

DOI 10.15407/zoo2026.04.446

UDC 595.796:502.7

PHYTOINDICATION-BASED ANALYSIS OF THE ECOLOGICAL NICHE OF *LASIUS FULIGINOSUS* (HYMENOPTERA, FORMICIDAE) IN RIPARIAN AND MESOPHILOUS FORESTS

S. Stukalyuk^{1, *}, I. Goncharenko^{1, 2} & M. Kozyr¹

¹ Institute for Evolutionary Ecology, National Academy of Sciences of Ukraine, Lebedeva St., 37, Kyiv, 03143 Ukraine

² Department of Medical Biology and Sports Dietetics, National University of Ukraine on Physical Education and Sport; Fizkultury st., 1, Kyiv, 03150 Ukraine
E-mail: asmoondy@gmail.com

* Corresponding author:

S. Stukalyuk (<http://orcid.org/0000-0002-9775-0750>)

I. Goncharenko (<https://orcid.org/0000-0001-5239-3270>)

M. Kozyr (<https://orcid.org/0000-0002-5135-7937>)

urn:lsid:zoobank.org:pub:A6FFF4F9-C9A6-4583-A984-FE8185F40942

Phytoindication-based analysis of the ecological niche of *Lasius fuliginosus* (Hymenoptera, Formicidae) in riparian and mesophilous forests. Stukalyuk, S., Goncharenko, I. & Kozyr, M. — The aim of this study was to characterise the ecological niche of *Lasius fuliginosus* (Hymenoptera: Formicidae) along phytoindication gradients, and to determine the relationship between its foraging activity and the structure of the vegetation in riparian and mesophilous forests in Kyiv region. Fieldwork was conducted from July to August 2025 across 36 *L. fuliginosus* colonies (20 in the Holosiivskyi National Nature Park and 16 on Zhukiv Island). Standard 20 × 20 m plots were used for simultaneous geobotanical surveys and quantitative assessments of foraging intensity (number of workers passing per minute on trails and tree trunks). Environmental conditions were evaluated using eight standardised Didukh phytoindication scales. Statistical analyses included Generalized Additive Models (GAMs), Generalized Linear Models (GLMs), Principal Component Analysis (PCA) and Permutational Multivariate Analysis of Variance (PERMANOVA). The multivariate ecological niche of *L. fuliginosus* exhibited a pronounced microclimatic specialization, with temperature and moisture acting as the primary narrow limiting factors. The narrowest ranges were observed for temperature (Tm: 56–64 points, median: 60.5) and soil moisture (Hd: 43–54 points, median: 48), indicating strict avoidance of extreme xerophytic and waterlogged conditions. The number of forage trees per plot (1–6) had no significant impact on ant abundance ($p = 1.0$), whereas plant species richness exhibited a distinct nonlinear threshold pattern modelled using GAM. A significant increase in foraging activity was observed exclusively when moving from low (7–

13 species) to moderately low (13–16 species) richness ($p < 0.05$). PCA and PERMANOVA revealed a highly significant and distinct environmental segregation between the niche configurations of riparian willow-poplar forests and mesophilous oak-hornbeam forests ($F_{1,34} = 18.86$, $R^2 = 0.36$, $p = 0.001$). However, due to high ecological plasticity, the actual intensity of foraging did not differ significantly between the two forest types ($W = 171$, $p = 0.1526$), despite a higher median abundance in riparian zones (445.5 workers per minute) than in mesophilous stands (279.5 workers per minute). *L. fuliginosus* is tightly associated with stable, moderately warm and humid forest microhabitats, serving as an effective bioindicator for monitoring ecosystems under anthropogenic pressure.

Key words: *Lasius fuliginosus*, ecological niche, phytoindication, Didukh scales, foraging activity, riparian forests, mesophilous forests, Kyiv Region.

