the distance to forage trees in different biotope types, **W** is for number of workers, **Wr** is for range (min-max) of values of number of workers, **L** is for distances to forage trees.

Ant_type	Ant_species	Biotope	N	W	Wr	L
D	*Crematogaster subdentata*	**Urban**	**113**	**79.3±55**	**7–254**	**4.78±3.01**
D	*Lasius brunneus*	**Natural**	**14**	**27.1±23.7**	**5–87**	**3.75±2.15**
D	*Lasius brunneus*	**Urban**	**6**	**12.3±8.3**	**3–23**	**4.59±3.34**
D	*Lasius fuliginosus*	**Natural**	**18**	**45±46.1**	**2–198**	**5.28±2.44**
D	*Lasius fuliginosus*	**Urban**	**56**	**21±32.2**	**1–208**	**7.83±3.95**
H	*Camponotus vagus*	**Natural**	**92**	**36.8±33.2**	**6–171**	**5.02±3.82**
H	*Camponotus vagus*	**Urban**	**29**	**34.7±30.1**	**6–118**	**7.29±3.5**
H	*Formica cinerea*	**Semi-urban**	**54**	**52.2±51.6**	**1–191**	**3.6±3.45**
H	*Formica cinerea*	**Urban**	**180**	**32.5±42.1**	**2–294**	**4.84±3.23**
H	*Formica polyctena*	**Natural**	**220**	**121±103.8**	**6–530**	**8.52±7.08**
H	*Formica rufa*	**Natural**	**228**	**181.7±127.8**	**10–600**	**6.4±5.45**
H	*Lasius emarginatus*	**Natural**	**126**	**18.8±15.2**	**3–105**	**1.89±2.88**
H	*Lasius emarginatus*	**Urban**	**50**	**18.2±18.1**	**3–90**	**0.05±0.01**
H	*Lasius neglectus*	**Urban**	**322**	**110.9±59.3**	**10–320**	**0.27±0.32**
H	*Lasius niger*	**Urban**	**226**	**18.5±12.6**	**2–62**	**1.41±0.78**

distances to trees in urban environments are smaller for the above species (Table 5).

For *Lasius emarginatus*, the reverse situation is observed: for the same average number of workers, distances are greater in natural biotopes than in urban habitats ones. This may be because colonies of this species found in urban areas are in all cases exclusively under trees. Under natural conditions, red wood ants adopt a strategy of long distances to trees, which is related to the large size of their colonies. *Lasius niger*, and especially *L. neglectus*, implement the opposite strategy in urban habitats (they settle near forage trees). In urban environments, *Crematogaster subdentata* can nest at considerable distances from forage trees. However, this is because this species is a dendrobiont (or arboreal species) and nests in trees; secondly, it has a network structure of nests in supercolony conditions, which can be located at different distances from forage trees.

Analysis of the rate of ant visits to different tree species

Fig 4 shows the top 10 tree species most visited by ants. The first 4 places are occupied by local species (oak, pine, maple, linden), followed by introduced and invasive species (locust, larch), then again by local species (Pallas pine, white poplar and willow in Crimea) and fruit trees (mulberry). A disadvantage of such an analysis may be the different frequency of occurrence of the trees themselves (in an oak forest it is not possible to visit a pine tree). Therefore, we can say that the visit rate is not so much a result of "popularity" of trees among ants, but also a result of different rates of occurrence to the trees themselves. Results of distribution of tree visits by different ant species are presented in more detail in Table 6.

Camponotus vagus is most common on oak and pine, *Crematogaster subdentata* on mulberry, *Formica cinerea* on pine and to a lesser extent on linden. Red wood ants are most common on pine and oak, but also on larch and maple. *Lasius brunneus* is mainly found on oak, *L. fuliginosus* on oak and willow, *L. emarginatus* on oak, maple and linden, *L. niger* on maple and linden, *L. neglectus* on Pallas pine and white poplar. Thus, the studied ant species show different preferences for forage trees, although some of them may overlap (oak, pine, maple and linden). Table 7 shows girth values of the most visited trees and distances from the nests to these trees.

