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CHANGES IN THE STRUCTURE OF NEST COMPLEXES OF THE RED WOOD ANTS *FORMICA RUFA* AND *F. POLYCTENA* (HYMENOPTERA, FORMICIDAE) IN URBAN FORESTS

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Changes in the Structure of Nest Complexes of the Red Wood Ants *Formica rufa* and *F. polyctena* (Hymenoptera, Formicidae) in Urban Forests. Stukalyuk, S., Goncharenko, I. & Kozyr, M. — The aim of this work is to evaluate changes in the structure of nest complexes of two species of red wood ants: *Formica rufa* Linnaeus, 1761 and *F. polyctena* Foerster, 1850, in the city of Kyiv (Ukraine) using morphometric indicators, as well as to evaluate their dynamics. In 2014–2022, nest complexes of two species of red wood ants (*Formica rufa*, *F. polyctena*) were observed in urbanised forests within the city of Kyiv. A total of 472 *F. rufa* and 411 *F. polyctena* nests were studied in 7 nest complexes (4 — *F. polyctena*, 3 — *F. rufa*). The total volume of *F. polyctena* nests were found to decrease by 2020–2021, while the volume of *F. rufa* nests remained at the same level or even increased. This suggests that *F. rufa* is more resistant to changes in forestry conditions.
Key words: Red wood ants, monitoring, nest complexes, *Formica rufa*, *Formica polyctena*.

Introduction

Red wood ants (*Formica rufa* group) are dominant among the ant species of the forest zone of the temperate zone of the Palaearctic Region (Radchenko, 2016; Seifert, 2018). Red wood ants can live in solitary anthills, but can also form huge nest complexes (or supercolonies) comprising hundreds of anthills. Nest complexes are a group of nests of the same species, the forage areas of which, in contact, form a territorial continuum (Zakharov, 1991, 2015). Red wood ants are effective entomophages. These species could be useful as biological control agents in forest pest management (Pavan, 1959, 1979; Grimalsky and Lozinsky, 1979; Frizzi et al., 2018; Trigos-Peral et al., 2021). In addition, red wood ants are involved in the biogenic cycling of substances in the soil due to their nest-building activity (Gosswald, 1981; Tsikas et al., 2021). Red wood ants are the key ant species in large areas of Eurasian forests (deciduous and mixed forests, taiga) that need to be protected and the state of their nest complexes monitored. This depopulation process can be observed in red wood ant colonies that are separated by large distances (Balzani et al., 2022). In the 1970–1980s, an attempt was made to mass relocate red wood ants in the former USSR (Operation *Formica*). However, as early as 2015, mass mortality of entire nest complexes of red wood ants was observed, at least in Russia (Zakharov, 1991, 2015).

The main factors negatively affecting red wood ants are anthropogenic. These include such negative consequences of human activities as deforestation or forest fragmentation, forest fires, which have become more frequent and are constantly increasing in size, and chemical pollution of the environment (Domisch et al., 2005; Zakharov, 2015). The habitat of red wood ants is degraded, microclimatic conditions and trophic chains are disturbed. This inevitably leads to the degradation of red wood ant nest complexes and their extinction. The areas of territories that are optimal for nesting shrink; there is also fragmentation of territories and a decrease in the food supply (Zakharov, 1991). In areas of active recreation, most anthills are usually destroyed by humans. This is confirmed by data from Dlussky, who found that within a 50 km radius of Moscow (Russia), up to 95 % of red wood ant anthills were damaged to some degree (Dlussky, 1967). On the other hand, no such destruction was observed within the boundaries of Kyiv (Ukraine) and most anthills were intact (Stukalyuk et al., 2021), so it cannot be argued that anthill destruction is widespread in urbanised forests. Red wood ants are particularly vulnerable because their nests are clearly visible and foraging trails run along the soil surface, so many ants die when trampled in recreational areas (Zakharov, 1991, 2015).

Thus, the anthropogenic factor leads to a gradual decrease in the size of anthills, the number of anthills forming supercolonies, and the length and branching of their trail infrastructure (Soboleva, 2011; Zakharov, 2015). Cities, especially metropolitan areas, are unfavourable for the formation of nest complexes, as are ants of other species, due to the scarcity of suitable nesting habitat, high recreational pressure and pollution (Friedrich and Philpott, 2009). In cities such as Helsinki (Finland) and Moscow (Russia), red wood ants are known to be either absent or represented by solitary small anthills (Vepsäläinen et al., 2008; Putyatina et al., 2017). In other European cities, such as Kyiv and Lviv, not only single anthills of red wood ants were found, but also their nest complexes (Stukalyuk et al., 2021; Doroshenko & Nazaruk, 2022). For example, 883 nests (472 *Formica rufa*, 411 *Formica polyctena*) were surveyed in the urbanised forests of Kyiv during 2015–2020, the area of the city is 840 km^2, i. e., approximately 1 anthill per 1 km^2 (Stukalyuk et al., 2021). Such a high rate may be related to the relatively large area of green spaces in Kyiv — 55 % of the city area, of which 44 % is urbanised forest (Didukh & Alioshkina, 2012). It should be noted that more than half of the anthills of red wood ants in Kyiv are concentrated in nest complexes (Stukalyuk et al., 2021). Nest complexes show greater plasticity to adverse factors and are more durable than individual anthills (Zakharov, 1991).