Introduction

Ants (Hymenoptera, Formicidae) are a vital part of forest ecosystems. They act as bioindicators of environmental health, ecosystem engineers and important links in food webs. Their high abundance, diverse life strategies and ability to alter soil and vegetation structure mean that ants significantly influence nutrient cycling, soil composition, seed dispersal and the regulation of other invertebrate populations (Folgarait, 1998; Sanders & van Veen, 2011; Rocha et al., 2024). As ecosystem engineers, ants create and maintain microhabitats, thereby enhancing local biodiversity and promoting the resilience of forest communities to human impacts (De Almeida et al., 2020; Rocha et al., 2024). Vegetation structure and climate gradients also play an important role in shaping ant communities (Uhey et al., 2020). In forest ecosystems, ants respond to changes in temperature, humidity, light and vegetation structure, making them effective indicators of forest degradation, climate shifts and disruptions in trophic interactions (Andersen, 1997; Lawes et al., 2017; Uno et al., 2010; Subedi et al., 2021). Of particular interest among forest dendrobiont species is *Lasius fuliginosus* (Latreille, 1798) — the only representative of the subgenus *Dendrolasius* Ruzsky, 1912 in Europe (Radchenko, 2016).

The subgenus *Dendrolasius*, to which this species belongs, has an Amhipaleartic range, whereas *L. fuliginosus* itself is distributed across the western and central part of this range (Radchenko, 2005). In Europe, it extends to latitudes of 64–65 °N in Scandinavia and Finland, and south to Spain. In Greece, it is only found in high-mountain forests. To the east, its distribution extends from the European part of Russia to southern part of West Siberia, northern Kazakhstan, the Caucasus and Transcaucasia (Czechowski et al., 2002; Zakharov, 2015). In Ukraine, *L. fuliginosus* is distributed throughout the entire territory, including the forest, forest-steppe and steppe zones, as well as the Crimean mountains. In the forest and forest-steppe zones it is mainly confined to broad-leaved and mixed forests, whereas in the steppe zone it occurs exclusively in intrazonal forests (e. g. floodplain and ravine forest stands). It occurs less frequently in coniferous stands, as well as in urban or forest parks (Radchenko, 2016; Stukalyuk et al., 2022a). *L. fuliginosus* is one of the dominant species of ant in forest communities (Dobrzańska, 1966; Márkó et al., 2013; Ślipiński et al., 2014; Stukalyuk, 2017). It prefers shaded, moderately humid habitats and is oligothermic with respect to the thermal regime (Seifert, 2018). *L. fuliginosus* colonies can be very large, containing hundreds of thousands to 2.5 million workers (Dobrzańska, 1966; Czechows-

ki et al., 2002; Zakharov, 2015; Radchenko, 2016; Seifert, 2018; Stukalyuk et al., 2022 b). As a territorial species, *L. fuliginosus* actively defends its foraging areas and trails. Long-term observations have shown that this species can coexist with another dominant territorial species, *Formica polyctena* Foerster, 1850, for long periods with minimal territorial overlap. However, it does significantly influence the community structure of subordinate ant species (Czechowski et al., 2013).

While most colonies are monogynous (Elst & Gadau, 2018), oligogyny and polygyny have also been suggested (Czechowski et al., 2002). *L. fuliginosus* is an active trophobiont that is closely associated with aphid colonies, and these colonies constitute a significant portion of its protein-rich diet (Depa et al., 2022; Dobrzańska, 1966; Zakharov, 2015). Foraging areas are guarded and there are permanent foraging trails leading to trees with aphids (Dobrzańska, 1966; Czechowski et al., 2002; Stukalyuk et al., 2022 b). Nests are usually located at the base of trees or in trunk cavities; they are less often found in stumps and logs, and cases of soil nests are extremely rare (Seifert, 2018). These nests are built from 'cardboard' made of shredded wood soaked in honeydew, containing species-specific fungi, and they resemble a sponge in structure (Maschwitz & Hölldobler, 1970; Vaessen et al., 2026). Part of the nest may be underground in the roots of the tree where the ants hibernate (Zakharov, 2015). Settling in buttresses facilitates access to aphid colonies on the same and neighbouring trees. *L. fuliginosus* is capable of active thermoregulation in spring, accelerating brood development (Stukalyuk et al., 2026). *L. fuliginosus* prefers to build nests in living trees.

