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STUDY OF ECOLOGICAL CHARACTERISTICS OF *LASIUS NIGER* (HYMENOPTERA, FORMICIDAE) USING VEGETATION DATA

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Study of Ecological Characteristics of *Lasius niger* (Hymenoptera, Formicidae) Using Vegetation Data. Stukalyuk, S., Goncharenko, I. & Kozyr, M. — When assessing the condition of *Lasius niger* (Linnaeus, 1858) nest complexes, plant communities should be considered. The aim of this work is to analyse ecological characteristics and structure of *L. niger* nest complexes using vegetation data. The study was conducted in Ukraine, in June 2017 (a nest complex on a territory near Vyshneve, Kyiv Oblast, 502 nest mounds) and in June 2022 (Chaika, Kyiv Oblast, 72 nest mounds, Stara Ushytsia, Khmelnytskyi Oblast, 134 nest mounds). Morphometric parametres of the mounds (diameter, height), their relative position and size classes in squares of 100 m^2 were studied. At the same time, vegetation plots were carried out. Differences in the structure of *L. niger* nest mounds discussed previously are at least partly result from differences in the ecological conditions of the localities. Of the six ecological indicators (Hd — Tm), three — soil acidity and nitrogen, and the hemeroby indicator, which assesses the degree of anthropogenic pollution — have a significant influence on the abundance of *L. niger* nest mounds. These factors were shown to have a significant influence on the ant colony volume indicator. For most indicators, except moisture and light, the optimum for *L. niger* was close to 50 points (middle of the scale). For the anthropogenic factor, the range of values was the widest, which indirectly confirms the relative tolerance of this species to the anthropogenic influence of moderate intensity and allows its existence in urban conditions where competitive pressure from other species is lower. The sign of regression coefficient, especially the positive sign for the acidity and nitrogen indicators, demonstrates positive effect of these factors on the ant colony structure indicators.
Key words: indicators, ants, optimum, acidity, hemeroby, nitrogen, urban conditions.

Introduction

One of the best-studied ant species in the Palearctic is the black garden ant (*Lasius niger* (Linnaeus, 1758)). *L. niger* is a widespread species, its range extends from Atlantic Ocean to Transbaikalia (Seifert, 2020). It prefers to occupy open areas: meadows, pastures, forest edges (Czechowski et al., 2012), on small islands in the Gulf of Finland (Czechowski et al., 2013). Furthermore, *L. niger* is one of the few ant species that has successfully colonised urban areas. For example, it is the most common and abundant ant species in the cities of Warsaw (Poland, Ślipiński et al., 2012), Helsinki (Finland, Vepsäläinen et al., 2008) and Kyiv (Ukraine, Radchenko et al., 2019; Stukalyuk et al., 2019; 2020). Such a wide distribution is possible due to a combination of several factors: plasticity in nest building on different types of substrates (soil, moss, tree debris), as well as symbiotic relationships with aphid species (by data of Novgorodova and Ryabinin, 2015 — with 65 species of aphids; by data of Stukalyuk et al., 2022 — with 43 species of aphids). Under urban conditions, *L. niger* actively uses stones as solariums for accelerated brood development (Stukalyuk and Radchenko, 2022).

The colony size of a single nest mound usually does not exceed 10,000 workers, but in the most favourable habitats it can reach up to 70,000 (Zakharov, 2015). As a rule, *L. niger* colonies are polycalic, with a central nest and several auxiliary nests. In meadows and pastures, nests look like earth mounds up to 40 cm high and 60–70 cm in diameter. In cities, however, *L. niger* anthills are underground and almost never take the form of earth mounds. The nest mounds are connected by a system of tunnels or trails. There may be from a few to tens of thousands of nest mounds within a single nest complex (Stukalyuk et al., 2022). In the latter case, *L. niger* ants, like *Lasius flavus* (Fabricius, 1782), can determine the type of micro-relief (Zryanin, 1998). Soil type is highlighted as the main factor limiting the abundance and distribution of ant species living in open areas (Zryanin, 2003). Dimensional (morphometric) parametres of *L. niger* nest mounds depend on mechanical composition of soil and soil type: on sandy soils their height is lower than on loamy soils (Zryanin, 1998). Shading also plays a role: nest mounds are higher in shaded habitats than in lit ones (Dlussky, 1981). Thus, *L. niger* nest mounds can have different linear dimensions depending on the type of soil, its composition and illumination level.

Despite what is known about biology of this ant species, a number of questions remain unanswered. In particular, there is lack of data on the spatial distribution of *L. niger* nest mounds relative to each other (Higashi et al., 1987; Zryanin, 1998; Holec et al., 2006). For large colonies of *L. niger*, including hundreds and thousands of nest mounds, mechanisms of their formation are unclear. Despite the fact that trophobiotic relationships between *L. niger* and aphids have been well studied, few studies link vegetation (geobotanical plots) and morphometric parametres of nest mounds. Finally, from a geobotanical point of view, characteristics of *L. niger* ecological niche, factors influencing size of nest mounds and structure of *L. niger* nest complexes have not been analysed.

The aim of this study is to analyse ecological characteristics and structure of *L. niger* nest complexes using vegetation data. We also intend to test a methodology for assessing ecological parametres of the *Lasius niger* niche, based on a methodology from a related biological science, the phytoindication methodology used by botanists.

Objectives of the study include: a) analysis of the size characteristics of nest mounds in different populations; b) analysis of the ways in which the large nest complex of *L. niger* appeared; c) study of the characteristics of the spatial distribution of *L. niger* nest mounds relative to each other within the large nest complex; and d) evaluation parametres of the ecological niche (6 to 10) of the Lasius niger species according to phytoindication estimation.

Material and Methods

Study region and sample size

The study was conducted in June 2017–2022 on the territory of two regions of Ukraine: in Kyiv Oblast (two locations, near Vyshneve (50°38’98.00” N, 30°33’55.52” E) and Chaika, 50°41’57.72” N, 30°30’29.15” E) and in Khmelnytskyi Oblast (Stara Ushytsia, 48°61’57.79” N, 27°04’79.20” E).