The aim of the work is to study changes in the structure of nest complexes of the red wood ants *Formica rufa*, *F. polyctena* on the example of the city of Kyiv (Ukraine) using morphometric indicators and also to evaluate their dynamics.

The hypothesis of the study is that the degradation and extinction of red wood ant nest complexes in urbanised forests is caused by the complex effects of the anthropogenic factor.

Material and Methods

Research region and measurement technique. Kyiv is a suitable model site for monitoring red wood ant nest complexes within the city borders. The authors monitored seven nest complexes of two species of red wood ants, *Formica rufa*, *F. polyctena*, for 8 years. The study was conducted in July–August 2014–2022 on the territory of Kyiv. Monitoring was carried out on 7 nest complexes of red wood ants, 3 — *Formica rufa*, 4 — *F. polyctena* (fig. 1). The nest complexes (3 out of 4) of *F. polyctena* were located in the north-western outskirts of the city, while all complexes of *F. rufa* were located in the south-western outskirts. All complexes were located on the territory of two large forests — Golosiivsky (with the Feofaniya forest fragment) and Svyatoshinsky. Golosiivsky forest is a deciduous forest dominated by oak (*Quercus robur* L.), hornbeam (*Carpinus betulus* L.)

and maple (*Acer platanoides* L.). The Svyatoshinsky forest is a mixed forest, where the tree layer is dominated by pine (*Pinus sylvestris* L.), oak, and less often by hornbeam and maple.

A total of 513 *F. polyctena* and 484 *F. rufa* nests were studied during all years of observation.

The nest complexes of the red wood ants have been subjected to various anthropogenic impacts. In Feofaniya (*F. rufa*, nest complex No. 1, fig. 1), these are deforestation and clearing of the area around the church under construction since 2015, recreation, cleaning of dead wood and its processing into wood chips, and the organisation of the construction of a residential area nearby.

In 2020 on the territory of the Observatory (*F. polyctena*, Golosiivsky forest, No. 4) the forest was cleared, the dead wood was processed and the shrub layer was cut. In the Golosiivsky forest for *F. rufa* (No. 3), since 2017 the clearing has been overgrown with young trees, the forest has been littered with fallen trees, and the shading has increased. This nest complex was located on the edge of a 20 metre wide clearing. Logging was carried out in 2010.

In the Golosiivsky forest (*F. rufa*, No. 2) there is a plantation of an introduced species of larch (*Larix decidua* Mill.). The age of larch planting is 40–60 years (tree trunk diameter is on average 0.4–0.7 m).

In the Svyatoshinsky forest (*F. polyctena*, No. 3) the area has been subjected to constant littering and trampling due to recreational and economic activities (landfills of food, household and construction waste in the forest.). The other two complexes of *F. polyctena* in the Svyatoshinsky forest (No. 1 and 2, fig. 1) were under standard forest conditions, i.e. sanitary cuttings were made and the ants settled in the vicinity of the clearings.

Different numbers of nest complexes were measured in different years. In 2013, 2014 the monitoring of *F. rufa* complex No. 1 was carried out, in 2015 — complexes of *F. rufa* No. 1, 2. In 2016, all nest complexes of both species were measured, with the exception of *F. rufa* No. 3; in 2017, the nest complexes of *F. rufa* No. 3 and *F. polyctena* No. 1 were measured. In 2019, *F. rufa* complexes 2, 4, *F. polyctena* complexes 2, 3, 4 were monitored. In 2021, all nest complexes were measured, and in 2022 — with the exception of *F. polyctena* complex No. 1, which was mined as a result of the hostilities with Russia that began on 24 February 2022. Despite the fact that it was not always possible to measure all 7 complexes in the different years of the study, it is still possible to calculate average morphometric indicators, as they characterise each ant species in the given area as a whole. In the field, the following basic morphometric indicators of nests were measured: minimal and maximal diameters and height (in metres, m). The accuracy of diameter and height measurements is up to 5 cm. All measurements were made according to the method of K. V. Arnoldi (1979).

