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HABITAT ANALYSIS OF *Formica rufa* AND *Formica polyctena* (HYMENOPTERA; FORMICIDAE) PREFERENCES IN KYIV CITY, UKRAINE ACCORDING TO VEGETATION

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ABSTRACT

The habitats of two species of Red Wood Ants (RWA, *Formica rufa* Linnaeus, 1761, *Formica polyctena* Foerster, 1850) were assessed in urbanized forests in Kyiv city (Ukraine). Descriptions of vegetation in the study sites of RWA were used for phytoindicative assessment of environmental conditions according to eight factors. The aim of this study is to analyze the ecological requirements of two species RWA in the urbanized forests of Kyiv using the phytoindication approach. The study was conducted in 2020-2022 on the territory of two forest areas in Kyiv, represented by deciduous (Golosiivsky forest) and mixed forests (Svyatoshinsky forest). Seven RWA nest complexes were found and mapped, three nest represent *Formica rufa* (152 anthills) and four nest complexes represent *F. polyctena* (132 anthills). It has been established that anthills are located near trees, usually conifers. In mixed forests, anthills are larger in both species. The height and diameter of the anthill are directly proportional to the number of forage trees visited. Ecological analysis of habitats of RWA using a phytoindication approach revealed the following factors significant for RWA: a) natural habitats ($F=95.066$, $P\text{-value} = 1.9e-11$), *F. polyctena* is more sensitive to the anthropogenic factor; b) humidity of habitats ($p\text{-value} = 2e-09$). The ecological humidity amplitude is wider in *F. rufa* ($sd = 0.98$ in *F. polyctena* vs $sd = 3.85$ in *F. rufa*); c) thermal regime ($P\text{-value} = 7.7e-04$), *F. polyctena* has a higher value (mean = 57.02). The amplitude value for the thermal regime is wider in *F. rufa* ($sd = 2.36$ in *F. polyctena* vs $sd = 6.85$ in *F. rufa*), i.e., *F. rufa* is a more eurytopic (plastic) species. There is no separation of the habitats of the two species of RWA, and, despite the difference in optima, the ecological amplitudes of *F. polyctena* and *F. rufa* largely overlap.

Keywords: Red Wood Ants, morphometric characteristics, anthills, forage trees, urbanized forests, conifers.

ABSTRAK

Habitat kepada dua spesies Semut Kayu Merah (RWA, *Formica rufa* Linnaeus, 1761, *Formica polyctena* Foerster, 1850) telah dinilai di hutan bandar di Bandar Kyiv (Ukraine). Perihal ke atas vegetasi di tapak kajian RWA telah digunakan sebagai penilaian fitoindikatif keadaan persekitaran mengikut lapan faktor. Kajian ini dijalankan untuk menilai keperluan ekologi dua spesies RWA di hutan bandar Kyiv menggunakan pendekatan fitoindikator. Kajian ini telah dijalankan pada 2020-2022 di teritori di dua kawasan hutan di Kyiv, mewakili *deciduous* (hutan Golosiivsky) dan hutan campur (hutan Svyatoshinsky). Tujuh sarang RWA kompleks telah ditemui dan dipetakan, di mana tiga sarang mewakili *F. rufa* (152 busut) dan empat sarang mewakili *F. polyctena* (132 busut). Busut telah dibina berdekatan pokok pada kebiasaannya konifer. Pada hutan campur, busut lebih besar di kedua-dua spesies. Ketinggian dan diameter busut berkadar langsung dengan bilangan dan pokok yang telah dilawati. Analisis ekologi habitat ke atas RWA menggunakan fitoindikator mendedahkan faktor signifikan ke atas RWA: a) habitat semulajadi ($F=95.066$, nilai $P = 1.9e-11$), *F. polyctena* adalah lebih sensitif kepada faktor antropogenik; b) kelembapan habitat (nilai $P = 2e-09$). Amplitud kelembapan ekologi lebih besar pada *F. rufa* ($sd = 0.98$ dalam *F. polyctena* vs $sd = 3.85$ pada *F. rufa*); c) regim terma (nilai $P = 7.7e-04$), *F. polyctena* lebih tinggi dengan nilai (purata = 57.02). Nilai amplitud untuk regim terma lebih besar pada *F. rufa* ($sd = 2.36$ pada *F. polyctena* vs $sd = 6.85$ pada *F. rufa*), i.e., *F. rufa* lebih eritopik spesies (plastik). Tiada pengasingan untuk habitat ke atas dua spesies RWA meskipun perbezaan yang optimum serta amplitud ekologi *F. polyctena* dan *F. rufa* bertindih dengan besar.

Keywords: Semut Kayu Merah, ciri morfometrik, busut, pokok pencarian, hutan bandar, konifer.

INTRODUCTION

Red Wood Ants (RWA) are one of the main components of forest ecosystems. Also, RWA participate in the cycle of biogenic elements in the soil (Ohashi et al. 2007; Wardle et al. 2011; Zakharov 1991; Zingg et al. 2018), contribute to its aeration due to nest-building activity, collect and move the seeds of some plant species (the phenomenon of myrmecochory), thereby facilitating their distribution (Boryakova & Melnik 2017). Modern studies of RWA using botanical data are mainly focused on forest inventory data, i.e., the age composition of forest stands, as well as the main tree species that form the tree layer, are considered (Cappelli 2015; Dyachenko 2017; Domisch et al. 2005; Kilpelainen et al. 2005; Shtuchnyy 2006).

To date, there are few studies of the state of nest complexes of RWA, in which detailed geobotanical descriptions (phytoindication approach) are involved. In some works, other ant species were chosen as the object of study (Bátori et al. 2019). Available works on RWA do not provide a complete analysis of habitat assessment based on geobotanical descriptions (Boryakova & Melnik 2017; Konopleva 2010; Rubashko et al. 2009). Meanwhile, a detailed study of the habitat of RWA can provide answers to questions about their adaptive potential, as well as about the most optimal forest biocenoses for them. The use of complete vegetation descriptions makes it possible to assess habitats and is important for the conservation of RWA, and may also favor their successful dispersal in the event of a decline in numbers.

The purpose of this study is to determine the habitat preferences of *Formica rufa* and *Formica polyctena* in the urbanized forests of Kyiv city (Ukraine) using a phytoindication approach. The objectives of the research were, a) to compare the linear parameters of anthills

in different forests types (mixed, deciduous); b) to study the possible relationship between the linear dimensions of anthills (height, average diameter) and the number of visited forage trees; c) to analyze the attendance of different species of trees by RWA; and d) to carry out an ecological analysis of the habitats of *F. rufa* and *F. polycтена* using the phytoindication approach.

MATERIALS AND METHODS

Study Sites

The study was conducted in 2020-2022 in the territory of Kyiv city, Ukraine. Golosiivsky forest (750 hectares) is mainly a deciduous forest (but with small mixed forests parts), while Svyatoshynsky forest is mixed (area 280 hectares). Oak (*Quercus robur*), maple (*Acer platanoides*) and hornbeam (*Carpinus betulus*) are the dominant tree species in the deciduous forest. Larch (*Larix decidua*) was planted in one of the locations of the Golosiivsky forest. In addition to these species, pine (*Pinus sylvestris*) is present in the mixed forest (Figure 1).