In total, sizes of 723 nest mounds from 26 nest complexes were measured (134 nest mounds in Khmelnytskyi Oblast, 72 in Chaika in 2022, and the 502 around Vyshneve in 2017). 36 geobotanical surveys of vegetation were conducted (14 from the nest complex near Vyshneve).

Methods of analysis of the collected material can be divided into myrmecological and botanical.

Research design

The article breaks into the following parts:

a) study of nest complexes without regard to vegetation obtaining calculation statistics, it is asymmetry and shape/size ratio;

b) size classification of nest mounds by 4 classes;

c) comparison of morphometric indicators between localities (ANOVA + boxplot);

d) conclusions about the general kind of nest mounds of this species and whether they differ between localities (they are in considerably different conditions);

e) comparison of nest mounds in terms of vegetation: an attempt to explain their differences in environmental conditions, which can be assessed using the phytoindication method (phytoindication calculation);

f) consideration of correlations between eco-factors and selection of indicators for further analysis; and

g) regression analysis of nest mound volume indicators as a function of phytoindication assessment of relative contribution (importance) by the indicators to the formation of response by nest mound volume conclusions regarding the influence of factors on the nest mound volume.

Structurally, the article has two parts. In the first part, the task was to describe *Lasius niger* ant colonies and compare morphometric indices of the colony in three different locations, geographically separated and ecologically different. In the second part, we carried out parametric evaluation of the *Lasius niger* ecological niche, taking into account the entire data set, in order to identify the factors that affect the colony structure of this species the most.

Myrmecological methods

Linear dimensions of the nest mounds included in the nest complexes (cross diameter at the widest and narrowest points and height) were measured. In the case of small nest complexes (up to 50 nest mounds), the entire nest complex territory was measured; in the case of large nest complexes, the territory was divided into transects along which measurements were taken. Sizes of nest mounds were measured within 10 × 10 m squares (100 m^2, quadrats). In total, 76 quadrats were measured in 26 nest complexes. All complexes were divided into two size categories: 2 to 50 nest mounds per complex (25 complexes) and more than 50 nest mounds (one complex containing about 15 000 nest mounds, of which 502 were measured in 4 transects).

The large nest complex B near Vyshneve was studied using the transect method. In order to assess possible dependence of the nest size on the local density of nest mounds, in groups of the selected sectors representing each of the four density categories (1–5 nest mounds (IV density zone); 6–10 (III); 11–15 (II) and 16–20 (I)) we set up 10 × 10 m quadrats in a linear (transect) system (fig. 1).

We searched a total of 42 quadrats and found 502 nest mounds: density category IV — 10 quadrats set up, 43 nest mounds found; III — 10 quadrats, 115 nest mounds; II — 9 quadrats, 143 nest mounds; I — 13 quadrats, 201 nest mounds.

Based on the measurements of nest mound sizes, 4 size classes were identified: 1 (mean diameter (d) = 5.0–26.0 cm, height (h) = 6.0–16.0 cm), 2 (27.0–33.0 cm (d); 17.0–22.0 cm (h)), 3 (34.0–39.0 cm (d), 23.0–29.0 cm (h)) and 4 (40.0–65.0 cm (d), 30.0–57.0 cm (h)). We assigned the first two size classes to small (young), the third to medium, and the fourth to large (and the oldest within the nest complex) nest mounds. From the morphometric indicators of the nest mounds, the following was calculated:

a) mean diameter, D, cm: (D1 + D2)/2 (formula 1),

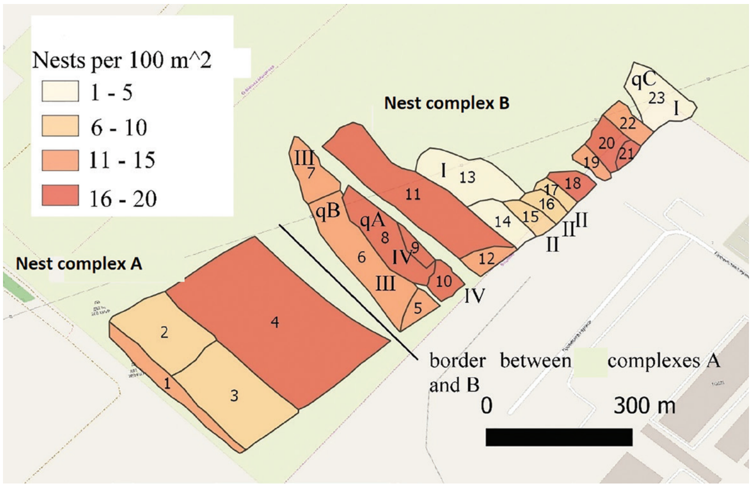

Fig. 1. Map showing two *Lasius niger* large nest complexes: A and B with quadrats of different densities of nest mounds. I–IV — transects.

b) size or volume, V, cm3: 3.14*D/2*H/3 (formula 2),

c) asymmetry value, A: abs(D1 — D2)/(D1 + D2) (formula 3) and

d) shape as a diameter to height ratio, S: D/H (formula 4).

To determine spatial arrangement of the nest mounds in relation to each other, each square was mapped. This was done using millimetre paper. Nest mound coordinates are given as X and Y. This method of determining nest mound position within the squares is more accurate than GIS methods, as the latter produces 2–12 metre error, which is a lot for a 10 x 10 metre square.

Botanical surveys

A botanical survey was carried out on sample plots using the standard method (Ramensky, 1938; Landolt, 1977; Mueller-Dombois and Ellenberg, 2002; Goncharenko and Didukh, 2003). Nest mounds were recorded and measured on the same plots. Sizes of the geobotanical sample plots ranged from 100 to 400 m^2. A total of 36 surveys (geobotanical plots) were carried out. The complete plant species composition and the layer structure were recorded. Species projective cover was recorded according to B. Mirkin scale (Mirkin and Naumova, 2014).