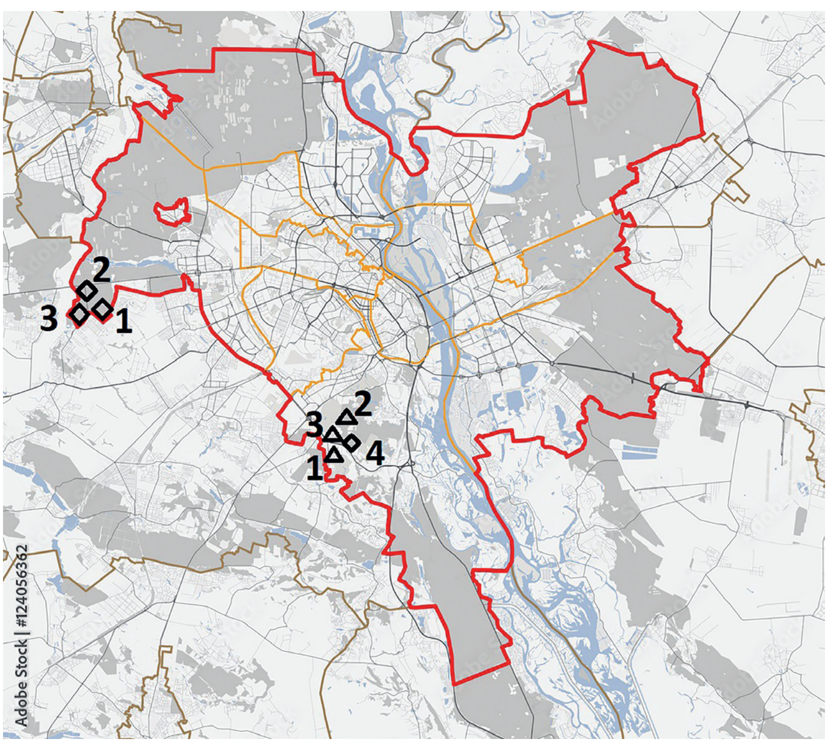

Fig. 1. Location of nest complexes of *Formica rufa* (diamonds), *F. polyctena* (triangles) on the territory of the city of Kyiv (Ukraine). The city limits are marked by a red line, the forest areas by dark grey. The numbers correspond to the serial number of each complex.

Obtaining calculated morphometric indicators. From the indicators of height and two diameters, the following were calculated:

— The average value of the diameter, D, m: (D1 + D2)/2 (Formula 1), where D1 —the maximal diameter of the nest, D2 —the minimal diameter.

— Volume, V, m^3: S×H/3 (Formula 2), where H is a height of the nest, S — nest base area.

— The asymmetry value, A: abs (D1 — D2)/(D1 + D2) (Formula 3).

— The shape as a ratio of diameter to height, S: D/H (Formula 4).

For each indicator, the semantic meaning of each class was different. For example, for the indicator of volume — from small to large nests; for the degree of asymmetry — from symmetrical to those with great asymmetry; for shape, estimated by the ratio of diameter to height — from elongated, usually old nests, to tall, growing, cone-shaped anthills. Asymmetry may represent functional status of the nest. Normally, viable and growing nests are symmetrical. In the case of systematic damage, overgrowth of the anthill with vegetation, depopulation occurs and the ants are not able to carry out construction activities evenly around the entire circumference of the nest. The shape of the nest is most often associated with the characteristics of the illumination. However, this parameter can also be used to compare the state of the nest — growing (high conical) nests have a smaller height/diameter ratio. Nests that have stabilised in their growth are characterised by a hemispherical shape, while decaying large nests may retain a diameter comparable to the growth period, but their height decreases as the central part of the nest sags as a result of a decrease in the ants' building activity.

Anthills classification by size, asymmetry, height and diameter ratio. In the next step, the anthills were classified into 5 classes according to the three most important indicators (size, asymmetry and shape). The classification (discretization) was carried out using the function of the K-means method. The class interval limits for each indicator are given in table. 1.

Statistical analysis. All statistical calculations were performed using the statistical environment R ver. 3.5.3 (https://cran.r-project.org). The classic ANOVA test (aov function of the base R installation) was used to test the hypothesis of no difference between the annual means. Multiple pairwise comparisons or post hoc analysis were performed using Tukey's test. Significant differences in the mean values of the anthill morphometric parameters were assessed by standard ANOVA (aov function in the base installation of R).

Results

As the monitoring focused on two ant species, *F. polyctena* and *F. rufa*, the differences between their nests were assessed according to the above morphometric parameters. It was assumed that there were significant differences in the average values of the morphometric parameters of the nests between these species. Obviously, in the colonies of two ant species, the distribution of nests according to the size classes identified in the course of the discretization also differs. For comparison, nests of different size classes (from small to large in volume) of each species were counted, as well as indicators of asymmetry and shape.

Anthills classification according to morphometric indicators

Table 1 shows the class interval boundaries for 5 classes identified by morphometric indicators, separately for anthill size (volume), shape as estimated by the ratio of diameter to height, and degree of asymmetry.