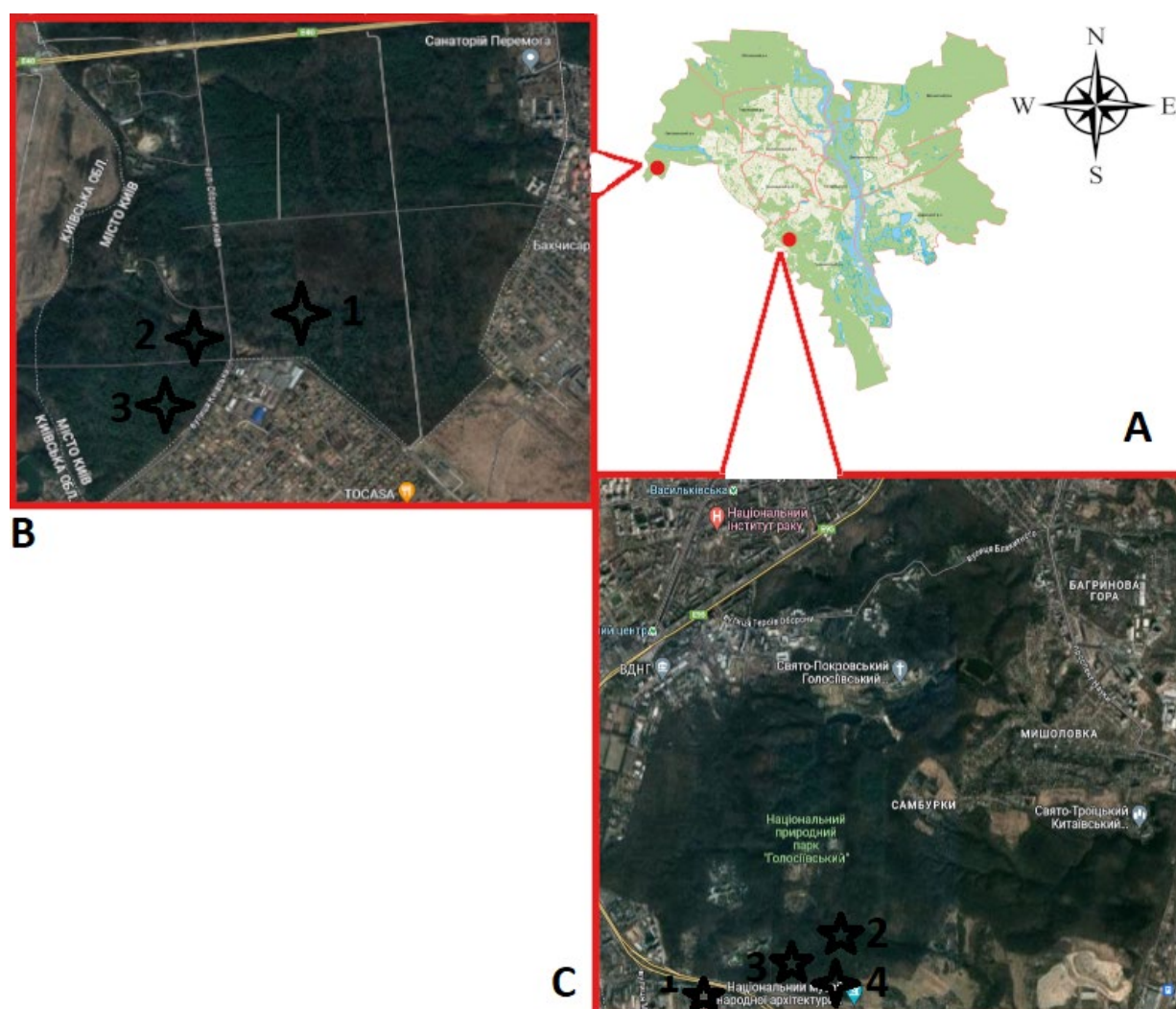


Figure 1. Location in Kyiv city (Ukraine, 1A) of nest complexes of *F. polycтена* (four-pointed stars, 1B – Svyatoshynsky forest) and *F. rufa* (five-pointed stars, 1C - Golosiivsky forest). The numbering is corresponded to the numbers of the complexes being studied

Myrmecological Methods

In both study sites, a total of seven nest complexes of RWA of two species were examined - *Formica rufa* (three complexes, 152 anthills in total) and *F. polyctena* (four complexes, 132 anthills). The affiliation of anthills to the type of forest (mixed, deciduous) was established based on geobotanical relieves. For each anthill, two diameters were measured (in the narrowest and widest parts of the anthill), from which the average diameter was calculated. The height of the anthill was also measured. Both parameters were measured in meters. Further, the diameter (D) and height (H) were used to calculate the volume index of the anthill, or V, m^3 , calculated by the formula: $3.14 \cdot D^2 \cdot H / 3$. The volume indicators of anthills were used to calculate their size classes, according to the K-means method. Thus, five size classes of anthills were obtained according to their volume.

A geobotanical relieves (or vegetation plots) was carried out next to each group of anthills. If the anthill was part of the complex, but was isolated from others, a separate vegetation plots was made for it, but if a group of anthills was located on the registration site, a vegetation plots was made for all of them. All nest complexes were mapped according to Zakharov's method (1991; 2015). On such maps, anthills, trails between them and to the forage trees are plotted on a scale (Figures 2A, 2B). Trees located within the forage area of the anthill, to which the trails of ants led, were considered fodder.

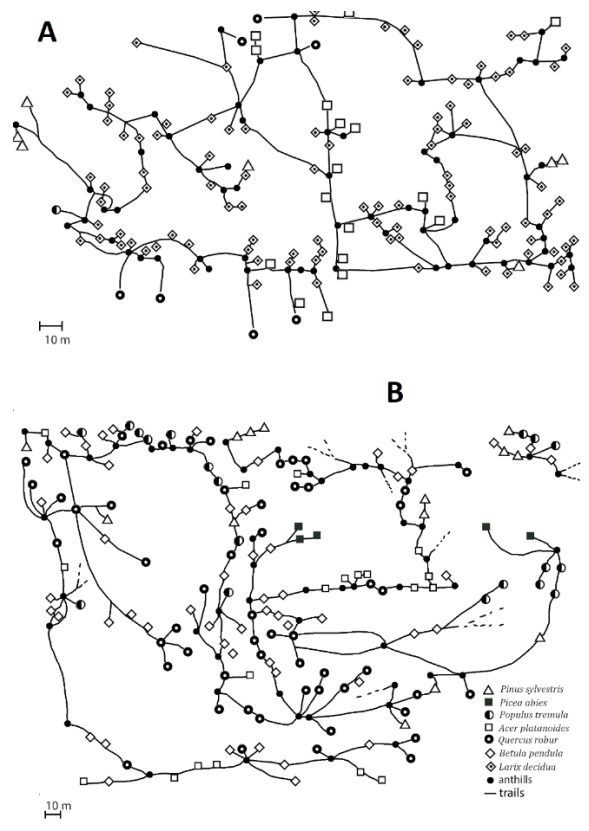


Figure 2. Mapping of the nest complex of *F. rufa* (A, Golosiivsky forest) and *F. polyctena* (B, Golosiivsky forest)

Analysis of the RWA Attendance of Different Species of Trees.

For each anthill, the species composition of forage trees was analyzed. The diameter and number of tree trunks of each species were also taken into account. For both species, the top

five visited tree species were measured, as well as the size class distribution of anthills for each tree species.

Syntaxonomic Scheme of The Vegetation of The Studied Objects

On the territory of the mentioned objects, we noted several associations that can be found in the syntaxonomic scheme (Dubyna et al. 2019; Kozyr 2012). Its location is indicated next to each association.

Cl. Carpino-Fagetea Jakucs ex Passarge 1968

Ord. Carpinetalia betuli P. Fucarek 1968

All. *Aceri campestris-Quercion roboris* Bulokhov et Solomesch et Laivins in Bulokhov et Semenishchenkov 2015

Ass. *Mercurialo perennis-Quercetum roboris* Bulokhov et Solomesch in Bulokhov et Semenishchenkov 2015

All. *Carpinion betuli* Issler 1931

Ass. *Galeobdolo lutei-Carpinetum* Shevchyk, Bakalina et Solomakha 1996

Cl. Quercetea roboris-Petraeae Br.-Bl. ex Tx. ex Oberd. 1957

Ord. Quercetalia roboris Tx. 1931

All. *Pino-Quercion* Medwecka-Kornaš et al. in Szafer 1959

Ass. *Quercu robori-Pinetum* W.Matuszkiewicz 1981

All. *Convallario majali-Quercion roboris* Shevchyk et Solomakha in Shevchyk, Solomakha et Voityuk 1996

Ass. *Melico nutantis-Quercetum roboris* Shevchyk et Solomakha in Shevchyk, Solomakha et Voityuk 1996

Methods of Vegetation Study

For the ecological analysis of the habitats of both RWA species, the following data on ants were recorded including species, size of anthills, size classes of anthills and species composition of vegetation on test plots. Sample plots ranged in size from 16 to 100 m², and the vegetation description technique was based on various literatures (Goncharenko & Didukh 2003; Landolt 1977; Mueller-Dombois & Ellenberg 2002; Ramensky 1938). A total of 135 vegetation plots were made in which 179 cases of *F. polyctena* and 88 cases of *F. rufa* were recorded. This number differs from the total number of anthills indicated above, since some of the anthills did not have forage trees.