Parametres of the ants' ecological niche were assessed using the same ecological indicators: based on a range of these indicators' values. All geobotanical plots where ant colonies were recorded were taken into account, and the optimum was assessed based on the values of the average ecological indices. The 'optimum' concept is conditional in this case, as the sites studied represent only part of the species' ecological niche. As the factors are scaled to a single 100-point scale, the range and optimum values can be compared between factors (Goncharenko et al., 2020). Wider range values indicate a greater amplitude for a specific factor. For anthropogenic factor it can be considered as tolerance to anthropogenic stress.

Next, ecological parametres (environmental variables) were calculated for the same sample plots using the phytoindicator methodology, which is widely used in botany (Ramensky, 1938; Tsyganov, 1983; Didukh & Plyuta 1994; Didukh, 2011). We used the plant indicator scales adapted to Ukrainian flora (Didukh, 2011). The following key plant factors were used in the evaluation Hd for humidity, Rc for soil acidity, Nt for nitrogen, Lc for light, and Tm for temperature. In addition, the hemeroby index (Hm, hemeroby) was used to assess anthropogenic pressure (Frank and Klotz, 1990). Hemeroby refers to result of cumulative (all types of) human impact on a phytocoenosis/ecosystem (Jalas, 1955; Hill et al., 2002; Yorkina et al., 2022). Higher hemeroby values correspond to more anthropogenically altered areas of the environment. For the 6 factors listed above, mean estimates of plots were calculated using the weighted average method, i. e. taking into account the projective cover of species. For comparability of scores between factors with different numbers of points in the scales, they were first reduced to a single 100-point scale (Goncharenko, 2017; Churilov et al., 2020; Goncharenko et al., 2022), and then the site (phytocoenosis) average was calculated. Phytoindication is not a direct method of assessing the environment, but it is based on ecological scales which characterise the relationship between plants and environmental parameters in a relative (score or rank) basis.

The resulting indicators were treated as independent (influencing) factors, with nest mound volume as a dependent variable. The volume indicator was chosen because it is adequately indicative of ant colonies and takes into account both diameter and height of the nest mounds.

Statistical analysis

Tukey's test was used for paired comparisons (average number of mounds per square between complexes with up to 50 mounds and complexes with more than 50 mounds). Mound locations were tested for spatial randomness using a classical chi-squared test for spatial scatter based on quadrat counts. A 10 m × 10 m grid was used. Changes in the number of points along the transects were quantified using the Kolmogorov-Smirnov test, a classical method for analysing point patterns. Randomness of spatial point patterns was analysed using the L-function, a transformation of Ripley's K-function (Besag, 1977). The p-value was calculated from 9999 replications of the Monte Carlo test (Ripley, 1977, 1981; Baddeley et al., 2014). Spatial statistical analysis was performed in R using the 'spatstat' package (Baddeley et al., 2015).

As three different localities were included in the study to determine differences in colony structure, and their morphometric indices were compared using a standard ANOVA (aov function in the basic R installation). All calculations were performed using the statistical environment R ver. 3.5.3 (https://cran.r-project.org). Multiple pairwise comparisons, called post hoc analysis, were performed using Tukey's test.

The dependence of nest mound volume on environmental factors was assessed using regression analysis. A multiple regression model and the function lm(v ~ Hd + Rc + Nt + Lc + Hm + Tm) embedded in basic R were used. A custom relweights function by Tyler Rinker, available on GitHub (https://github.com/trinker/Regression/blob/master/R/relweights.R), was used to estimate relative contribution (significance) of environmental variables to nest mound volume. Implementation of this function involves evaluating a portion of the total R^2 of the regression model explained by each of the independent variables (predictors).

Results

Phytocenotic characteristics of vegetation

The communities of plants are actually formed in the place of agricultural activity. However, in some localities (Chayka, Vyshneve) the agricultural activity was completely stopped about 10 years ago, and in the territory of Stara Ushytsa — ploughing was stopped 2–5 years ago, and grazing, mowing and burning continue with varying intensity. The first two localities are mainly flat massifs with a one- or two-storey grass cover of 50–80 % and a height of 30–90 cm, depending on the test site, while the third is usually located on gentle slopes, where there is moderate livestock grazing and mowing or burning. Grasslands in the area of Staray Ushytsa are also one- or two-storeyed, only occasionally three-storeyed, and the height is mostly 45–110 cm. Typically, 5–16 plant species were observed on a test plot in Vyshneve, and the total species composition consisted of 35 species. In the study plots near Chayka there are 7–16 (42 in total), and in Staraya Ushytsa 8–22 (55 in total) species. A total of 105 plant species were recorded in the phytocenoses of the studied areas. The above data are confirmed by our visual observations, and also by the analysis of Supplementary Table 1 with geobotanical plots, and indicate that the territory of the first two sites had suffered significant damage to the vegetation cover, in particular long-term ploughing, while the third site was not subjected to such interventions, because livestock grazed there and grass was mown, or in some places (abandoned homesteads) ploughing took place 15–20 years ago.

Analysing Supplementary Table 1 (https://doi.org/10.5281/zenodo.8419358), it is clear that the richer the species composition of the phytocenosis, the longer it is not exposed to the influence of strong anthropogenic factors and, above all, the quicker it returns to a natural or semi-natural composition. The presence of species such as *Cirsium arvensis*, *Artemisia absinthium, Phalacroloma annuum*, *Calamagrostis epigeios* is a clear indicator of successional processes at present and anthropogenic influence in the past. If the impact ceases and enough time pass, the participation of these species in the formation of natural coenoses will decrease significantly, but we doubt that these species will disappear completely, given the location of these areas near populated areas. The Supplementary_Table 1 also shows that the coenoses have been invaded by alien aggressive species, especially species-transformers: *Ambrosia artemisiifolia*, *Solidago canadensis*, *Acer negundo*. This leads to the formation of these species, which are different from the natural coenoses, and which quickly take over the surrounding areas. The presence of such species as *Pilosella officinarum*, *Galium verum*, *Hieracium umbelatum*, *Potentilla argentea,* species of the genus *Euphorbia* indicates the gradual xerophytization of the coenoses, which will be replaced by steppe meadows or grassland steppes. And if for Stara Ushytsia, this is quite natural, but for the areas near Kyiv (Chayka, Vyshneve) it confirms once again the change of climate to a more arid one. The presence of *Pinus sylvestris*, *Populus tremula*, *Betula pendula* and *Salix cinerea* in the phytocenoses clearly shows that these areas will soon become secondary forest massifs.