Table 1. Intervals of values of three morphometric indicators (in brackets) for 5 classes (by size, shape and degree of asymmetry) of anthills

Class code	Volume (size) classes	Shape classes	Asymmetry classes
1	small (0.01–0.12)	high (0.38–2.10)	almost symmetric (0.00–0.09)
2	(0.12–0.25)	(2.10–2.97)	(0.09–0.21)
3	(0.25–0.41)	(2.97–4.64)	(0.21–0.35)
4	(0.41–0.67)	(4.64–9.31)	(0.35–0.53)
5	large (0.67–1.23)	lengthy (9.31–18.75)	with big asymmetry (0.53–0.75)

Table 2. The number of anthills of various classes (see designations in table 1) in colonies of two ant species (total number in *Formica polyctena* (N = 513, *Formica rufa* N = 484)

Ant_species	Class	1	2	3	4	5	Comment
Formica polyctena	asymmetry	**309**	133	45	21	5	Symmetrical
Formica polyctena	Shape	103	**225**	163	21	1	Most typical form (2nd grade)
Formica polyctena	volume (size)	85	**165**	144	91	28	Dominated by the middle size class (2nd class)
Formica rufa	asymmetry	**327**	94	24	4	2	Symmetrical
Formica rufa	Shape	186	**189**	83	19	7	Most are tall and typically domed
Formica rufa	volume (size)	171	**176**	102	31	4	Dominated by small and medium size class (1st and 2nd class)

Note. The maximum value of each indicator is highlighted in bold.

Table 2 shows the distribution of nests by size, shape, and degree of asymmetry for two species, *Formica polyctena* and *Formica rufa*.

Symmetrical nests predominate in both species (table 2). In terms of shape, both species are dominated by the 2nd class, where the ratio of diameter to height ranges from 2.10 to 2.97 (table 1). In terms of size classes, the 2nd class is the most numerous (nests of small size — 0.12–0.25 m^3). For *Formica polyctena*, however, the distribution centre is closer to the middle size class (table 2).

Morphometric parameters of two ant species

Table 3 presents the basic statistical indicators of the nest morphometric measurements in the two species studied, as well as the results of the ANOVA evaluation of the differences between the species.

The value of the F-statistic shows the greatest differences in diameter and volume. In particular, the volume and diameter of *Formica rufa* nest complexes are on average slightly smaller than those of *Formica polyctena* (0.2 and 0.3 m^3, respectively). The smallest differences are observed in the shape (ratio of diameter to height). The values of the asymmetry coefficient fluctuate in a fairly wide range from 0 to 0.71 for *Formica rufa* and from 0 to 0.75 for *Formica polyctena*, but there are no major differences in this indicator between the species.

Table 3. Comparison of anthills of 2 species of red wood ants (*Formica polyctena* and *Formica rufa*) in terms of morphometric parameters (diameter, height, volume (size), degree of asymmetry, shape), as well as F statistics of the ANOVA test to assess differences between the two species

Ant_species	*Formica polyctena*				*Formica rufa*				ANOVA F statistic
Variable	Mean	Sd	Min	Max	Mean	Sd	Min	Max	
Diameter, m	1.2	0.461	0.13	3.35	0.8	0.366	0.13	2	F = 153.736***
Height, m	0.4	0.169	0.05	0.9	0.4	0.179	0.02	1.1	F = 38.536***
Volume, m^3	0.3	0.205	0.01	1.23	0.2	0.142	0.01	1.01	F = 95.118***
Asymmetry	0.1	0.115	0	0.75	0.1	0.088	0	0.71	F = 25.67***
Shape, D/H ratio	2.8	0.991	0.93	9.5	2.6	1.674	0.38	18.75	F = 3.734*

The colonies structure comparison by morphometric parameters in different years

The dynamics of changes in the morphometric parameters of the colonies over the years of observation are shown in table 4.

Counting and additive indicators, such as the number of nests in the colony and their total volume, have undergone greater changes than average and correlative (shapes and asymmetries) — more stable indicators (table 4). As a result, these indicators are more sensitive when monitoring the state of ant nest complexes.

Figure 2 shows the changes in the average size (volume) of the nests over the years of observation. Insignificant fluctuations alternate with periods of relative stability of the indicator, when no statistically significant differences are observed.

Opposite trends were found for two species of red wood ants (fig. 3, A, B).

While for *F. rufa* the volume and number of anthills increased (mainly due to the growth of complex No. 1), for *F. polyctena* both indicators show a steady decline (fig. 3, B). The decrease in the number of *F. polyctena* anthills in 2022 is also due to the fact that measurements of nest complex 1 were not carried out. In 2017–2021, the number of nests in the nest complex was stable and amounted to 64–66 nests. If there were no drastic changes in the number of nests in 2022, the total number of *F. polyctena* nests should not have exceeded the level of 2021. Thus, in 2021 the number of nests of this species decreased compared to 2016, but not significantly. Significant changes have taken place in the nest volume of *F. polyctena* — it has decreased significantly by 2021 (fig. 4).