Methods for Analyzing the Relationship Between Indicators of Anthills and Vegetation

Ecological analysis was carried out using the phytoindication technique, which is widely used by botanists (Didukh & Plyuta 1994; Didukh 2011; Ellenberg 1974; Ellenberg et al. 1991; Frank & Klotz 1990; Ramensky 1938; Tsyganov 1983). As a basis for the assessment, we chose ecological scales of plant species (Didukh 2011). The calculation was based on the average scores of plant species. According to recent studies, the scales, due to their different scales for different indicators, are first reduced to a single 100-point scale, and then the average score of plant species of each phytocenosis is calculated, weighted by the values of the projective plant cover (Churilov et al. 2020; Goncharenko 2017; Goncharenko et al. 2022).

Statistical Analysis

Statistical calculations were carried out using the statistical environment R ver. 3.5.3 software (<https://cran.r-project.org>). The arithmetic mean of the morphometric indicators and the

standard deviation were calculated for each ant species. The ANOVA test was used to identify differences between the two ant species. Multiple paired comparisons (so-called post hoc analysis) were performed using Tukey's test. Bivariate regression was used to identify a possible relationship between the number of forage trees and the linear dimensions of the anthill. We calculated the mean values and standard deviations for eight phytoindicators (Hd–Kn), and also used an ANOVA test to assess the differences in these indicators between both RWA. We have used the following indicators: Hd – moisture, Rc – soil acidity, Sl – total salt regime, Nt – nitrogen soil content, Lc – availability of light, Nv – naturalness value, Tm – temperature value, Kn – continentality. Phytoindication is not a direct means of assessing the environment. Instead, it relies on ecological scales that represent the relationship between plants and environmental parameters in a relative score or rank basis.

Indicators of moisture, acidity, salinity and nitrogen relate to the assessment of soil conditions. An important factor for the existence of plants is the availability of light, which is estimated by the Lc indicator. The Tm and Kn indicators measure the relationship between plants and climatic factors (Didukh 2011). Scales of the relationship of plants to the anthropogenic factor assess the degree of their tolerance to human influence, in particular, such a scale is the scale of the naturalness value, or Nv, proposed by Borhidi (1995).

RESULTS

Comparison of Linear Parameters of Anthills in Different Forests Types (Mixed, Deciduous)

In mixed forests, anthills are usually found near coniferous trees (Figure 2A, larch, pine), in deciduous forests - usually near oaks (Figure 2B). Ants in the mixed forest can enter areas without conifers, but anthills are not built there (Figure 2A, lower part of the complex). Anthills of *F. rufa* and *F. polyctena* in mixed forests have larger parameters of both height (Figure 3A) and average diameter (Figure 3B) compared to deciduous forests (Table 1).

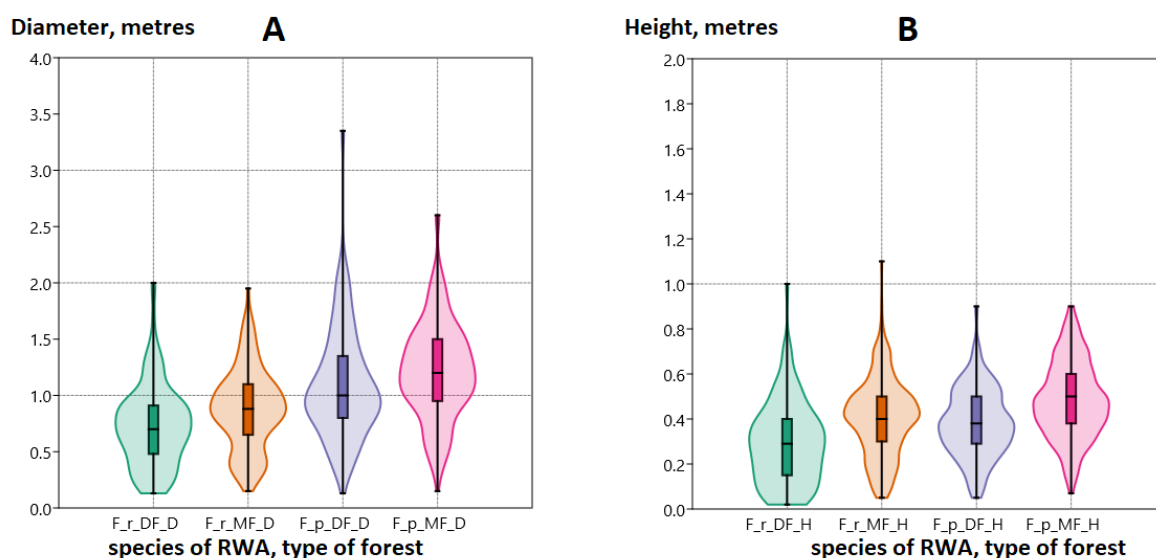


Figure 3. Comparison of linear dimensions (height, H, A, average diameter, D, B, meters) of *F. rufa* (F_r), *F. polyctena* (F_p) anthills in deciduous (DF) and mixed forests (MF)

Table 1. Results of Tukey's test for pairwise comparison of diameter (D) and height of anthills of *F. rufa* (F r) and *F. polycтена* (F p) in deciduous (DF) and mixed (MF) forests

Height, metres				
	F_r_DF_H	F_r_MF_H	F_p_DF_H	F_p_MF_H
F_r_DF_H		2.63E-10	3.23E-06	0
F_r_MF_H	9.425		0.4884	1.64E-08
F_p_DF_H	7.133	2.005		2.40E-10
F_p_MF_H	15.66	8.488	9.445	
Diameter, metres				
	F_r_DF_D	F_r_MF_D	F_p_DF_D	F_p_MF_D
F_r_DF_D		0.001532	0	0
F_r_MF_D	5.171		2.97E-08	0
F_p_DF_D	11.36	8.346		0.002545
F_p_MF_D	16.28	14.76	4.977	

Legend: Significant comparisons are bold.

In terms of diameter in mixed and deciduous forests, the difference between the anthills of *F. rufa* is greater than that of *F. polycтена*. The difference in height between mixed and deciduous forests is greater than the difference between the diameters of anthills for both species taken separately. No relationship was found between the trunk diameter of forage trees and the linear dimensions of anthills.

The Relationship Between the Linear Dimensions of Anthills (Height, Average Diameter) and the Number of Visited Forage Trees

There were no significant differences between the number of visited forage trees in both species of RWA (*F. rufa*, on average 2.39 ± 0.18 trees per anthill, maximum 14 trees, *F. polycтена*, 2.34 ± 0.14 , maximum 11 trees). However, there is a regression relationship between the height of the anthill of each individual species and the number of trees visited (Figures 4A, 4B).