The ecological niche of a species is traditionally considered in terms of two complementary concepts: Grinnellian (the fundamental niche, which is determined by abiotic environmental conditions and resource availability) and Eltonian (the realised niche, which takes into account trophic interactions and biotic relationships) (Grinnell, 1917; Elton, 1927; Soberón, 2007). Phytoindicator scales (Ellenberg et al., 1991; Didukh, 2011) are a widely used tool for quantitatively assessing the Grinnellian niche of animals since plant community composition and structure indirectly but reliably reflect key microclimatic, soil moisture, acidity, nitrogen content, illumination and naturalness of habitat gradients. All of these factors directly influence the choice of nest site, foraging activity and the success of colonies in ants. The system developed by Didukh (2011) is an adapted and improved version of European approaches. Based on an analysis of over 3,300 Ukrainian flora species, it takes into account not only optima, but also the full ranges of species tolerance. It also allows for synphytoindication, which is the calculation of weighted average ecological indices based on the projective cover of each species in the geobotanical description. This enables the composition and structure of plant communities to indirectly reflect the aforementioned key gradients. Unifying various scales into a single 100-point system (Goncharenko, 2017; Churilov et al., 2020; Goncharenko et al., 2022) ensures high data comparability and enables the identification of limiting factors with sufficient accuracy. The effectiveness of the phytoindication approach for studying the ant niche has been confirmed by a series of studies in Ukraine. For instance, an analysis of the ecological preferences of various Formicidae species using vegetation data from the Chernihiv region revealed notable differences in tolerance levels. *Lasius niger* (Linnaeus, 1758) and *Formica cinerea* Mayr, 1853 exhibited the greatest adapt-

ability, whereas *Formica rufa* Linnaeus, 1761 had a more restricted niche associated with stable forest environments (Stukalyuk et al., 2026). This approach has also been successfully applied to assess the niche of *Lasius niger* in Kyiv and Khmelnytskyi regions. Here, soil acidity, nitrogen content and the degree of anthropogenic transformation were found to be significant predictors of nest complex structure (Stukalyuk et al., 2024). Previously, a similar approach was applied to two species of red wood ants (*Formica rufa* and *F. polyctena* in urbanised forests in Kyiv. This study identified differences in their sensitivity to moisture and thermal conditions (Stukalyuk et al., 2024). These studies have shown that phytoindication can be used to link ant distribution and activity with vegetation gradients, which is particularly valuable in heterogeneous landscapes. Despite the significant amount of information available on the biology of *L. fuliginosus* (behaviour, colony structure, trophic relationships with aphids and temporary social parasitism) (Buschinger, 2009; Czechowski et al., 2013; Zakharov, 2015; Seifert, 2018), the quantitative analysis of its ecological niche using phytoindicators has yet to be conducted. The urbanised forests of the Kyiv region in Ukraine, such as the oak-hornbeam forest of Holosiivskyi and the floodplain forest of Zhukiv Island, are valuable models for studying the influence of anthropogenic pressure on dominant ant species in urban environments as their forest stands are typical in terms of composition and age.

This study aims to characterise the ecological niche of *Lasius fuliginosus* along phytoindication gradients, and to identify the relationships between its foraging activity and the structure of the vegetation in riparian (willow-poplar) and mesophilous (oak-hornbeam) forests in Kyiv.