Table 4. Morphometric parameters of *Formica rufa* and *Formica polyctena* nest complexes in different years

Ant_species	Year	N	v_total	v_avg	d_avg	h_avg	shape_ratio	asymmetry
Formica polyctena	2016	164	53.11	0.32	1.20	0.46	2.69	0.12
Formica polyctena	2017	64	19.76	0.31	1.26	0.44	2.97	*0.08*
Formica polyctena	2019	116	38.68	0.33	1.23	0.46	2.80	0.12
Formica polyctena	2021	128	29.25	*0.23*	*1.00*	0.40	*2.65*	0.11
Formica polyctena	2022	41	*11.05*	0.27	1.22	*0.40*	3.43	0.08
Min (*Formica olyctena*)		41.00	11.05	0.23	1.00	0.40	2.65	0.08
Max (*Formica polyctena*)		164.00	53.11	0.33	1.26	0.46	3.43	0.12
Formica rufa	2013	33	5.75	0.17	0.85	0.37	2.85	0.06
Formica rufa	2014	63	6.13	0.10	0.57	0.23	3.72	0.06
Formica rufa	2015	60	11.45	0.19	0.92	0.36	2.71	0.10
Formica rufa	2016	78	14.31	0.18	0.85	0.37	2.45	0.07
Formica rufa	2017	12	2.55	0.21	1.03	0.38	3.58	0.08
Formica rufa	2019	94	17.12	0.18	0.82	0.37	2.39	0.08
Formica rufa	2021	71	16.30	0.23	0.86	0.44	2.16	0.09
Formica rufa	2022	73	16.61	0.23	0.95	0.43	2.34	0.06
Min (*Formica rufa*)		12.00	2.55	0.10	0.57	0.23	2.16	0.06
Max (*Formica rufa*)		94.00	17.12	0.23	1.03	0.44	3.72	0.10

Designations: N is the number of anthills in the nest complex, v_total is the total volume (the sum of the volumes of individual anthills), v_avg, d_avg, h_avg are the average values of volume, diameter and height (by years), shape ratio and asymmetry are the correlative indicators of shape and asymmetry.

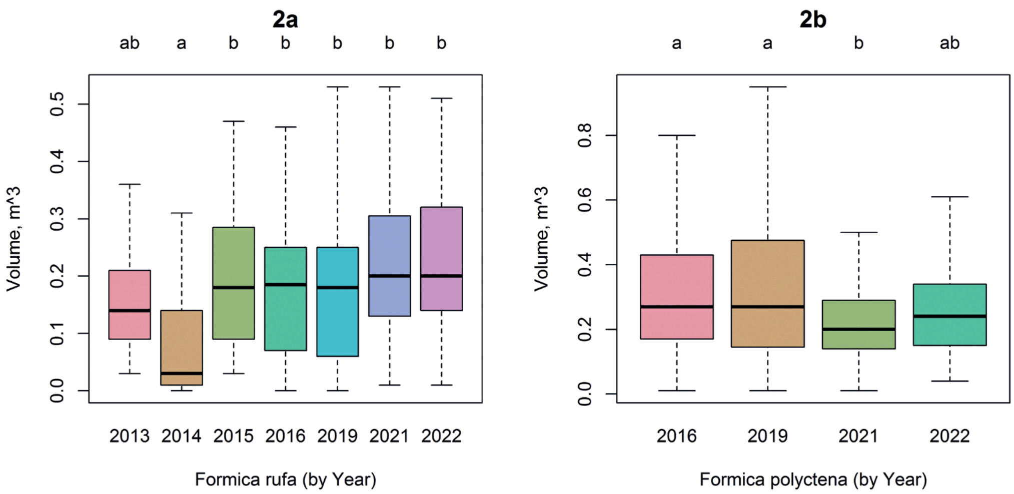

Fig. 2. Comparison of anthill sizes (volume) of two species (*Formica rufa*, fig. 2, a and *Formica polyctena*, 2, b) by years of observation. Only the years in which observations were made are shown. The designations of the results of Tukey's paired comparisons are coded with the letters shown above the figures (see Materials and methods).

Figure 4 shows the degradation trends for the nest complexes of *F. rufa* No. 1 (4, A, B), *F. polyctena* No. 4 (4, C, D).

For *F. rufa* No. 1, there was a sharp decrease in the average diameter of anthills in 2014, and on the contrary, an increase since 2015 (fig. 4, A). In 2016, this indicator remained at approximately the same level, and in 2021 it decreased again. In 2022, this nest complex