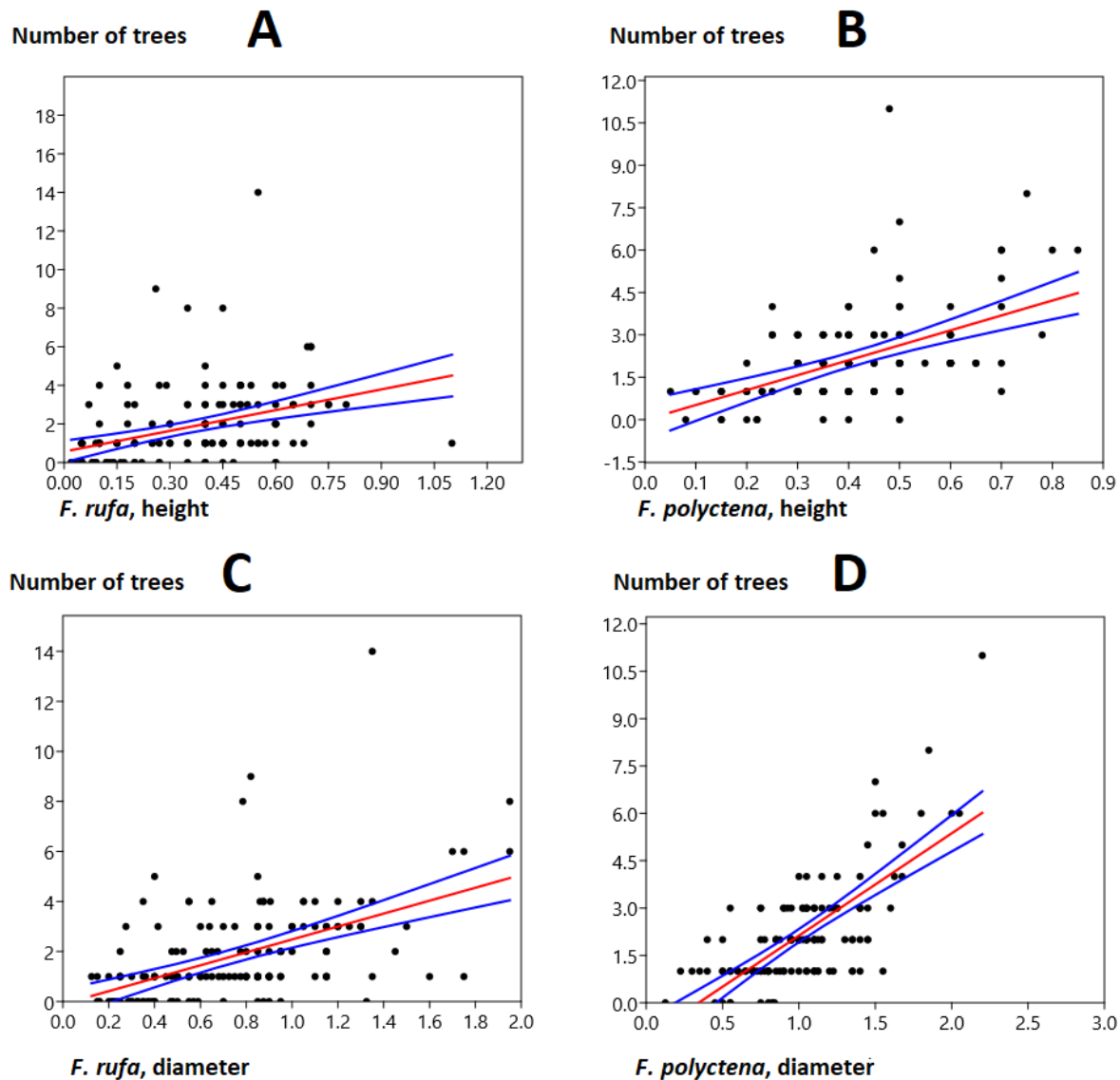


Figure 4. Regression relationship between sizes (4A, B, height, h; 4C, D, average diameter, D, meters) of an anthill and the number of forage trees visited (N) in *F. rufa* (F_r), *F. polycтена* (F_p). 4A: $r=0.38$, $r^2=0.14$; $P\leq 0.0001$; $df=150$, $F=26.2$; 4B: $r=0.49$, $r^2=0.24$; $P\leq 0.0001$; $df=130$; $F=42.8$; 4C: $r=0.51$; $r^2=0.26$; $P\leq 0.0001$; $df=150$; $F=53.1$; 4D: $r=0.71$, $r^2=0.51$; $P\leq 0.0001$; $df=130$; $F=136.7$

This dependence is more pronounced for both ant species for the means diameter (Figure 4C, 4D), i.e. the larger the anthill, the greater the number of trees visited by the colony. It is interesting to note that 37 anthills of *F. rufa* and 9 of *F. polycтена* did not have a single forage tree.

Analysis of the Attendance of Different Species of Trees For RWA.

There are 96 species of plants belonging to 46 families were found, of which 26 are trees, 13 are shrubs, and 57 are herbaceous plants. Table 1 lists the top five forage tree species preferred by *F. polycтена* and *F. rufa*, as well as indicators related to trees (trunk diameter) and ants (anthill volume and size classes, frequency and proportion of visits). The projective cover of *Carpinus betulus* varies widely (8-90%), but it is usually the dominant species with more than 25-35%. Despite such a significant role in the creation of phytocoenoses, this species is of little

interest to RWA. In both species of RWA, anthills of classes cl2-cl5 are located near coniferous, less often deciduous tree species (Table 2).

Table 2. Top 5 tree species visited by ants

ant_species	tree_species	Tree indicators		Ants parameters			Anthill classes by size				
		d_min	d_max	N	v_sum	Prop	cl1	cl2	cl3	cl4	cl5
<i>Formica polycтена</i>	<i>Pinus sylvestris</i>	0.2	1.2	183	63.83	0.64	8	30	52	50	43
	<i>Quercus robur</i>	0.2	1.8	80	20.75	0.28	4	16	33	21	6
	<i>Acer platanoides</i>	0.15	0.4	13	6.08	0.05	0	2	1	2	8
	<i>Populus tremula</i>	0.2	0.6	9	1.5	0.03	2	1	5	1	0
	<i>Carpinus betulus</i>	0.3	0.4	1	0.73	0.01	0	0	0	0	1
<i>Formica rufa</i>	<i>Larix decidua</i>	0.2	0.7	102	32.86	0.38	10	9	22	50	11
	<i>Acer platanoides</i>	0.13	1.25	72	18.76	0.27	3	27	12	27	3
	<i>Quercus robur</i>	0.3	4.5	60	13.04	0.22	9	21	15	10	5
	<i>Pinus sylvestris</i>	0.4	0.7	19	5.14	0.07	2	5	5	4	3
	<i>Populus tremula</i>	0.3	0.45	9	2.44	0.03	0	2	3	4	0

Legend: d_min, d_max – minimum and maximum trunk diameters (at chest height) of trees, in meters; n is the frequency of visits, prop is the proportion of visits to a given tree species; v_sum - total size (volume) of anthills, cl1 - cl5 - size classes of anthills.

In both species of RWA, the most visited are conifers - *Pinus sylvestris* and *Larix decidua*. This is due to the fact that these species usually grow on light sandy soils, which are also preferred by RWA. In terms of distributions, *F. polycтена* is a more selective species, as the top most visited *Pinus sylvestris* accounts for 0.64 or 64% of all visits, while *F. rufa* only 0.38 or 38%. Also note that *P. sylvestris* in *F. rufa* is only in 4th place in terms of attendance (19 cases, or 7%). As for broad-leaved species, the 2nd and 3rd place in both species is traditionally occupied by the main and most common species - *Quercus robur* and *Acer platanoides*.

Ecological Analysis of Habitats of 2 Ant Species According to Vegetation Phytoindication Data

Table 3 shows ecological assessments of the habitats of *F. polycтена* and *F. rufa* according to the phytoindication analysis of vegetation.

Table 3. Phytoindicative indicators of habitats in two RWA species *Formica polycтена* and *Formica rufa* according to vegetation analysis, as well as F statistic ANOVA test of group differences between these species

Ant_species	<i>Formica polycтена</i>		<i>Formica rufa</i>		ANOVA F statistic	
	Variable	Mean	Sd	Mean		Sd
Hd		48.01	0.98	45.24	3.85	F=82.203***
Rc		51.62	3.3	50.82	5.72	F=2.099
Sl		26.51	1.85	26.58	3.45	F=0.041
Nt		46.2	4.11	45.56	7.63	F=0.791
Lc		51.3	3.28	51.47	5.36	F=0.102
Nv		56.77	4.7	46.86	11.84	F=95.066***
Tm		57.02	2.36	54.41	6.85	F=20.959***

Kn	41.64	3.74	42.4	6.33	F=1.494
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Designations of environmental factors: Hd – moisture, Rc – soil acidity, Sl – total salt regime, Nt – nitrogen soil content, Lc – availability of light, Nv – naturalness value, Tm – temperature value, Kn – continentality. Statistical significance markers: * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$.