This is characteristic of the phytocenoses studied in Chayka. Mass presence of grasses *Poa pratensis*, *Agrostis canina*, *Agrostis capillaris*, *Calamagrostis epigeios*, *Dactylis glomerata*, *Elytrigia repens, Festuca pratensis, Festuca rubra, Phleum pratensis, Poa pratensis* on grassy areas will most likely lead to formation of corresponding associations or phytocenoses with their dominance. In woody coenoses, their role and projective coverage will be greatly reduced. Vegetation data in the form of plots were analysed by us to assess the ecological characteristics of *Lasius niger* with different phytoindicators (Material and Methods section).

Density and size of nest mounds per 100 m² in complexes of different sizes

Depending on their size, complexes may have different nest mound densities per 100 square metres (fig. 2).

Small complexes, up to 50 nest mounds have low nest mound density, while in the nest complex B nest mounds have high density on the territory (fig. 2). The number of large nest mounds in complexes of different sizes serves as a diagnostic sign of ant dispersal. The difference in the average number of nest mounds per 100 square metres between each of the first three zones and zone I of the nest complex B is significant: between IV and I ($p \leq 0.001$), between III and I ($p \leq 0.001$), between II and I ($p \leq 0.001$). Thus, zone I has lower density of nest mounds in comparison with the other nest complex B zones.

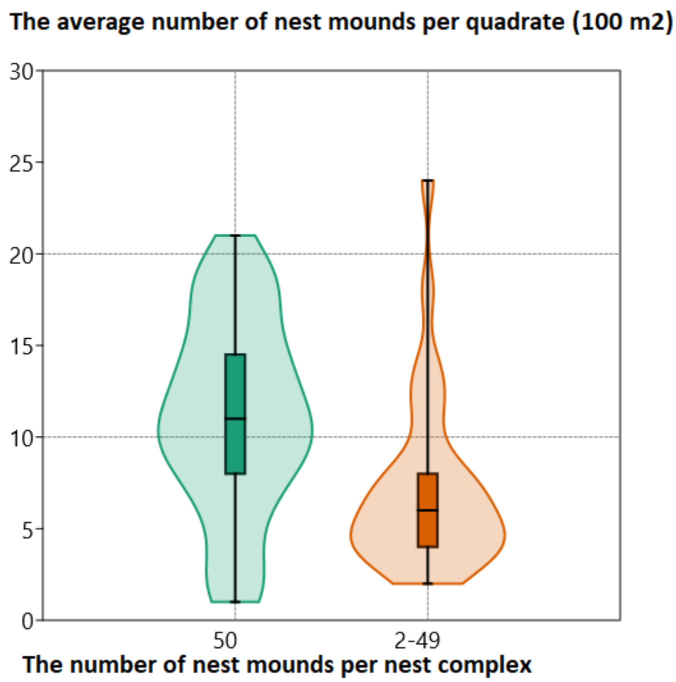

Fig. 2. Average number of nest mounds per 100 square metres in complexes of different sizes (up to 50 nest mounds and more than 50 nest mounds). P = 0.0001 (Tukey's pairwise).

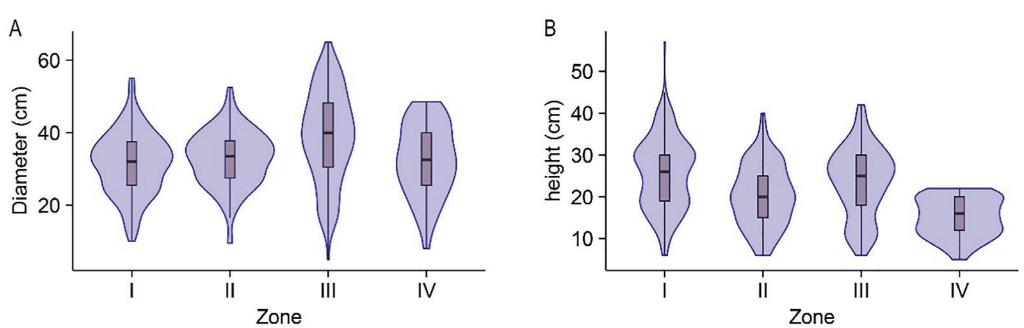

Fig. 3. Morphometric parametres of *Lasius niger* nest mounds in the nest complex B territory. I to IV are zones with different nest mound density per 100 m². A — diameter, B — height.

Zone I and III nest mounds in the nest complex B have greater average height and diameter compared with the other two zones ($p \le 0.001$–0.0001, fig. 3, A, B).

This indicates that zone I and III nest mounds may have been the original sites from which boundaries of the large nest complex B were extended.

Another indicator of how the nest complex B boundaries were expanding is the number of the largest (and oldest) nest mounds, corresponding to size class 4 in heights and diameter. Analysis of the number of such mounds in each of the 10 x 10 m squares in the four density zones showed that the majority of such mounds were in zone III and zone I (by diameter). In terms of diameter, size class 4 mounds in zone III are larger than those in size class I ($p \le 0.01$); in zone III larger than those in zone II ($p \le 0.001$); and in zone III larger than those in zone IV ($p \le 0.001$). In terms of height, zone I has the highest number of nest mounds per square: more than in zone II ($p \le 0.01$), in zone III ($p \le 0.04$) and in zone IV ($p \le 0.0001$). The number of nest mounds in zones II and III is not much different; the lowest number of large nest mounds was recorded in zone IV.

It follows that the nest complex B was formed as a result of settling and merging of nest mound groups in zones I and III. Finally, after zone II, zone IV was occupied, and its development brought zones III and I into contact and merged them into subcomplex B.

The number of nest mounds of different size classes can be an important diagnostic sign for the time interval when one of the four zones of sub-complex B was formed (table 1).

Most medium and large nest mounds of size classes 3–4 are found in zones I and III of subcomplex B, their number is lower in zone II, and they are minimally represented in zone IV. As for the small nest mounds of size classes 1 and 2, most of them are located in zones I and II, which may indicate their intensive occupation. In zone IV, the number of small nest mounds is also minimal, indicating that the ants have just started to disperse here.