The top 10 tree species visited by ants represent 86% of the total recorded visits, with *Quercus robur*, *Pinus sylvestris*, and *Acer platanoides* accounting for 54% of the cases. These observations reflect the frequency of ant visits but do not account for the availability of different tree species

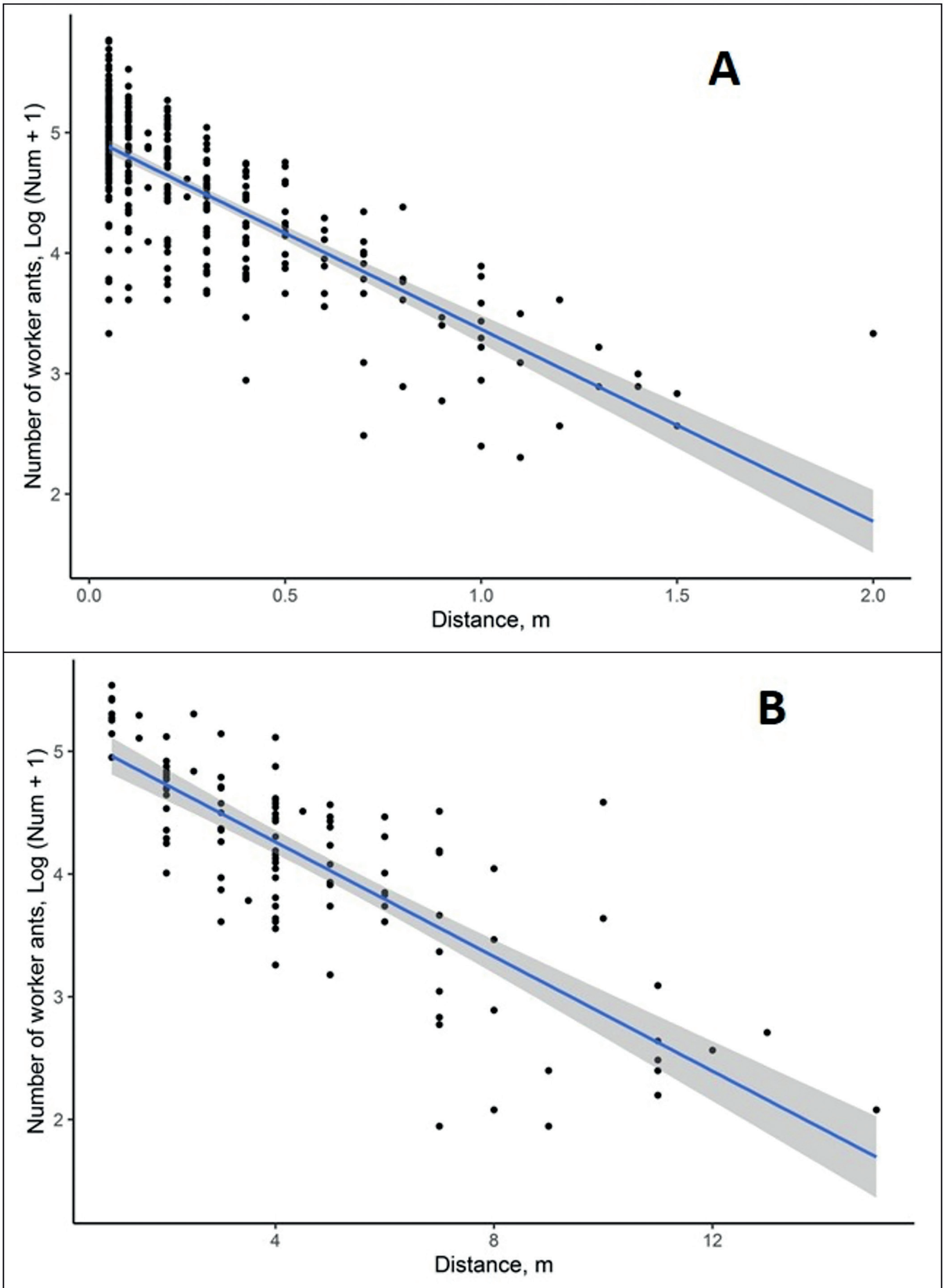

Fig. 3 – Regression model for dependence of the number of workers on distance in two model species. **A** is for *Lasius neglectus***, B** is for *Crematogaster subdentata*. The figures show regression plots of the number of workers (logarithm) on the distance to the food tree. The number of workers is logarithmic because the values and their range are too significant and vary widely. The fit was made with a linear model.