The significant differences in the preferences of *Formica polyctena* and *Formica rufa* are observed in three indicators: a) humidity, b) the degree of naturalness of the plant species composition, and c) the thermal regime (indirectly indicates the extent to which a habitat is warming). Visual comparison of the optimal factors between *Formica polyctena* and *Formica rufa* is presented in Figure 5.

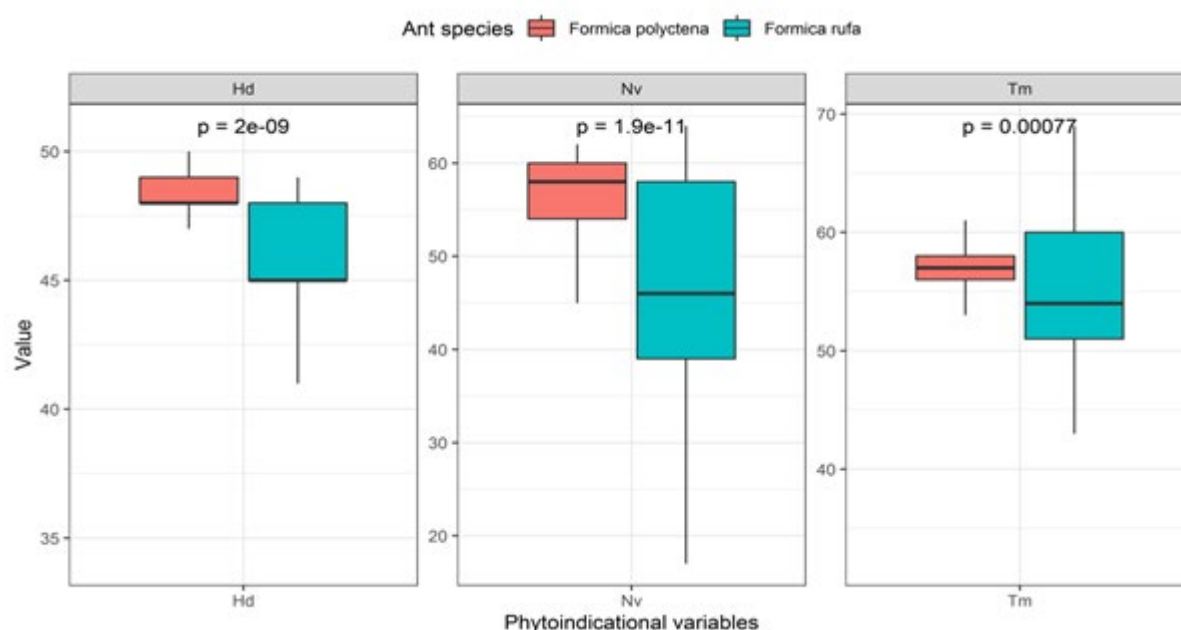


Figure 5. Comparison of habitats of *F. polyctena* and *F. rufa* according to phytoindication. Only the factors for which the greatest differences in means are observed are shown. The designations of the factors are the same as in Table 2. In addition, the values of the significance level of the ANOVA test are indicated

Judging by the value of F statistics and the level of significance, the greatest differences are observed in the degree of naturalness of habitats, Nv (Table 3). In botany, this indicator usually correlates with the magnitude of the anthropogenic load and the degree of transformation of the flora of the coenosis. Figure 5 shown that *F. polyctena* is much more sensitive to the anthropogenic factor, since this species was recorded in cenoses with higher naturalness (Table 3). At the same time, for both species, the assessments on the scale of natural habitats are close to the middle of the 100-point scale (about 50 points), which indicates that both of these species are generally quite tolerant to the anthropogenic factor, which is why they are found within the boundaries of a large city at the presence of woody (forest and forest-park) vegetation.

Significant differences were also observed in habitat humidity, Hd (Table 3, Figure 5). At the same time, the optimum in *F. polyctena* was observed in slightly more humid conditions (Table 3). Perhaps this is not directly related to the level of humidity, but rather to the difference

in the species composition of phytocoenoses and fodder herbaceous plants growing under these conditions. In general, for both species, the moisture conditions should be characterized as mesophytic. Also, it should be noted that, both in terms of the natural factor and in terms of humidity, the breadth of the ecological amplitude in *F. rufa* is wider (in terms of humidity, see Table 3).

Differences in terms of thermal regime, T_m (Table 3, Figure 5) are also significant, although less pronounced than in the two previous factors. The thermal regime, which also indirectly characterizes the degree of warming of habitats, has a higher index in *F. polyctena* (Table 3). This generally characterizes this species as more eurytopic (plastic). Given the small difference in T_m (Table 3) and the much wider amplitude in *F. rufa*, this does not lead to separation of the habitats of these two species. On Figure 5, despite the difference in optima, the ecological amplitudes of *F. polyctena* and *F. rufa* overlap to a large extent.

DISCUSSION

Preferences of RWA in the Forest Depending on Its Composition, Age and Presence of Clearings

Formica rufa and *F. polyctena* studied by us had similar habitat requirements, at least in urbanized forests. Despite this, there may be differences between different species of RWA - for example, *Formica aquilonia* Yarrow, 1955 prefers forest areas with mature trees (140 years old) and with more shading, compared to *Formica lugubris* Zettersted, 1840, which is more common on forest edges (Punttila et al. 1994). In our study, the two largest nest complexes of *F. polyctena* were located in a mixed forest, the main layer of which consisted of pines up to 180 years old (Svyatoshinsky forest). In the deciduous forest (Golosiivsky forest), the main tier is made up of oaks aged 180-300 years. Thus, the presence of mature or overmature trees is an important condition for the existence of nest complexes of RWA (Berberich et al. 2022). Our data on the preference for visiting coniferous trees confirm the results obtained for RWA in Bulgaria, where spruce and pine were the top visits (Antonova & Marinov 2021). In Switzerland, the tree most visited by RWA is spruce (85% of the trees were visited, the rest were not), larch (69%), followed by two species of pine (46-58%) (Cappelli 2015). Finally, among deciduous species, RWA select oak, as well as birch (Robinson et al. 2008), which is also confirmed by us, although maple occupies the second place in our study region after oak in terms of attendance. The attendance by ants of different tree species is directly related to the species of aphids living here. Thus, in the region of our study, eight species of aphids were noted on oak, five species on maple, 11 species on birch (eight species are attractive to ants), five species on pine, and only one species on hornbeam (Stukalyuk et al. 2020a). Apparently, for RWA, conifers are more attractive than deciduous trees, since in general, forage trails were found on oak in all ant species in the Kyiv region two times more often (40% of all trees) than in pine (20% of trees). Forage trails were also more common on maple (29%) than on pine (Stukalyuk et al. 2020a). The presence of a hornbeam in the forest, according to our assumption, is a negative factor for RWA, since this tree species is unattractive to ants.

There is a direct relationship between the age of stands and the density of anthills of RWA: in young stands it is minimal, while in mature forests it is maximum (Kilpelainen et al. 2005). Other studies indicate that the density of anthills in young 5-year-old pine plantations and mature 120-year-old spruce forests is the same, but the volume of anthills in forests is greater (Domisch et al. 2005). In medium-aged stands, 30–40 years old, RWA have minimal activity (Gibb & Johansson 2010); for 20-year-old stands, it is indicated that no anthills were found there (Domisch et al. 2005). Some species of RWA may prefer stands of different ages

- for example, *F. aquilonia* settles in old-aged stands, while *F. lugubris* develops in younger ones. This is due to the fact that the first species is more competitive, while the second one spreads faster (Borkin et al. 2012).