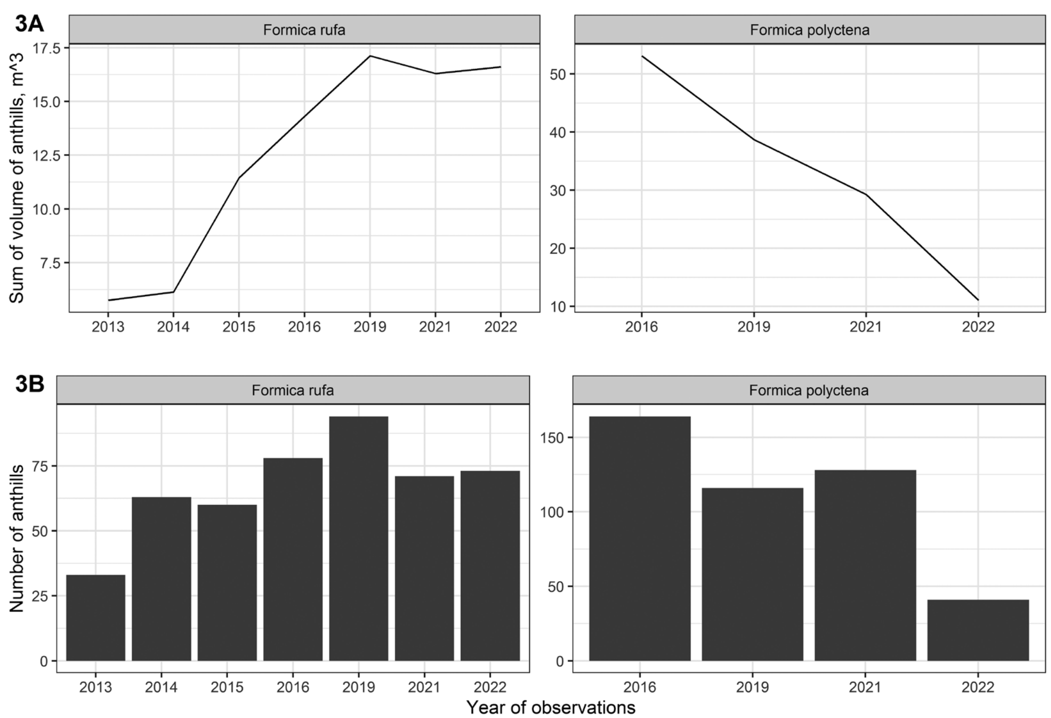

Fig. 3. Dynamics of changes in total volume (3, A) and number of anthills (3, B) in nest complexes by year of observation. 2017 is not included in the graphs due to the low number of nest complexes observed in that year.

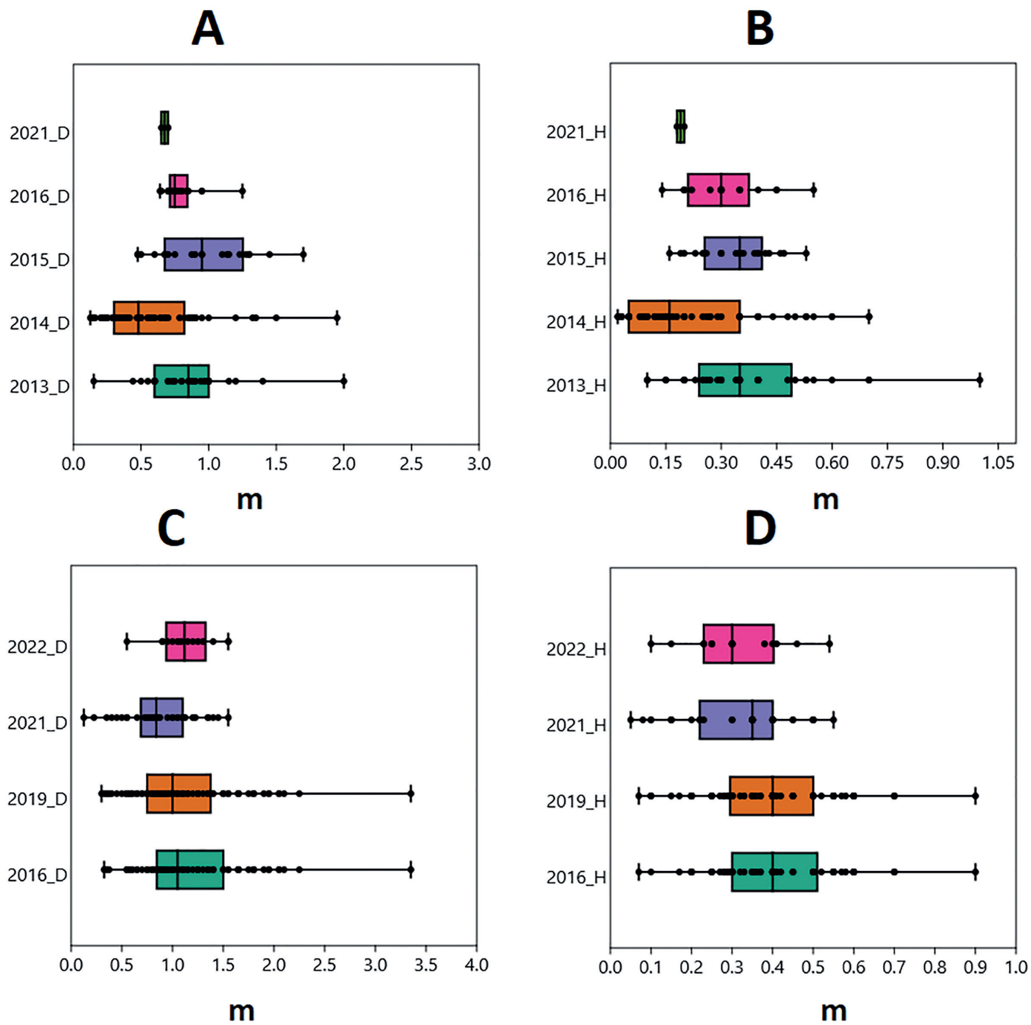

Fig. 4. Degradation of the *Formica rufa* complex No. 1 (Feofaniya) in terms of average height (4, A) and diameter (4, B) under conditions of intensive construction and recreation; 4, C, D — diameter and height near the nest complex of *F. polyctena* No. 4 (surroundings of the Observatory), under conditions of felling of the shrub layer and processing of fallen trunks and branches into wood chips.

completely disappeared. The trend in average height is similar (fig. 4, B). The number of anthills changed more, doubling since 2014 (from 33 to 63) and decreasing 3 times since 2015 (21 in 2017, 17 in 2016). In 2021, only 2 anthills will remain.