Zones with high density of nest mounds may indicate more favourable habitat, while low-density zones may indicate less favourable habitat. Attractiveness of the sites for ants may be a consequence of differences in the composition of plant communities.

Nest aggregation

The chi-squared test applied to 4 transects in the large complex at Vyshneve did not reject the null hypothesis that mounds were evenly distributed across the 10 m x 10 m quadrats. However, results of the Kolmogorov-Smirnov test indicate that the number of mounds changes along transect 1 ($P = 0.0086$). The empirical L-function suggests that the pattern deviates insignificantly from complete spatial randomness,

Table 1. The number of nest mounds of four size classes in height and diameter in four zones of nest complex B

Density zone per 100 m^2	Parameter	Class 1	Class 2	Class 3	Class 4
I	Height	31	45	45	80
	Diameter	56	57	53	35
II	Height	38	32	26	19
	Diameter	21	36	35	23
III	Height	31	27	48	37
	Diameter	25	17	25	76
IV	Height	25	18	0	0
	Diameter	13	11	7	12

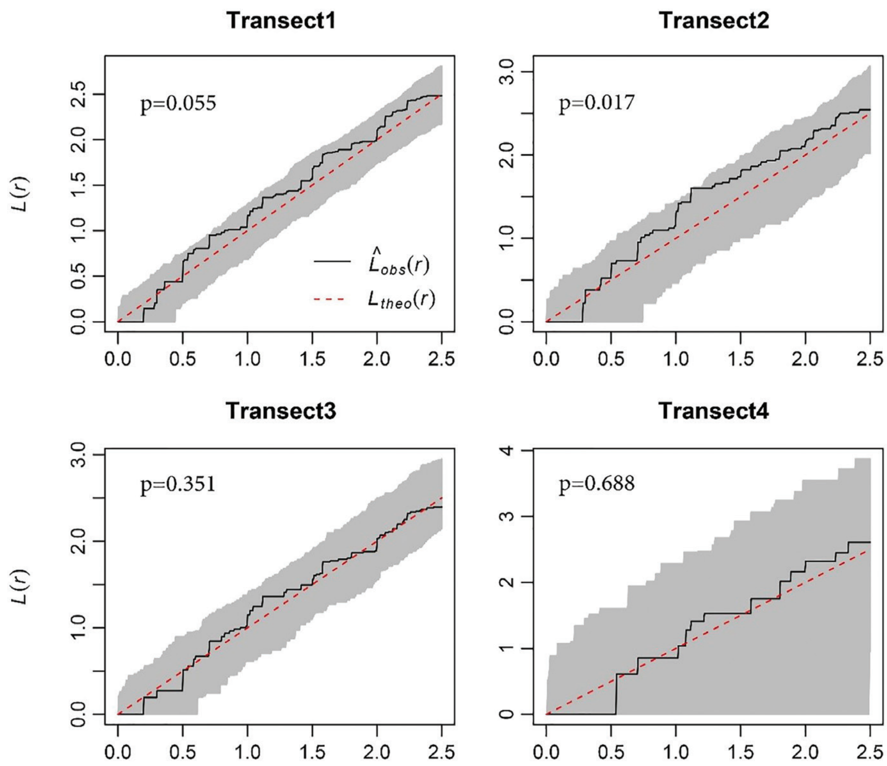

Fig. 4. The empirical L-function (solid lines) and expected value assuming the points are completely random (dashed lines). Gray shadow denotes an envelope of 9999 simulations for theoretical L-function. The p-values were extracted from the Maximum Absolute Deviation test for a spatial point pattern.

but the mounds along transect 2 clustered at a distance of approximately 1.2 m (fig. 4). Note that the clustering distance of 1.2 m is close to that between ploughed furrows, and mounds are often seen on ploughed furrows. We did not find pronounced aggregation between nest mounds in nest complex B. Similar calculations were not made for nest complexes of smaller size.

Table 2. Morphometric parametres of *Lasius niger* nest mounds in the studied area

Variable	Location	Diameter, cm	Height, cm	Volume, c^m3	Asymmetry, D1/D2 ratio	Shape, D/H ratio
Mean	Ch	30.4	18.9	352.4	0.1	1.9
Sd		11.975	10.092	279.723	0.087	0.822
Min		5	3	7.85	0	0.938
Max		59.5	41	1183.257	0.5	5.833
Mean	U	33.3	28.1	530.8	0.1	1.4
Sd		9.959	13.471	367.141	0.056	0.642
Min		11	7	57.567	0	0.6
Max		59	70	1881.907	0.333	4
Mean	V	34.3	22.9	437.4	0.1	1.6
Sd		10.472	8.521	246.455	0.083	0.627
Min		5	5	18.317	0	0.658
Max		65	57	1694.815	0.458	5
F-statistic		F = 4.431**	F = 23.684***	F = 10.724***	F = 12.656***	F = 14.676***

Morphometric parametres of *Lasius niger* nest mounds

There is a significant difference between the sites for all the morphometric indices (table 2).

This indicates significant differences in the structure of the studied colonies of this species, which can be explained mainly by the different ecological conditions of the sites.

Figure 5 shows comparison results for the morphometric indices of the *Lasius niger* colonies in the 3 studied sites.

The Stara Ushytsia nest mounds are significantly (slightly) larger in volume and height. At the same time, they have lower diameter to height ratio d/h, and the colonies' asymmetry rate is lower too.

When compared with table 2, the minimum volume values of the Chaika nest mounds are flat. As mentioned above, one of the analysis points was to investigate the *Lasius niger* ecological niche, for which data was obtained from vegetation through phytoindicator assessment.

Ecological niche parametres (6 to 10) of the *Lasius niger* species according to phytoindicator assessment

Table 3 shows results of the indicators calculated as averages for the individual surveys where *Lasius niger* ants were recorded in each of the three sites studied.