In addition to the age of the stand, its condition is of great importance - even in spruce forests with a tree age of 85-100 years, with an average tree condition category of 3.5, most *F. aquilonia* anthills degrade or stop growing and decrease in number. To a large extent, this is facilitated by the mass drying up of spruces due to the activity of the bark beetle, as well as damage by the root fungus, which entails a reduction in the trophic base of ants (Shtuchnyy 2006).

Kilpelainen et al. (2005) found that the maximum density of anthills in Finland is characteristic of spruce and birch forests. In our study, the presence of coniferous trees is also critically important for RWA; birch trees are among the trees visited by ants, although oaks and maples retain the primacy among deciduous species. Apparently, the choice of the most visited tree species by ants will differ in different climatic zones (Nur-Zati 2018).

Equally important is the presence of suitable coniferous introducers, for example, larch, from the planting of which the development and expansion of the boundaries of the *F. rufa* complex No. 2 began. Figure 2A demonstrating that the majority of trees visited by RWA from this nest complex are larches, a plant species introduced to this region. (See Figure 2A). Similar data that coniferous introducers may be suitable for another species, *F. lugubris*, have already been obtained earlier (Procter et al. 2015). Among the introduced species, larch is indicated as a tree species suitable for RWA by other authors (Robinson et al. 2008).

The loss of conifers from the mixed forest composition negatively affects the size of *F. polyctena* nest complexes (Juhász et al. 2020). Thus, for RWA living in mixed forests, the conservation of coniferous trees is critical. Coniferous-dominated mixed forests are best suited for the conservation of RWA nest complexes (Fitzpatrick et al. 2020; Frizzi et al. 2022; Sondej et al. 2018; Stukalyuk et al., 2023; Stukalyuk & Kozyr, 2024). In our case, this type of forest corresponds to Svyatoshinsky, in which two complexes of *F. polyctena* with 35 and 100 anthills of large size classes have been preserved. The main layer in the forest is formed by pines.

Ruderal herbaceous plants appear during forest thinning by unsystematic logging and bark beetle outbreaks, reducing the survival probability of RWA anthills by more than a third (Véle & Frouz 2023). Ruderal plant species in the forest replaces grasses and forbs, resulting in degradation of anthills due to overgrowing (Golosova 2008). Overgrowing of anthills with herbaceous plants (including ruderal species) also negatively affects their survival, as the temperature decreases and humidity increases in them (Véle & Holusa 2008).

Too high density of anthills, for example, *F. aquilonia*, can have a negative impact on the species diversity and abundance of ground beetles, as well as various epiphytes growing on tree trunks (mosses, lichens) (Thunes et al. 2018). Under clearcut conditions, fallen trunks can be colonized by other ant species, and the presence of RWA does not affect their numbers (Włodarczyk et al. 2009). *Formica aquilonia* anthills in cleared areas are smaller in size compared to the control in areas of mature forest (Sorvari & Hakkarainen 2005).

Anthills near trees, as noted by us and confirmed by other authors, are often associated with the availability of a valuable resource, aphid colonies. The size of the *F. lugubris* anthill is directly linked to the number of forage trees available, which relates to the availability of

aphid colonies (Hill et al. 2018). This is also confirmed by our data for two RWA species (*F. rufa*, *F. polyctena*). Apparently, this dependence is typical for all species of RWA. At the same time, ants will not necessarily visit the most massive trees with a large diameter near the anthill, since such a resource can be quickly depleted. Therefore, trees of the same diameter located further away will also be actively visited by ants (Gibb et al. 2016).

Influence of Microclimatic Factors on the Adaptive Potential of Nest Complexes of RWA.

The study of *F. polyctena* anthills of different sizes showed that small anthills are more dependent on direct solar insolation, while active thermoregulation becomes the main warming factor for large anthills (Rosengren et al. 1987; Stukalyuk et al., 2020b). Shading is directly related to the size of *F. polyctena*, *F. rufa*, and *F. aquilonia* anthills, and their size decreased with increasing distance from the nearest tree (Chen & Robinson 2014; Sondej et al. 2018). We found that for *F. polyctena* the degree of warming up (thermal mode) is more important than for *F. rufa*. The highest density of anthills of RWA was noted for sandy soils (Kilpelainen et al. 2005), which was also confirmed in this study. Clearcut areas radically change microclimatic conditions, which is one of the reasons for the reduction in the number of *F. aquilonia* anthills in these territories (Sorvari & Hakkarainen 2007). Slope exposure, climatic conditions, and forest structure affect the distribution of RWA in mountainous regions, while among the factors that do not have a pronounced influence, one can name the species diversity of plants, the area of forest fragments, and the distance to the edge (Vandegheuchte et al. 2017). A global increase in temperature (including at the level of local habitats) can also be a factor that determines the development of nest complexes of RWA (Fitzpatrick et al. 2020).

Prospects for the Phytoindication Approach in The Study of Nest Complexes of RWA

The geobotanical approach has previously been used in ant research, but with different goals. It has been established that the main number of myrmecochore plants is concentrated in the zone 2-5 m from the *F. aquilonia* anthills, while standard sites of 1 m² Brown-Blanque were used (Boryakova & Melnik 2017). The use of the phytoindication approach to assessing the state of *F. aquilonia* anthills showed that the most significant factor was illumination, which was inversely related to their state (Konopleva 2010). This may be due to the fact that *F. aquilonia* is a shade-tolerant species (Radchenko 2016); therefore, for *F. rufa* and *F. polyctena*, we did not find a pronounced effect of illumination (Stukalyuk & Maák, 2023), although the thermal regime may indirectly indicate the importance of warming up anthills. On the other hand, in this study, the natural habitat, humidity and thermal regime were found to be the most significant factors.

Konopleva (2010) also indicated the most optimal biotopes for ants, based on geobotanical relevés: a blueberry spruce forest, a green moss pine forest surrounded by spruce forests. The least favorable for *F. aquilonia* were aspen and linden forests, as well as tall grass, lichen, and green moss lingonberry pine forests (Konopleva 2010). According to our data, mixed forests (Ass. *Quercus robur*-*Pinetum*) are the most favorable for *F. rufa* and *F. polyctena*, oak forests are the least favorable (Ass. *Mercurialis perennis*-*Quercetum*, Ass. *Melico nutantis*-*Quercetum roboris*), and any deciduous forests with hornbeam participation are unfavorable (Ass. *Galeobdolon lutei*-*Carpinetum*). It is interesting to note that anthills (for example, *F. rufa*) form specific meadow-edge plant communities, which can increase the capacity of the habitat and floristic diversity (Rubashko et al. 2009). The southern or northern exposure of the slope also has a significant impact on the vegetation, as well as on the distribution of ants, according to their preferences (Bátori et al. 2019).

In general, the approach of environmental assessment with the involvement of phytoindication data is very promising, due to the universality, simplicity and possibility of such an assessment over large areas and for the purpose of monitoring. The phytoindication technique has solid evidence and years of experience in the use of vegetation for ecological assessment. Accumulating data for more ant species, diverse vegetation, and larger areas will enable wider scale evaluations and comparisons. This includes predicting the conservation of ant colonies alongside changes in vegetation, which plays a pivotal role in the environment.