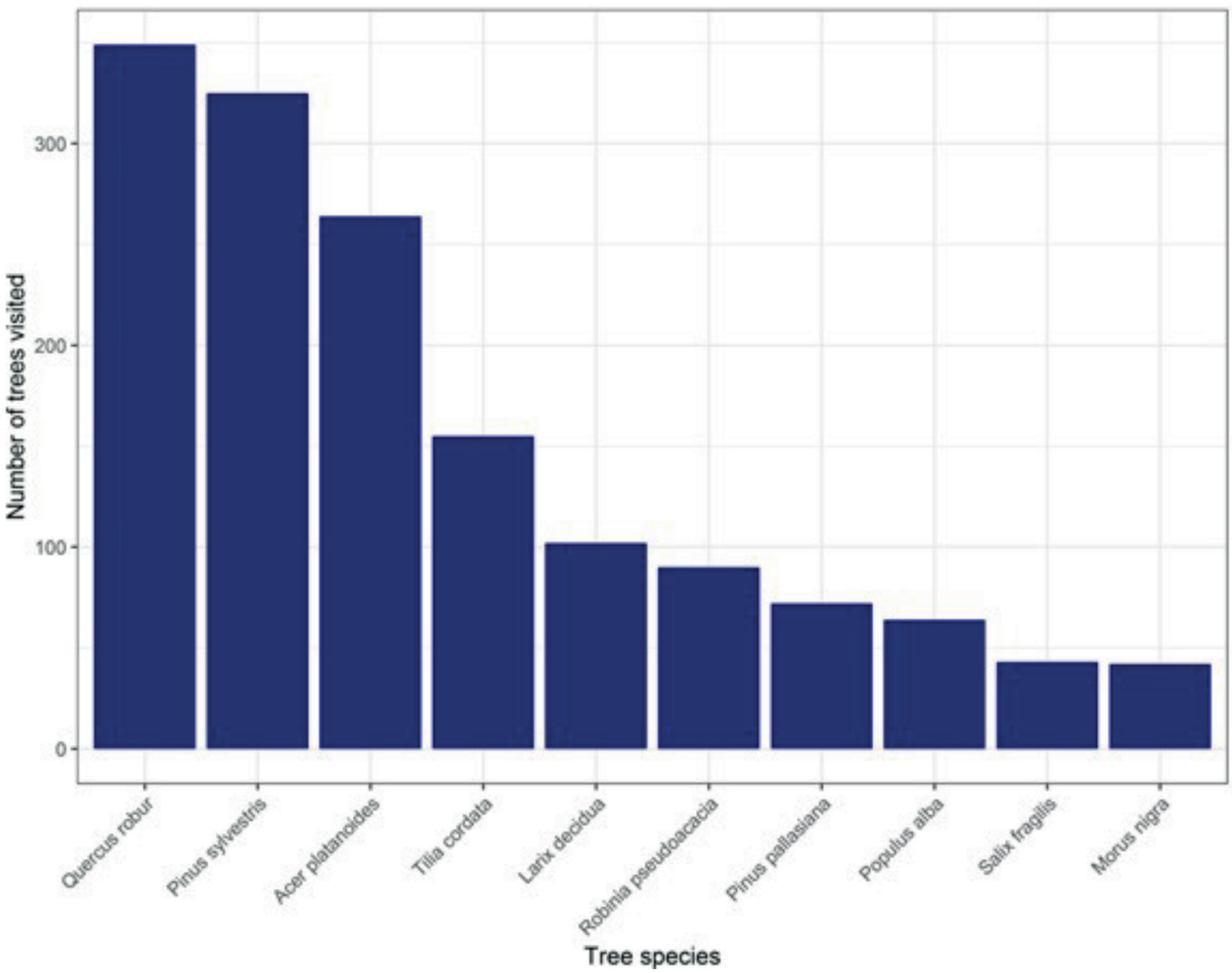

Fig. 4 – Distribution of indicators of ants visiting different tree species (top 10).

in each biotope. As a result, it remains unclear whether these patterns indicate specific preferences or opportunistic foraging based on the availability of tree species in natural, semi-urban, and urban areas. The most frequently visited trees for most species are those with a girth of about 1 m (diameter column in Table 7). The differences in distances to forage trees are somewhat greater. The shortest distances are for poplar (*Populus alba*) and Pallas pine (which hosts *Lasius neglectus*), the longest are for willow (*Salix fragilis*). This is partly because poplars grow in dry areas and willows in wetter areas, mainly in the lower reaches and valleys of rivers.