ANOVA results show that there are significant differences in ecological conditions between the three sites. This suggests that differences in the structure of *Lasius niger* nest mounds discussed above are, at least in part, due to differences in the ecological conditions of the localities. It should be noted that presence of *Lasius niger* at all three sites indicates a high degree of ecological plasticity.

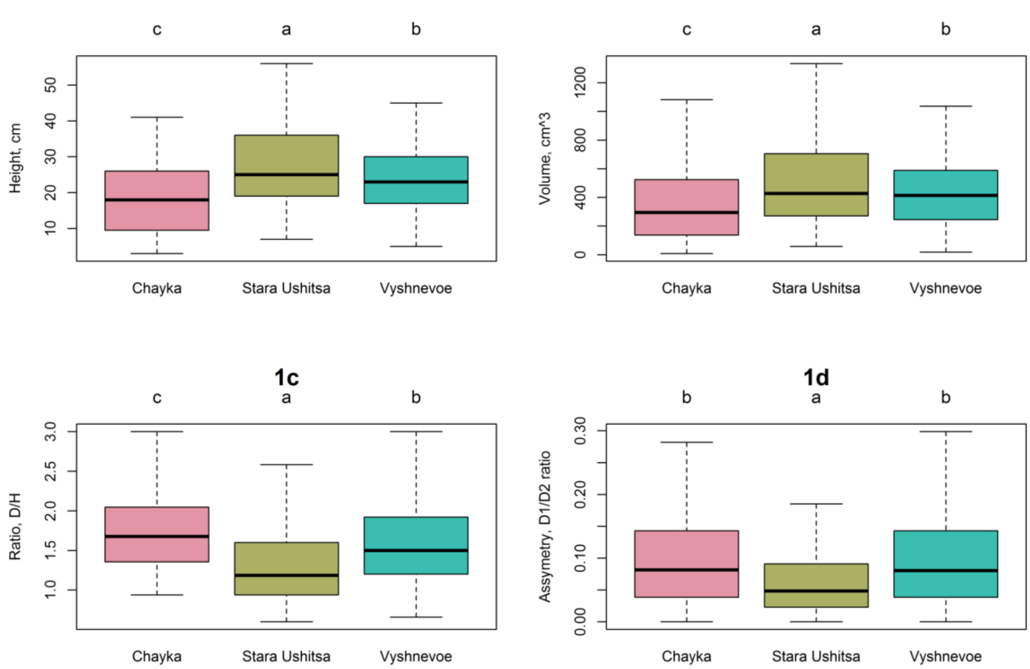

Fig. 5. Box plots showing differences in morphometric parametres of *Lasius niger* nest mounds between the three studied sites. The letters above the graphs indicate results of Tukey's comparison test. a — height, cm, b— volume, cm^3, c — ratio D/H, D — asymmetry (D1/D2 ratio).

Table 3. Comparison of six phytoindicator variables in the three studied sites where *Lasius niger* colonies were registered

Variable	Location	Hd	Rc	Nt	Lc	Hm	Tm
Mean	Ch	45.71	50.27	52.38	62.07	44.8	53.44
Sd		3.39	2.83	3.44	2.53	2.8	1.7
Mean	U	44.11	54.67	57.15	66.4	47.16	54.5
Sd		3.97	3.32	5.46	1.1	4.46	2.26
Mean	V	40.1	51.1	63.4	66.21	56.67	57.17
Sd		2.27	2.31	6.29	2.2	8.43	1.31
F-statistic		F = 206.379***	F = 113.656***	F = 147.159***	F = 131.108***	F = 144.425***	F = 287.244***
p-value		1.41E-71	1.26E-43	2.61E-54	2.79E-49	1.83E-53	1.92E-92

Note. Hd is humidity, Rc is soil acidity, Nt is nitrogen, Lc is light value, Hm is hemeroby, Tm is temperature value.

The next step was to investigate which of the environmental factors assessed by the phytoindicators had effect on the nest mound size and to what extent. This was done using regression analysis. Nest mound volume was used as the response variable and ecological indicators of the geobotanical sites where the nest mounds were located were used as the influencing variables.

Table 4 shows regression analysis results for the *Lasius niger* nest mound volume as a function of ecological habitat parametres (based on phytoindicator assessment).

We see that of the 6 ecological indicators (Hd — Tm), three — soil acidity and nitrogen, as well as the hemeroby indicator, which assesses the degree of anthropogenic load — have significant impact on the volume of *Lasius niger* nest mounds. From the ecological point of view, we believe that the influence of soil characteristics on nest mounds indicators is mediated. That is, it is primarily the vegetation (species composition and community structure) that changes as a function of soil characteristics. And vegetation as a whole and individual plants play a dual role for ants. On the one hand, plants provide food for ants and aphids. On the other hand, the vegetation plays an important role not only for the ants but also for the whole community. In addition, indicators of soil structure, particularly texture, are likely to correlate with changes in soil properties. This affects ants' ability to build nest mounds (which is easier on sandy soils). Thus, the influence of environmental parametres on ant colony structure indicators is wide-ranging.

Table 4. Regression statistics (1 to 5) and ecological niche parametres (6 to 10) of the *Lasius niger* species according to phytoindicator assessment

Abbreviation	Variable	Estimate	Std. error	Statistic	p. value	sigSymbols	Mean	Min	Max	Range	Range rank
Column number		1	2	3	4	5	6	7	8	9	10
Hd	Humidity	–3.6	5.6	-0.6	5.21E-01		42.5	36.5	49.9	13.4	4
Rc	Soil acidity	9.1	4.6	2.0	4.59E-03	**	52.2	43.2	61.6	18.4	3
Nt	Nitrogen	6.0	2.2	2.7	7.02E-03	**	58.3	42.8	73.6	30.8	2
Lc	Light	–5.6	6.3	–0.9	3.78E-01		64.8	57.7	69.6	11.9	6
Hm	Hemeroby	–3.5	2.0	–1.7	3.00E-02	*	50.9	35.2	89.0	53.8	1
Tm	Temperature	–12.0	9.2	–1.3	1.95E-01		55.7	50.7	63.8	13.1	5

Discussion

Distribution and characteristics of *Lasius niger* nest complexes in the study region