CONCLUSION

Based on this study, we observed that the location of anthills is favored by two factors: a) being close to a tree; b) a coniferous tree. For two species of RWA (*F. rufa* and *F. polycytena*), mixed forests are a more favorable habitat than deciduous ones; therefore, their anthills in mixed forests are larger. In addition, the height and diameter of the anthill are directly related to the number of forage trees visited by one colony. Among the most visited tree species are conifers - pine (*Pinus sylvestris*) and larch (*Larix decidua*). Introduced conifers (larch) can serve as effective refugiums for the preservation of nest complexes of RWA in deciduous forests. Among deciduous, oak (*Quercus robur*) and maple (*Acer platanoides*) are the most frequented by ants. An ecological analysis of the habitats of RWA using a phytoindication approach made it possible to identify the most significant factors. The naturalness of habitats affects *F. polycytena* sensitivity to anthropogenic factors. Humidity is the second factor influencing habitat suitability. *F. polycytena* thrives in more humid habitats. Conversely, *F. rufa* is capable of surviving in habitats with a wider moisture range. The third factor, thermal regime, is higher for *F. polycytena*. *F. rufa* has a greater amplitude width under thermal conditions, indicating that it is a more eurytopic (plastic) species. Despite differences in optima, there is no separation between the habitats of the two RWA species, and the ecological amplitudes of *F. polycytena* and *F. rufa* largely overlap.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Ethics Declarations

No ethical issue is required for this research.

Data Availability Statement

Data available on: <https://docs.google.com/spreadsheets/d/1ANk9qTK4e2zvWPd1I-ORutnUfin6-DzH/edit?usp=sharing&ouid=109923867036522210210&rtpof=true&sd=true>

Authors' Contributions

Stanislav Stukalyuk (SS) conceptualized this research and designed experiments; SS, Mykola Kozyr (MK) and Igor Goncharenko (IG) participated in the design and interpretation of the data; SS, MK and IG wrote the paper and participated in the revisions of it. All authors read and approved the manuscript.

REFERENCES

- Antonova, V. & Marinov, M.P. 2021. Red wood ants in Bulgaria: Distribution and density related to habitat characteristics. *Journal of Hymenoptera Research* 85: 135-159.
- Bátori, Z., Vojtkó, A., Maák, I.E., Lőrinczi, G., Farkas, T., Kántor, N., Tanács, E., Kiss, P.J., Juhász, O., Módra, G., Tölgyesi, C., Erdős, L., Aguilon, D. J. & Keppel, G. 2019. Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. *Scientific reports* 9(1): 7176.
- Berberich, G.M., Berberich, M.B. & Gibhardt, M. 2022. Red wood Ants (*Formica rufa*-group) prefer mature pine forests in Variscan granite environments (Hymenoptera: Formicidae). *Fragmenta Entomologica* 54(1): 1-18.
- Borhidi, A. 1995. Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica* 39(1–2): 97–181.
- Borkin, K., Summers, R. & Thomas, L. 2012. Surveying abundance and stand type associations of *Formica aquilonia* and *F. lugubris* (Hymenoptera: Formicidae) nest mounds over an extensive area: Trialing a novel method. *European Journal of Entomology* 109(1): 47-53.
- Boryakova, E.E. & Melnik, S.A. 2017. Spatial distribution of small mammals depending on the influence of red wood ants (Hymenoptera, Formicidae) and vegetation cover in the conditions of the Nizhny Novgorod Cis-Volga region. *Science for Education Today* 7(3): 177-193.
- Cappelli, S. 2015. Tree Choice of Red Wood Ants. PhD Thesis, University of Zurich, Zurich, Switzerland.
- Chen, Y.-H. & Robinson, E.J.H. 2014. The relationship between canopy cover and colony size of the wood ant *Formica lugubris* - implications for the thermal effects on a keystone ant species. *PLoS ONE* 9(12): e116113.
- Churilov, A., Goncharenko, I., Kravchenko, O., Kovalevskyi, S.B., Marchuk, Y., Maevskyi, K., Kovalevskyi, S., Marchuk, O., Shevchuk, M. & Dubchak, M. 2020. Phytoindicative assessment and analysis of vegetation in disturbed areas after illegal amber mining in the Western Polissya of Ukraine. *Forestry Ideas* 26(1): 191-208.
- Didukh, Y.P. 2011. *The Ecological Scales for the Species of Ukrainian Flora and their Use in Synphytoindication*. Kyiv, Ukraine: Phytosociocentre.
- Didukh Y.P. & Plyuta, P.G. 1994. *Phytoindication of Ecological Factors*. Kyiv, Ukraine: Naukova dumka.
- Domisch, T., Finér, L. & Jurgensen, M.F. 2005. Red wood ant mound densities in managed boreal Forests. *Annales Zoologici Fennici* 42: 277-282.

- Dubyna, D., Dziuba, T.P., Iemelianova, S.M., Bagrikova, N.O., Borysova, O.V. & Borsukevych, L.M. 2019. *Prodromus of the Vegetation of Ukraine*. Kyiv, Ukraine: Naukova Dumka (In Ukrainian).
- Dyachenko, N.G. 2017. *Red Wood Ants of Belovezhskaya Pushcha*. Moskva, Russia: KMK Press (in Russian).
- Ellenberg, H. 1974. *Zeigerwerte der Gefäßpflanzen spflanzen Mitteleuropas*. Göttingen, Germany: Scripta Geobotanica.
- Ellenberg, H., Weber, H.E., Dull, R., Wirth, V., Werner, W. & Paulisen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Göttingen, Germany: Scripta Geobotanica.
- Fitzpatrick, B.R., Baltensweiler, A., Düggelin, C., Fraefel, M., Freitag, A., Vandegehuchte, M.L., Wermelinger, B. & Risch, A.C. 2020. The distribution of a group of keystone species is not associated with anthropogenic habitat disturbance. *Diversity and Distributions* 27: 572-584.
- Frank, D. & Klotz, S. 1990. *Biologisch-Ökologische Daten Zur Flora der DDR*. 2nd Edition. – Halle: Martin-Luther-Universität Halle-Wittenberg.
- Frizzi, F., Masoni, A., Santedicola, M., Servini, M., Simoncini, N., Palmieri, J. & Santini, G. 2022. Intraspecific relationships and nest mound shape are affected by habitat features in introduced populations of the red wood ant *Formica paralugubris*. *Insects* 13: 198.
- Gibb, H. & Johansson, T. 2010. Forest succession and harvesting of hemipteran honeydew by boreal ants. *Annales Zoologici Fennici* 47(2): 99-110.
- Gibb, H., Andersson, J. & Johansson, T. 2016. Foraging loads of red wood ants: *Formica aquilonia* (Hymenoptera: Formicidae) in relation to tree characteristics and stand age. *Peer Journal* 4: e2049.
- Golosova, M.A. 2008. Bioindication of the state of forest ecosystems in terms of environmental parameters of anthills. *Forestry bulletin* (1): 117-120.
- Goncharenko, I.V. 2017. *Phytoindication of Antropogenic Impact*. Dnipro, Ukraine: National Academy of Sciences of Ukraine, State Institution (Institute for Evolutionary Ecology of NAS of Ukraine) [In Ukrainian]
- Goncharenko, I.V. & Didukh, Y.P. 2003. The Braun-Blanquet approach: History and current trends. *Scientific Papers of National University of Kyiv-Mohyla Academy* 21: 82-91 [In Ukrainian]
- Goncharenko, I.V., Solomakha, I.V., Shevchyk, V.L., Dvirna, T.S., Tymochko, I.Y. & Solomakha, V.A. 2022. A phytoindicational assessment of the vegetation of afforestation belts in the Middle Dnipro Region, Ukraine. *Environmental & Socio-economic Studies* 10(2): 30-39.
- Hill, J.L., Vater, A.E., Geary, A.P. & Matthews, J.A. 2018. Chronosequences of ant nest mounds from glacier forelands of Jostedalbreen, southern Norway: Insights into the