We found no significant correlations between tree size and distance from nests. Under natural conditions, r^2=0.148 (F=15.713, df=90) for *Camponotus vagus*, r^2=0.003 (F=0.816, df=218) for *Formica polyctena* and r^2=0.242 (F=14.116, df=226) for *F. rufa*. In the urban habitats of Crimea, r^2=0.232 (F=90.111, df=298) for *Lasius neglectus*, indicating preference of this invasive species for settlements near large trees. No difference in the sizes of nesting and forage trees was found for the ants that colonise trees, except for *L. fuliginosus* (1.88 m and 1.4 m, p = 0.044). At the same time, the sizes of nesting trees may differ; *L. fuliginosus* inhabits larger trees (1.88 m) than *L. brunneus* (1.33 m, p=0.008) and *Crematogaster subdentata* (1.2 m, p=0.0008), but there is no such difference for *Lasius emarginatus* (1.72 m, p=0.458), *L. brunneus* inhabits smaller trees than *L. emarginatus* (1.72 m and 1.33 m, p=0.007), *L. emarginatus* inhabits larger trees in comparison with *C. subdentata* (1.72 m and 1.2 m, p=0.0004). For forage trees there is no difference in size between species, except for *L. fuliginosus / C. subdentata* (1.4 m and 0.92 m, p=0.003).

It was also found that different ant species have different numbers of forage trees visited by one colony on average (ANOVA p-value = 1.282E-34, Table 8).

Table 8 shows that in the urban habitats of Crimea, the largest number of trees is controlled by *Crematogaster subdentata*, 2 times more than *Lasius neglectus* colonies.

Thus, the studied ant species utilize different settlement strategies in urban, semi-urban, and natural habitats. Both

Table 6 – Distribution of tree visits by different ant species.

tree_species	*Camponotus vagus*	*Crematogaster subdentata*	*Formica cinerea*	*Formica polyctena*	*Formica rufa*	*Lasius brunneus*	*Lasius emarginatus*	*Lasius fuliginosus*	*Lasius. neglectus*	*Lasius niger*	**Count**
Acer campestre									**1**		**1**
Acer negundo	**3**										**3**
Acer platanoides			**24**	**12**	**62**	**1**	**53**	**4**		**108**	**264**
Aesculus hippocastanum									**1**		**1**
Ailanthus altissima									**8**		**8**
Albizia julibrissin									**14**		**14**
Betula pendula	**2**		**4**					**2**			**8**
Cedrus libani									**29**		**29**
Cotinus coggygria									**1**		**1**
Cupressus sempervirens									**11**		**11**
Elaeagnus commutata									**1**		**1**
Fraxinus excelsior		**10**							**13**		**23**
Gleditsia triacanthos									**2**		**2**
Juglans regia		**15**									**15**
Larix decidua					**102**						**102**
Malus domestica									**2**		**2**
Morus nigra		**42**									**42**
Pinus brutia									**15**		**15**
Pinus pallasiana									**72**		**72**
Pinus sylvestris	**64**		**109**	**147**	**5**						**325**
Pistacia mutica									**1**		**1**
Platanus orientalis									**1**		**1**
Populus alba									**64**		**64**
Populus nigra								**1**	**9**		**10**
Populus tremula			**8**								**8**
Prunus armeniaca		**12**									**12**
Prunus cerasifera									**12**		**12**
Prunus domestica		**9**							**1**		**10**
Prunus dulcis									**2**		**2**
Pyrus communis	**1**				**1**						**2**
Quercus robur	**36**		**34**	**60**	**57**	**13**	**87**	**34**	**1**	**27**	**349**
Robinia pseudoacacia	**11**	**13**	**1**				**14**	**3**	**9**	**39**	**90**
Salix fragilis		**12**				**1**		**30**			**43**
Thuja occidentalis									**3**		**3**
Tilia cordata			**54**		**1**	**5**	**22**		**21**	**52**	**155**
Ulmus glabra				**1**							**1**
Ulmus laevis	**4**								**28**		**32**
Sum	**121**	**113**	**234**	**220**	**228**	**20**	**176**	**74**	**322**	**226**	**1734**