In the studied area (Kyiv and Khmelnitsky Oblasts), large *Lasius niger* colonies with hundreds of nest mounds can be found everywhere: fields, gardens, tree plantations (especially young pine trees up to 3–4 m high), meadows, pastures and hayfields. It appears that *Lasius niger* mainly inhabits anthropogenically modified habitats. Similar large nest complexes can be found in the neighbouring Ukrainian Oblasts, Zhytomyr and Chernihiv. Absence of potential competitors (territorial dominant ant species) may favour the formation of such nest complexes. Nest complexes are found at the southern edge of the *Lasius niger* range, corresponding to the Ukrainian forest-steppe zone. Nest complexes of *Lasius niger* in native habitats are common in meadows (Radchenko, 2016). In fields, where nest heating is faster than in forests or meadows, the brood can develop faster and here *Lasius niger* is able to form nest complexes of maximum size. Radchenko (2016) points to the presence of earth mounds up to 1.5 m high (in the Carpathian Mountains) and high density of such mounds within Ukraine. Based on this, it can be assumed that in Eastern Europe large colonies of this species are common for forest-steppe territories and anthropogenic landscapes of Ukraine and Russia. The largest *L. niger* nest complexes form on ecotones, borders between pastures and fields (Seifert, 1993; Dauber and Wolters, 2004; Guseva and Koval, 2019).

The size of *L. niger* nest mounds is directly proportional to the amount of land it occupies and its population (Rasse and Deneubourg, 2001). In the large settlement, medium and large size nests predominated. We have shown that these factors play an important role, as their optimal combination enables the formation of large nest complexes. If we take the average worker population (10 000, Zakharov, 2015) and multiply it by the number of nest mounds in the large nest complex B we found, we get a population of 150 000 000 workers.

Seifert (2018) gives an average number of *L. niger* nest mounds of 43.5 to 108 nest mounds per 100 m^2. In our case, the average nest mound density in the large nest complex B territory is between 4 and 15 nest mounds per 100 m^2. It should be borne in mind, however, that we are giving figures for nest mounds only, without taking into account auxiliary nests or nests in the ground.

Nest mound size is directly related to colony age (Zryanin, 1998); therefore, analysis of the complex formation mode based on the number of large nest mounds is justified. Despite the fact that aggregation was only detected in one of the transects in the large *L. niger* nest complex B, other data indicate that it occurs in other nest complexes (Zryanin, 1998). At the same time, the distance between nest mounds is directly proportional to their size class. In polycalic colonies, nest aggregation may be more pronounced in *L. niger* than in other ant species (Higashi et al., 1987). Aggregation may be related to nest size: large nest mounds are chaotically arranged, while small and medium nest mounds are aggregated (Holec et al., 2006). This may confirm that the large nest complex B we studied evolved from the oldest (large) nest mounds, with new mounds built in between. Emergence of large *L. niger* nest complexes is probably associated with simultaneous dispersal of ants, or it may occur in several waves.

It is interesting to note that the location of nest mounds remains constant over the years, and their increase in linear dimensions is mainly recorded (Zryanin, 1999). As the linear dimensions increase, growth of *L. niger* nest mounds slows down (Zryanin, 2003), so they remain stable for many years.

Influence of environmental factors on the structure of *Lasius niger* colonies

Of course, contribution of the environmental factors influence on the ant colony structure varies. Some factors affect the colony structure more, others less, and this applies to three factors for which the influence is estimated to be reliable (Rc, Nt, Hm) as well as to all six. In our opinion, it is not entirely correct to judge directly on the basis of the absolute value of the regression coefficient. This is because this effect also depends on the range of ants' ecological amplitude. We cannot directly compare changes in nest mound volume for factors where the ant amplitude is wide and those where the amplitude is narrow. Therefore, we used an approach where relative importance of ecological factor is estimated by the magnitude of its contribution to the R^2 regression model determination coefficient (fig. 6).

The ranking of the variables according to their influence on the nest mound structure is in good agreement with the p-value of the regression analysis (table 4). Soil acidity, Hd, hemeroby, Hm, and nitrogen, Nt, are among the most influential variables. In addition, this graph visually conveys relative contribution of the variables. For example, soil acidity has a significant lead over the second factor (hemeroby), etc. This cross-estimation using different approaches is more robust. The regression coefficient for temperature, Tm, is the largest in absolute value (12.0, table 4). At the same time, relative contribution of Tm is small according to figure 6. This can be explained by the small amplitude of the Tm factor (Range column, table 4). On the one hand, a change in the temperature index by a single value will have significant effect on the volume of nest mounds. On the other hand, since the fluctuations of this indicator among the vegetation sites studied are relatively small, its

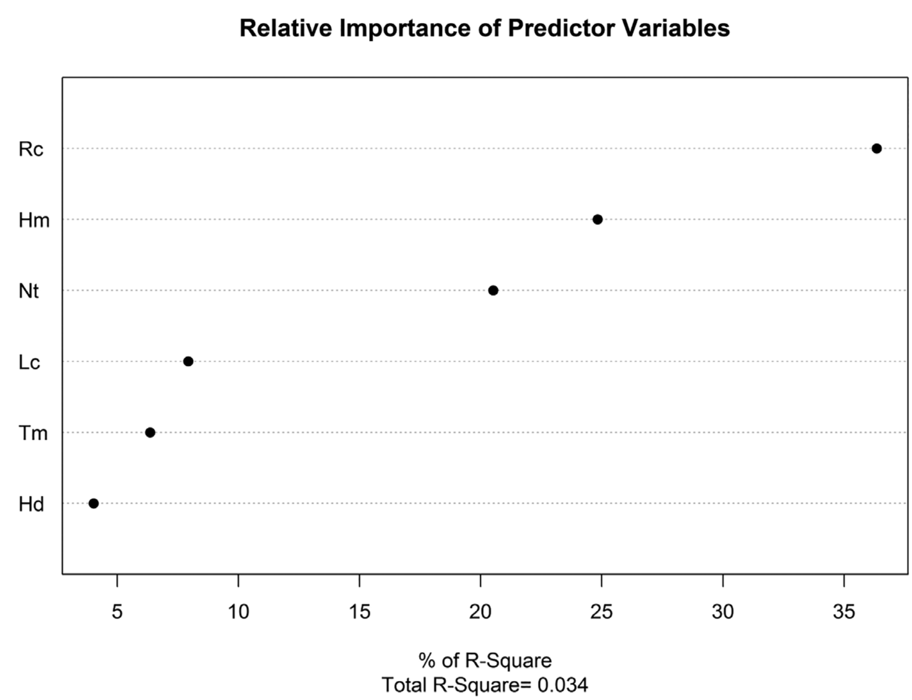

Fig. 6. Estimation of relative importance of environmental (predictor) variables in terms of their influence on the volume (dependent) variable of *Lasius niger* nest mounds.