For the *F. polyctena* nest complex No. 4, the average diameter and height were stable in 2016–2019 (fig. 4, C, D), as was the total number of anthills (77, 89). Since 2021, all these indicators have decreased, especially the number of anthills (37). In 2022, the average diameter and height indicators stabilised again, but the number of anthills more than doubled (14). The ants settled in piles of wood shavings, but this substrate proved to be unsuitable for their habitat as it was infested with the mycelium of the false honey agaric (*Hypholoma fasciculare*). More dramatic changes occurred in the nest complex of *F. rufa* (No. 3), which showed a stable growth until 2019 (21 anthills), after the winter of 2020–2021 only 1 anthill remained, and in 2022 the complex disappeared completely. The same happened with the nest complex of *F. polyctena* No. 3, which consisted of 13 anthills in 2016, 8 in 2019, and only 2 in 2021 and 2022. The anthills in this complex belonged to the 4th size class in 2019, and earlier — to the 3rd and 2nd size classes, i.e. before the final degradation of the landfill conditions.

Thus, 4 out of the 7 nest complexes studied in 2021 were either completely extinct or only a small number of unrelated, i.e. single, anthills remained.

Discussion

As a rule, the degradation processes in the nest complexes of red wood ants extend over years, since these complexes have their own safety margin. With gradual degradation, the total number of nests in the composition of the nest complex may increase, as previously demonstrated (Zakharov, 1991) and also confirmed by data on the example of *F. rufa* (No. 1). The nests of red wood ants in urban areas mostly have small nest mound volumes, up to 50 l, i. e. they are smaller in size compared to nests of natural populations (Vepsäläinen & Wuorenrinne, 1978). Only a quarter of the nests studied by these authors were quite large, up to 300 litres. Individual nests can be preserved even in the palisades of residential buildings, while small complexes can be preserved in urban forest areas (Omelchenko et al., 2010).

F. rufa in the conditions of Kyiv showed a tendency to increase the volume of nests, which is consistent with the data of Sorvari, who found that this species is more tolerant than *F. aquilonia Yarrow,* 1955, *F. lugubris* Zetterstedt, 1838, *F. pratensis* Retzius, 1783, *F. polyctena* to the presence of human buildings near their nests (Sorvari, 2022).

The categories of condition in nest complexes were most comprehensively studied by Zakharov (2015). He identified 5 categories: a) the phase of active growth of the complex. In this phase, 80–90 % of nests are interconnected in the form of exchange paths, mother and daughter nests are found throughout the complex, the proportion of growing nests with a conical dome can reach up to 80 %. Only *F. rufa* complex No. 2, which was created on the basis of larch planting, can be attributed to such complexes from this study, and it was from here that the ants began their further expansion. In addition, before its sudden death, *F. rufa* No. 3 belonged to the growing complexes until 2019 inclusive (2017 — 12 nests, 2019 — 21, 2021 — 1 nest, 2022 — 0). b). Stabilisation phase. Connected nests 70–80 %, conical nests up to 60 %, mother and daughter nests on the periphery of the complex. *F. polyctena* nos. 1, 2 can be attributed to this phase, at the time of 2022. c) The depression phase. There are only 30–60 % of the connected nests, less than half of the conical nests, mother and daughter nests are single. This phase now corresponds to the once large complex of *F. polyctena* No. 4 in the vicinity of the observatory (2016 — 77 nests, 2019 — 89, 2021 — 37, 2022 — 14). d) Degradation phase. The proportion of nests with a conical nest mound does not exceed 20%, and only up to 20 % of the nests are connected to each other; mother and daughter nests are absent. *F. rufa* complex No. 1 in 2015–2016 corresponded to this phase. e) Decay phase. There are no conical anthills, all nests are solitary, maternal nests and daughter nests are absent. In this phase, the complex of *F. polyctena* No. 3 was located, which broke up into several single large nests (2016 — 13 nests, 2019 — 8, 2021–2022 — 2 nests).

Under increasingly unfavourable conditions, nest complexes may adopt different strategies to prolong their existence and allow new growth. The first is the fragmentation of large nests into several smaller ones (Vepsäläinen & Wuorenrinne, 1978), which was observed in *F. rufa* complex No. 1 in 2013–2014 (fig. 4, A, B). Fragmentation may also be a response to irreparable damage to a large anthill. Fragmentation is not a universal survival mechanism, as most small nests die within the first year of existence (Zakharov, 1991). The second pathway, the strategy of population concentration, is the consolidation of several small nests into one large anthill, which can give rise to daughter nests if conditions change for the better (Zakharov, 2015). The implementation of this pathway was observed in the same *F. rufa* No. 1 complex in 2015 (fig. 4, A, B), as well as in *F. polyctena* No. 3.