red wood ants, as well as *Lasius fuliginosus*, control on average approximately the same number of trees in natural habitats, 1.5÷2.0 times more than *L. emarginatus*, *L. brunneus* and *Camponotus vagus*. In urban habitats, all species exercise control within a single tree, with the exception of *L. fuliginosus*, which has a larger number of trees compared with other species. In these habitats, *L. emarginatus* always controls one tree, which is 0.5 times less for the same species in natural habitats. For *L. fuliginosus*, the number of trees is 1.5 times higher in natural biotopes than in urban habitats; for *L. brunneus* and *C. vagus* this difference is insignificant.

In urban habitats, colonies of two species were most often found (*Lasius niger*, *Formica cinerea*, and also *L. neglectus* in Crimea), in natural habitats: red wood ants (this is due to the fact that the territories of nest complexes were studied), as well as *L. emarginatus*, and *C. vagus* were the most frequent.

Discussion

As shown in our paper, different ant species utilize different settlement strategies in different habitat types. These strategies are not so much related to the convenience of nesting as to the proximity of a perennial food source, i.e. forage trees. It follows that in urban habitats and semi-urban habitats biotopes, ants often settle closer to forage trees, and in natural biotopes, ants forage in greater numbers on forage trees despite the large distances between them. *Lasius neglectus* utilises a strategy of settling as close as possible to trees, which gives it quick access to them. In addition, *L. neglectus* nests may remain intact under trampling conditions if they are located at the base of trees. There may be tunnels between neighboring trees that also protect ants from negative influences. The data revealed a pronounced pattern for *L. neglectus*, where the number of workers decreases rapidly as the distance from the forage tree increases. This suggests that *L. neglectus* tends to settle very close to food sources. However, this observed pattern may not be solely due to a preference for trees. Other factors, such as the availability of alternative food sources in the area or fewer aphids present on the trees it visited, could also influence this behavior. Since the sampling design did not account for these potential variables, further investigation is needed to explore these alternative explanations.

Table 7 – Statistical indicators of the visit rate (girth of trees and distance to forage trees) for the 10 trees most visited by ants.

Tree_species	Girth	Distance	Count
Quercus robur	**1.31±0.9**	**5.47±6.03**	**349**
Pinus sylvestris	**0.48±0.27**	**6.4±5.79**	**325**
Acer platanoides	**0.93±0.61**	**3.2±3.6**	**264**
Tilia cordata	**0.85±0.48**	**2.22±2.43**	**155**
Larix decidua	**0.46±0.1**	**4.23±3.04**	**102**
Robinia pseudoacacia	**0.6±0.52**	**2.59±2.68**	**90**
Pinus pallasiana	**0.83±0.26**	**0.27±0.3**	**72**
Populus alba	**1.3±0.36**	**0.15±0.12**	**64**
Salix fragilis	**1.44±0.61**	**7.09±4.93**	**43**
Morus nigra	**0.97±0.4**	**5.32±2.65**	**42**

Ants often colonize areas available to them in urban areas: sand and soil along ditches, and roads skirts (Dijon et al. 2023). Red wood ants build highly visible nests and are only found in large natural forest remains in urban areas (Stukalyuk et al. 2022). In all cases, ant species surviving in urban environments have fewer trees in their foraging areas. This may be due to the fragmentation of urban habitats, where trees may be more widely spaced than in natural habitats. Therefore, in urban habitats biotopes, ant species that control a small number of trees, most often one, will predominate. The best examples are *Lasius niger* and *L. emarginatus*. The exception is the invasive species *Crematogaster subdentata*, which lives in trees and private houses and can create busy trails between its nests. Invasive ant species in urban environments can acquire new traits: supercoloniality, polygyny (Buczkowski 2010; Stukalyuk et al. 2021); in some cases, natural ant species can also acquire these traits (Stukalyuk 2018).