- distribution, succession and geo-ecology of red wood ants (*Formica lugubris* and *F. aquilonia*). *Holocene* 28 (7): 1113-1130.
- Juhász, O., Fürjes-Mikó, Á., Tenyér, A., Somogyi, A.Á., Aguilon, D.J., Kiss, P.J., Bátori, Z. & Maák, I. 2020. Consequences of climate change-induced habitat conversions on red wood ants in a Central European Mountain: a case study. *Animals* 10(9): 1677.
- Johansson, T. & Gibb, H. 2012. Forestry alters foraging efficiency and crop contents of aphid-tending red wood ants, *Formica aquilonia*. *PLoS ONE* 7(3): e32817.
- Konopleva, E.E. 2010. Structure and dynamics of the anthill complex of the northern wood ant *Formica aquilonia* Yarr. (Hymenoptera, Formicidae) under different forest conditions. *Bulletin of the Nizhny Novgorod University. N. I. Lobachevsky* (2-2): 407-412.
- Kozyr, N.S. 2012. Syntaxonomy of forest vegetation of the nature reserve fund of Kyiv. *International Online Symposium "Population Ecology of Plants. Current State, Points of Growth*, pp. 65-71.
- Kilpeläinen, J., Punttila, P., Sundstrom, L., Niemela, P. & Finer, L. 2005. Forest stand structure, site type and distribution of ant mounds in boreal forests in Finland in the 1950s. *Annales Zoologici Fennici* 42: 243-258.
- Landolt, E. 1977. *Okologische Zeigerwerte zur Schweizer Flora*. Zurich: Veroff. Geobot. Inst. ETH.
- Mueller-Dombois, D. & Ellenberg, H. 2002. *Aims and Methods of Vegetation Ecology*. New Jersey, USA: The Blackburn Press.
- Nur-Zati, A.M. 2018. Ants as indicator tools for tropical forest regeneration: A case study from Ulu Muda Forest Reserve. *Serangga* 23(3): 84-97.
- Ohashi, M., Kilpeläinen, J., Finér, L., Risch, A.C., Domisch, T., Neuvonen, S. & Niemelä, P. 2007. The effect of red wood ant (*Formica rufa* group) mounds on root biomass, density, and nutrient concentrations in boreal managed forests. *Journal of Forest Research* 12(2): 113-119.
- Procter, D.S., Cottrell, J., Watts, K. & Robinson, E.J. 2015. Do non-native conifer plantations provide benefits for a native forest specialist, the wood ant *Formica lugubris*? *Forest Ecology and Management* 357: 22-32.
- Punttila, P., Haila, Y., Niemela, J. & Pajunen, T. 1994. Ants communities in fragments of old-growth taiga and managed surroundings. *Annales Zoologici Fennici* 31: 131-144.
- Ramensky, L.G. 1938. *Introduction to a Comprehensive Soil-Geobotanical Study of Lands*. USSR: Selkhozgiz, Moskva.
- Radchenko, A.G. 2016. *Ants (Hymenoptera, Formicidae) of Ukraine*. Kyiv, Ukraine: Schmalhausen Institute of zoology NAS of Ukraine (In Russian).

- Robinson, E.J., Tofilski, A. & Ratnieks, F.L. 2008. The use of native and non-native tree species for foraging and nesting habitat by the wood-ant *Formica lugubris* (Hymenoptera: Formicidae). *Myrmecological News* 11: 1-7.
- Rosengren, R., Fortelius, W., Lindstrom, K. & Luther, A. 1987. Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. *Annales Zoologici Fennici* 24: 147-155.
- Rubashko, G.E., Khanina, L.G. & Smirnov, V.E. 2009. Dynamics of plant groups of *Formica rufa* anthills. *Ants and Forest Protection. Materials of the 13th All-Russian Myrmecological Symposium, August 2009.*
- Seifert, B. 2018. *The Ants of Central and North Europe*. Germany: Lutra Verlags und Vertriebsgesellschaft, Tauer.
- Shtuchnyy, N.A. 2006. Relationship between the life processes of the northern wood ant (*Formica aquilonia*) and the processes occurring in the forest environment. *Forestry Bulletin* (2): 71-74.
- Sondej, I., Domisch, T., Finér, L. & Czechowski, W. 2018. Wood ants in the Białowieża Forest and factors affecting their distribution. *Annales Zoologici Fennici* 55: 103-114.
- Sorvari, J. & Hakkarainen, H. 2004. Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*. *Animal Behavior* 67(1): 151-153.
- Sorvari, J. & Hakkarainen, H. 2005. Deforestation reduces nest mound size and decrease the production of sexual offspring in the wood ant *Formica aquilonia*. *Annales Zoologici Fennici* 42(3): 259-267.
- Sorvari, J. & Hakkarainen, H. 2007. Wood ants are wood ants: Deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. *Ecological Entomology* 32(6): 707-711.
- Sorvari, J. & Hakkarainen, H. 2009. Forest clear-cutting causes small workers in the polydomous wood ant *Formica aquilonia*. *Annales Zoologici Fennici* 46: 431-438.
- Stukalyuk, S.V., Kozyr, M.S., Netsvetov, M.V. & Zhuravlev, V.V. 2020a. Effect of the invasive phanerophytes and associated aphids on the ant (Hymenoptera, Formicidae) assemblages. *Halteres* 11: 56-89.
- Stukalyuk, S., Radchenko, Y., Netsvetov, M., & Gilev, A. 2020b. Effect of mound size on intranest thermoregulation in the red wood ants *Formica rufa* and *F. polyctena* (Hymenoptera, Formicidae). *Turkish Journal of Zoology* 44(3): 266-280.
- Stukalyuk, S., Gilev, A., Antonov, I. & Netsvetov, M. 2021. Size of nest complexes, the size of anthills, and infrastructure development in 4 species of red wood ants (*Formica rufa*, *F. polyctena*, *F. aquilonia*, *F. lugubris*) (Hymenoptera; Formicidae). *Turkish Journal of Zoology* 45: 464-478.

- Stukalyuk, S. & Maák, I. E. 2023. The influence of illumination regimes on the structure of ant (Hymenoptera, Formicidae) community composition in urban habitats. *Insectes Sociaux* 70(4): 423-437.
- Stukalyuk, S., Goncharenko, I. & Kozyr, M. 2023. Changes in the structure of nest complexes of the red wood ants *Formica rufa* and *F. polyctena* (Hymenoptera, Formicidae) in urban forests. *Zoodiversity* 57(5): 421-432.
- Stukalyuk, S. & Kozyr, M. 2024. Highways for red wood ants (Hymenoptera: Formicidae): a new method to increase the size of anthills. *Turkish Journal of Zoology* 48(2): 128-139.
- Thunes, K.H., Gjerde, I. & Skartveit, J. 2018. The red wood ant *Formica aquilonia* (Hymenoptera: Formicidae) may affect both local species richness and composition at multiple trophic levels in a boreal forest ecosystem. *Annales Zoologici Fennici*. 55: 159-172.
- Tsyganov, D.N. 1983. *Phytoindication of Ecological Regimes in the Conifer–Broadleaf Forest Subzone*. USSR: Nauka, Moskva.
- Vandegheuchte, M.L., Wermelinger, B., Fraefel, M., Baltensweiler, A., Duggelin, C., Brändli, U. & Risch, A.C. 2017. Distribution and habitat requirements of red wood ants in Switzerland: Implications for conservation. *Biological Conservation* 212: 366-375.
- Véle, A. & Holusa, J. 2008. Impact of vegetation removal on the temperature and moisture content of red wood ant nests. *Insectes Sociaux* 55: 364-369.
- Véle, A. & Frouz, J. 2023. Bark beetle attacks reduce survival of wood ant nests. *Forests* 14(2): 199.
- Wardle, D.A., Hyodo, F., Bardgett, R.D., Yeates, G.W. & Nilsson, M.C. 2011. Long-term aboveground and belowground consequences of red wood ant exclusion in boreal forest. *Ecology* 92(3): 645-656.
- Włodarczyk, T., Zmihorski, M. & Olczyk, A. 2009. Ants inhabiting stumps on clearcuts in managed forest in western Poland. *Entomologica Fennica* 20: 121-128.
- Zakharov, A.A. 1991. *Organization of Communities in Ants*. Russia: Nauka, Moscow (In Russian).
- Zakharov, A.A. 2015. *Ants of Forest Communities, their Life Cycle and Role in Forests*. Russia: KMK Scientific Press, Moskva (In Russian).
- Zingg, S., Dolle, P., Voordouw, M.J. & Kern, M. 2018. The negative effect of wood ant presence on tick abundance. *Parasites & vectors* 11: 1-9.