We test the following hypotheses: (1) The temperature and humidity niche of *L. fuliginosus* will be the narrowest, acting as the main limiting factor in its distribution; (2) Foraging activity is higher in better-lit, moderately humid microhabitats; (3) Riparian forests support greater *L. fuliginosus* activity than mesophilous forests; and (4) Plant species richness positively affects the overall *L. fuliginosus* activity up to a certain threshold, beyond which the effect ceases. For this study, parallel geobotanical descriptions were conducted alongside a quantitative census of the foraging activity of 36 *L. fuliginosus* colonies within standard 25 × 25 m plots. This was followed by the calculation of phytoindicator values and multivariate statistical modeling, including GLM, GAM, PCA and PERMANOVA.

Material and Methods

Study Area and Sampling Design

The study was conducted in July and August 2025 in the urban forests of Kyiv, Ukraine. It included 36 colonies of *Lasius fuliginosus*, 20 of which were found in the mesophyll oak-hornbeam forest of the Holosiivskyi Forest and 16 of which were found in the floodplain forests of Zhukiv Island. The Holosiivskyi Forest's main tree species are oak (*Quercus robur* L.), maple (*Acer platanoides* L.) and hornbeam (*Carpinus betulus* L.). Oak also predominates in the floodplain forests, followed by white poplar (*Populus alba* L.) and elm (*Ulmus* sp.) less commonly. The study was conducted at the same time (10:00–13:00 Kyiv time) in clear, cloudless weather. Geobotani-

cal descriptions were also conducted when describing each *L. fuliginosus* colony. The sites were selected to cover different forest types, tree species compositions corresponding to the two forest types, and microhabitats ranging from illuminated forest edges to poorly illuminated areas deep within the forest.

Vegetation Assessment

The projective cover of trees, shrubs and herbs was recorded as a percentage of the surface area for each plot. Tree species were identified, and their abundance was estimated based on their cover. The plant species richness of each plot was calculated as the number of different species encountered during the survey. Derived indices were calculated based on the primary data: total projective cover of trees, shrubs and herbs; the number of trees on the plot; the number of tree species; and total plant species richness. Additionally, phytoindication values from the Phi database were used for soil reaction, nitrogen content, humidity and temperature regime. No direct measurements of these environmental factors were carried out; their values had already been recorded based on vegetation characteristics. Environmental parameters were calculated for each plot using the widely used phytoindication technique in botany (Ellenberg et al., 1991; Didukh & Plyuta, 1994; Didukh, 2011). Scales adapted to the flora of Ukraine were selected (Didukh, 2011). To assess the key indicators of the ecological niche of *L. fuliginosus*, the following key plant factors were used: Hd — humidity; Rc — soil acidity; Sl — total salt regime; Nt — soil nitrogen content; Lc — light availability; Nv — naturalness value; Tm — temperature value; and Kn — continentality. All scales were standardised to a single 100-point scale for ease of comparison (Goncharenko, 2017; Churilov et al., 2020; Goncharenko & Yatsenko, 2020; Goncharenko et al., 2022).

Ant Sampling and Colony Characterization

The search for *L. fuliginosus* colonies was conducted using the route method. The observer examined tree trunks within 10-metre strips, paying particular attention to old, hollow trees. Each 100-metre strip was examined, after which the next 10-metre strip was examined. The observer gradually moved further away from the forest edge.

When a *L. fuliginosus* nest was found, the number of forage trees accessed by ant trails, as well as the number of trails, was recorded. A total of 109 forage trees were found. Additionally, the number of ants moving along the trails and trunks of the forage trees per minute was counted. For each colony, this count was performed once (with three measurements taken for each foraging path within the colony) during the specified time period (10:00–13:00). Since the measurements were taken in mid- to late summer (July and August), inter-seasonal effects were excluded. The number of ants moving along the foraging trail in both directions was counted. The species of foraging tree and the total number of tree species visited in each foraging area were also recorded. The distance between the detected colonies was at least 100 metres. Based on this and the lack of road connections between adjacent nests, it was concluded that they did not represent a single colony.

Data Management

All data were stored in a Microsoft Excel file divided into the following four main sheets: – ‘Relevés’ containing vegetation descriptions with species and cover;

- ‘Ants’ containing ant counts on trees and trails and the number of trees and trails;
- ‘Phi’ containing phytoindicator values for each plot;
- ‘Layer’ containing the total cover of the herbaceous, shrub and tree layers.