In all cases, main sources of resources for ants are large trees, which corroborates this previously established evidence (Stukalyuk & Maák 2023). Larger trees may support more aphid colonies compared to younger trees, providing a potentially richer food source for ants. However, this hypothesis was not directly tested in the present study and requires further investigation. It has been suggested that the abundance of aphids may increase along the urbanization gradient, although this does not appear to correlate with the abundance of ants, as noted in a single case study by Korányi et al. (2021). Large free-standing trees may drive ant biodiversity in cities (Mendonça-Santos et al. 2023). This is particularly true for arboreal ants in the tree-associated communities we studied. Tree species and size are determinants of the abundance of ants and other invertebrates (Yasuda & Koike 2009). Sizes of tree plantations in parks may also contribute to increase ant biodiversity, as may the proximity of these parks to forested areas (Carpintero & Reyes-López 2014; Liu et al. 2019; Santos et al. 2019).

Table 8 – Average number of forage trees controlled by one colony for different ant species in the studied habitats.

Species	Mean	Std. error	Stand. Dev.	Number of colonies
Lasius neglectus, **urban**	**2.525926**	**0.236716**	**2.750386**	**135**
Crematogaster subdentata, **urban**	**5.8**	**0.680433**	**3.726883**	**30**
Camponotus vagus, **Natural**	**1.508197**	**0.111186**	**0.868388**	**61**
Camponotus vagus, **Urban**	**1.26087**	**0.093618**	**0.448978**	**23**
Formica polyctena, **natural**	**2.528736**	**0.17898**	**1.669418**	**87**
Formica rufa, **natural**	**2.340206**	**0.200882**	**1.97846**	**97**
Formica cinerea, Sub-**Urban**	**2.16**	**0.286822**	**1.434108**	**25**
Formica cinerea, **Urban**	**1.730769**	**0.11451**	**1.167777**	**104**
Lasius niger, urban	**1.141414**	**0.029541**	**0.415685**	**198**
Lasius fuliginosus, **Natural**	**2.766667**	**0.28641**	**1.568732**	**30**
Lasius fuliginosus, **Urban**	**1.857143**	**0.318372**	**1.458962**	**21**
Lasius brunneus, **Urban**	**1.24**	**0.104563**	**0.522813**	**25**
Lasius brunneus, **Natural**	**1.375**	**0.13282**	**0.751343**	**32**
Lasius emarginatus, **Natural**	**1.518072**	**0.086329**	**0.786493**	**83**
Lasius emarginatus, **Urban**	**1**	**0**	**0**	**50**

An interesting result is the different distances between ant nests and trees of different species. This may be a consequence of the influence of microclimatic factors (soil composition and moisture, soil and air temperature: Uno et al. 2010), which can differ significantly under different trees (coniferous or deciduous), which also provide different shading (Sanusi et al. 2010; Wang et al. 2019). It is noteworthy that ants tend to settle closer to trees providing better shading (e.g., maple and linden, Table 8) and farther from trees with weaker shading (e.g., oak, pine, larch). This observation is based on visual assessments of tree canopy density and shading during the study. For willow, the data presented mainly concern *Lasius fuliginosus*, which lives in tree trunks and can build tunnels to forage trees; the close distances to Pallas pine and white poplar are due to peculiarities of *L. neglectus* settlement. In addition, different ant species prefer different tree species, but some of them can overlap (oak, pine, maple and linden). At the same time, different distances from the nest to the source of food resources in ants are associated with the effective distance to which they can mobilise for the resource, and this is a species-specific feature (Stukalyuk & Akhmedov 2022). The same work emphasizes the difference in effective mobilization distances for the same species in different types of biotopes.

Thus, in urban and other types of biotopes, ants settle in an optimal zone for themselves, but maintain proximity to a potential resource source (i.e. a tree). This dependence is more pronounced in urban habitats. In addition, in urban habitats, trees are often planted without taking into account their requirements for specific environmental conditions, while in natural environments trees obviously grow in suitable environments. Such features of the distribution of vegetation in urban environments contribute to the stressful conditions for trees, which can lead to their weakening compared to natural populations, allowing for the development of honeydew-producing hemipteran colonies (e.g., aphids, mealybugs, scales) on them (Lubiarz et al. 2011).