contribution is small too, as we can see in figure 6. In other words, it can be said that the regression coefficients (table 4) refer more to the general (fundamental) ecological amplitude, while the estimate based on R^2 (fig. 6) refers more to the realised one.

The sign of regression coefficient (table 4) gives important information about direction of factor influence on the nest mound volume. For example, increase in Rc (soil acidity) correlates with increase in nest mound size, as does increase in Nt (nitrogen). This suggests positive effect of these factors on ant colonies. As mentioned above, this effect is not necessarily direct. In particular, soil acidity is higher in pine forests, where soils are light, and this contributes to the formation of large ant colonies. For the effect of nitrogen, see Zryanin, 2003. Accumulation of organic matter in *L. niger* nest mounds is related to the leaching regime of the soil on loams. The situation is reversed in the *Lasius flavus* nest mounds, which have dense walls and water with organic matter is mainly leached into the soil around the mounds (Zryanin, 2003). Nest mound density in this species is higher than in *L. niger* or *Formica sanguinea* Latreille, 1798 (Wu et al., 2010).

On the contrary, effect of hemeroby, which indicates anthropogenic pollution, is negative (negative sign in the regression coefficient with Hm, table 4). In other words, as expected, anthropogenic influence is detrimental to the colony structure of the native ant species.

At the same time, there is another aspect of assessing the ecological niche of *Lasius niger*, which is the range of amplitude for each factor (variable). In terms of amplitude range, the factors are ranked in the 'Range rank' column, table 4. Looking at the values in the range column, Hm (anthropogenic pressure) has the largest amplitude (range = 53.8). In other words, despite the negative effect of the anthropogenic factor, ants' tolerance to it is quite high. This, in particular, allows them to exist in urban areas (Blinova, 2008, 2012; Putyatina, 2011; Antonov, 2012; Stukalyuk et al., 2020). Smaller amplitude we find for the factors of humidity, brightness and temperature (Hd, Rc, Tm range from 11.9 to 13.4, table 4). In other words, this type of estimation gives us an insight of the realised niche rather than the potential (fundamental) one. Perhaps, it is within this range of environmental conditions that competition with other species is the lowest. Therefore, the species may have a wide amplitude in other factors, but its optimum is squeezed into a relatively narrow range. *L. niger* has a wide thermal preference (Zryanin, 2003); therefore, our data on this factor can be considered relevant for open areas, without taking into account young pine plantations and other habitats that we did not study. As far as hemeroby is concerned, this may be a significant competitive advantage over other ants that are more sensitive to anthropogenic impacts, e. g. *Lasius emarginatus*, *Formica polyctena*. And it allows *Lasius niger* to form large colonies in urban environments (Stukalyuk et al., 2022).

As we have scaled all environmental factors to a uniform 100-point scale, it is possible to directly compare the optimal (mean) value of the environmental indicators. For most of them, the mean value (Table 4) is close to the middle of the scale, i.e. 50 points, neutral soils and medium-rich, etc. Only humidity deviates slightly downwards (mean Hd = 42.5) and lightness upwards (mean Lc = 64.8). As mentioned above, such estimates should be interpreted through the prism of the habitat-forming influence of vegetation. In particular, higher humidity values tend to promote plant height and canopy density. This, in turn, may inhibit nest mound formation. With regard to lightness, Lc, this factor in the phytoindicator correlates with the proximity of the upper layers of communities, trees and shrubs. A higher Lc value indicates 'light' forests, especially coniferous, as well as forest edges, which are more favourable for *Lasius niger*. Darkness associated with dense forests, deciduous forests and forests with dense shrub layers will be less favourable. The influence of light, like all other factors, must be considered through all possible biocenosis relationships (Stukalyuk and Maák, 2023). For example, proximity of tree layer has a negative effect on the growth of plants in the lower (herbaceous) layer, which also plays an important trophic role for ant. All this shows that only a comprehensive approach to interpretation of mathematical models can explain the relationship between colony structure and ecological indicators derived from phytoindicators.

Conclusions

Our results should be considered from two perspectives. On the one hand, inclusion of phytoindicators in the assessment of ant species ecological niche provides information which is difficult to assess using conventional myrmecological methods. Such assessment is possible, and is based on substantial understanding of the biocenosis structure, where ants and vegetation are part of the same biological system. Also, considering that the phytoindicator approach is rather simple and not time-consuming — that is why it is extensively used by botanists — it will be possible to use it for long-term and multi-purpose assessments. To sum up, the indicators obtained from phytoindication for ants should be interpreted in terms of the impact on vegetation, which plays a habitat-forming role.

For *Lasius niger*, on the other hand, we have not only obtained descriptive characteristics of the ecological niche in which the species occurs, but also information on how certain indicators affect the ant nest mound sizes. Acidity, nitrogen and hemeroby were shown to have a significant influence on the ant nest mounds volume indicator. This assessment is multi-criteria based. Average intensity of ecological factor, amplitude and direction as indicated by the regression coefficient sign are important. For most indicators, except humidity and light, the optimum for *Lasius niger* was close to 50 points (middle of the scale). For the anthropogenic factor, the value range was the widest, which indirectly confirms relative tolerance of this species to anthropogenic influence of moderate intensity, and allows its existence in urban conditions where competitive pressure from other species is less. The regression coefficient sign, especially positive sign for the acidity and nitrogen indicators, means positive influence of these factors on the ant nest mounds indicators.

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