At the same time, ants from this complex in at least 2 nests settled in hollows of oak trees in the canopy at a height of 10–15 m, apparently such vertical migrations can be adaptive in response to increasing shading (Stukalyuk, 2017).

Active recreation of urban forests increases the influence of two factors: a) the likelihood of forest fires as a result of improper fire management; b) soil compaction. According to some data, the density of soil can increase twofold, up to 1.2–1.3 g/cm^3, and on human trails this indicator approaches the density of asphalt and amounts to 2.0 g/m^3 (Golosova, 1998). Therefore, the density of the human trail network can negatively affect the species diversity of ants and other groups of invertebrates (Melliger et al., 2018). In recreational areas, the regime of surface water runoff changes and winter soil freezing can occur to a depth of 0.2–0.4 m (Golosova, 1998). Active recreation led to the degradation and death of *F. rufa* complex No. 1, and only the degradation stage from 2014 was covered. Before this period, according to our observations in 2006–2009, this complex contained about 80–100 nests with an average nest mound diameter of 0.8–1.0 m. The transformation of forest areas into a rubbish dump also negatively affects the condition of nests, as was shown for *F. polyctena* complex No. 3.

The littering of the forest with fallen tree trunks and branches is also important, as between 1 and 7.5 % of red ant nests can be damaged each year by fallen tree trunks during strong storms (Zakharov, 2015). Apparently, this factor has influenced the degradation of the *F. rufa* No. 1 complex. Improper forest management also has a negative impact — immediately after the cutting of the shrub layer and the removal of fallen tree trunks and their subsequent processing into chips, the large complex of *F. polyctena* No. 4 disintegrated. The nest complexes of *F. rufa* No. 2, *F. polyctena* No. 1, 2 remained at the same level throughout the years of observation. This may be due to the fact that they are located deep in the forest, far from motorways and other sources of pollution; active recreation is not practised here. In addition, in these areas the clearings are of a sanitary nature, i. e. the trunks of fallen dry trees are removed.

In highly fragmented forest areas of more than 25 ha, *F. polyctena* assemblages tend to decrease while *F. rufa* assemblages increase (van Buggenum, 2022). In the case of Kyiv, no nests of these species were found in forests smaller than 150 ha (Radchenko et al., 2019).

Forest type is also important for the condition of nest complexes. Especially in deciduous forests, *F. polyctena* not only shows smaller linear sizes of nests, but also lower viability (Juhász et al., 2020). This is also confirmed by the present research data: most of the territory of the *F. polyctena* No. 3 complex was in a deciduous forest, and the surviving nests remained only in the territory of a mixed forest with pine in the main tree layer. The same is true for the *F. rufa* complex No. 1, located in a deciduous forest.

The surviving nest complexes of the red wood ant in Kyiv city are located in the territory of the Golosiivsky National Natural Park, which includes the Svyatoshinsky forest in addition to the Golosiivsky forest. It is possible that the lack of development and mass recreation in these areas, as well as the availability of suitable conditions (forest composition, microclimatic conditions) contributed to the preservation of three complexes of red wood ants. The remaining 3 large complexes of red wood ants within the city of Kyiv have from 30 to 80 nests each. According to some data, such complexes form bands 15 km wide and 100 km long and tend to be located in the latitudinal direction (Gilev, 2011). Therefore, such complexes should be sought in the vicinity of Kyiv or along its latitude, in the west — in the Zhytomyr Region, and in the east of Ukraine — in the Chernihiv Region. The consideration of such complexes and their inventory can help to understand the real status of red wood ant populations on the territory of Ukraine.

Conclusion

Red wood ant nest complexes are particularly vulnerable in urbanised forests, where the impact of the anthropogenic factor is most pronounced. Opposite trends are observed in the nest complexes of two species of red wood ants (*F. rufa*, *F. polyctena*) inhabiting the territory of urbanised forests in Kyiv. While the total volume of *F. polyctena* nests show a decreasing trend, the opposite trend is observed for *F. rufa*. Of the 7 nest complexes studied, 2 remained stable (both *F. polyctena*), 1 showed a growth trend (*F. rufa*). All surviving nest complexes are located in the depths of the Svyatoshinsky and Golosiivsky forests, in an area with minimal human recreational and economic (mass felling) activity. In these areas limited (sanitary) felling of trees and removal of dead wood is carried out. The most unfavourable period for red wood ants was 2019–2022, when degradation or death of 4 nest complexes occurred (2 *F. rufa*, 1 *F. polyctena* disappeared, 1 *F. polyctena* degraded). Among the reasons that caused the degradation or death, we can mention the transformation of forest areas into a rubbish dump, the littering of the forest with fallen tree trunks, the cutting of the shrub layer, as well as active human construction and recreational activities. In order to preserve red wood ants in the urbanised forests of megacities, it is necessary to constantly monitor them and create protected areas (myrmecological reserves) based on the experience of other countries.

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