A common trend observed in all ant species is that their abundance is lower in urban habitats compared to natural ones. This could be related to various factors, including habitat modifications such as the presence of concrete, which may physically prevent nest founding. In addition, ants in urban habitats biotopes tend to settle closer to the source of resources (trees) (Ślipiński et al. 2012). This confirms with explicit data the previously established fact that ant nesting sites in urban environments are limited (Friedrich & Philpott 2009; Ślipiński et al. 2012). Ant colonies in urban habitat biotopes were found to be smaller (except for invasive species), which may be related to factors such as lower tree density per area unit (Buczkowski 2010). However, it is important to note that many native species can form large colonies in urban habitats as well, and further research is needed to better understand the factors influencing colony size in these environments. Furthermore, ant species are not randomly distributed in urban landscapes (Ślipiński et al. 2012). We have shown this in more detail using the example of ant species preferences for settlement distances from trees, as well as preferences for different tree types. The general trend is that ant species richness decreases with increasing urbanization gradients (Buczkowski & Richmond 2012). In our case, two species were most successful in urban landscapes: *Lasius niger* and

Formica cinerea. Finally, while in natural (and semi-urban) habitats the structure of ant communities is determined by environmental factors, in urban habitats the main factor determining the structure of these communities is the urbanization gradient (Ossola et al. 2015). The long-term functioning of such communities may be ensured by ant species that form the core of urban communities (Perez & Diamond 2019).

Conclusions

Distribution of Ants Around Forage Trees
The distribution of ants around forage trees depends on both the ant species and the habitat type. Most ant species show a negative relationship between the distance from trees and the number of workers, indicating that ants tend to decrease in number as the distance from the tree increases. However, *Camponotus vagus* was found to be an exception, likely due to its ability to form busy trails leading to trees located far from the nest.

Ant Settlement Patterns in Different Habitats
Ant settlement closer to food trees is more common in urban and semi-urban habitats than in natural ones. This could be attributed to the availability of suitable nesting sites, as urban environments often present fewer nesting options outside areas near trees, such as concrete surfaces. Further research is needed to determine whether this behavior is a preference for proximity to resources or a response to habitat constraints.

Ant Colony Size and Habitat Type
In natural habitats, higher numbers of ants and greater distances to forage trees are observed compared to urban and semi-urban habitats. This is likely because natural biotopes offer more space and resources for ants. However, the observed differences in foraging site structure suggest that ants adapt their settlement strategies to environmental conditions and resource availability.

Tree Preferences
Ant species exhibit different preferences for forage trees. While some species prefer native trees such as oak, pine, maple, and linden, others are more likely to visit introduced or invasive species such as *Robinia* and larch. This suggests that ants adopt adaptive strategies to use available resources. However, the frequency of tree visits might also be influenced by the varying occurrence of different tree species in each biotope, which may distort our understanding of true preferences.

Tree Size Preferences
Different ant species also show varied preferences for tree girth. For instance, *Lasius fuliginosus* is more commonly found in larger trees, likely because it nests in them, while other species prefer smaller trees. This could reflect different adaptive strategies based on habitat types, as ants in urban habitats may favor nearby resources due to their limited availability.

Forage Tree Visiting and Colony Size
Some ant species, particularly the invasive *Crematogaster subdentata*, are able to visit more forage trees at the same time than others, which may be linked to colony size and structure, as well as the availability of resources.

Urban Habitat Characteristics
Specific characteristics of urban habitats include a high concentration of ants around certain trees. In urban habitats, *Lasius niger* and *Lasius emarginatus* tend to visit only one tree on average, while in natural habitats, these species usually control more trees. This difference might be related to the limited availability of nesting sites in urban environments.

Acknowledgements – The authors are grateful to an unknown reviewer, who certainly contributed to improving the quality of our article. The authors are grateful to Prof. Paolo Audisio for his invaluable assistance in improving the structure of the article. The research leading to this publication has received funding from "Funding the development of priority research fields of the Ukraine" allowance number KPKVK 6541230.

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