Descriptive statistics were calculated for all colony parameters: minimum, 25th percentile, median, 75th percentile and maximum. These indicators were tabulated for further analysis and presentation of the results.

Derived variables (e. g. total ant abundance and plant species richness) were calculated in R and combined into a single dataset for analysis. During data cleaning, all missing values were removed and factor levels were standardised (for example, *Populus alba* and *Populus nigra* were combined into *Populus* sp.).

Statistical Analysis

Statistical data processing, modelling and visualisation were performed in R (version 4.5.2) (R Core Team, 2026). The ‘dplyr’ and ‘tidyr’ packages were used for data manipulation, and the ‘readxl’ and ‘openxlsx’ packages for data import. Graphics were generated using ‘ggplot2’ and ‘ggpubr’. Non-parametric statistical tests were conducted using the ‘rstatix’ and ‘ggsignif’ packages, while multivariate ecological analyses and non-linear modelling were performed with the ‘vegan’ and ‘mgcv’ packages.

The analysis was conducted in several progressive stages. First, descriptive statistics (minimum, maximum, median, 25(th) and 75(th) percentiles) were calculated for colony activity parameters (ant counts on trees and trails, total ant abundance) and plot structural traits (number of foraging trees and trails). Similarly, the ecological niche dimensions of *Lasius fuliginosus* were characterised by calculating the median and amplitude (minimum–maximum range) for each of the eight standardised Didukh phytoindication scales.

Secondly, the relationship between total ant abundance and vegetation structure was evaluated. As the variance-to-mean ratio indicated a highly aggregated, non-normal distribution with severe overdispersion, non-parametric approaches and advanced modelling were favoured over standard linear transformations. The effect of the number of foraging trees on total ant abundance was evaluated using an independent Wilcoxon rank-sum test (Mann–Whitney U test) with a Bonferroni adjustment for multiple pairwise comparisons. To evaluate the effect of plant species richness, two complementary approaches were utilised: (1) a categorical analysis where plant richness was divided into four categories and compared using a Wilcoxon rank-sum test with a Bonferroni correction; and (2) a continuous dynamic approach using a generalised additive model (GAM) with a quasi-Poisson error distribution and a log link function to capture nonlinear responses.

Thirdly, to evaluate the direct predictive power of macroclimatic and edaphic variables on ant foraging activity, a generalised linear model (GLM) within the quasi-Poisson family was fitted, with the Didukh environmental scales acting as predictors.

Fourthly, due to the poor predictive performance of linear modelling, the focus shifted to characterising the multivariate niche space. A principal component analy-

sis (PCA) was performed on the standardised matrix of the eight Didukh environmental scales to project and visualise the ecological niche space of *L. fuliginosus* in reduced dimensions. To strictly test for multivariate environmental niche segregation between the two macrohabitats (riparian willow-poplar forests versus mesophilous oak-hornbeam forests), a non-parametric permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances with 999 permutations was executed, complemented by non-metric multidimensional scaling (NMDS) to assess ordination stability.

Finally, the Wilcoxon rank-sum test (Mann–Whitney U test) was used to evaluate actual differences in total ant abundance between the two forest types. For all statistical tests, differences were considered significant at $p < 0.05$.

Results

Activity of *Lasius fuliginosus* in the Foraging Territory. Significant spatial heterogeneity in ant activity was observed between different colonies (see Table 1). The number of ants in trees ranged from 16 to 638 workers. Activity on trails also varied significantly (16–339).

The median abundance values in trees (145) and on trails (141) are very similar, suggesting that ants are distributed roughly equally between tree stands and trails. It can also be assumed that virtually all ants moving along ground roads ultimately reach forage trees. However, the upper quartile for trails (224.25) suggests that, in certain areas, above-ground activity may exceed that in trees. Total ant abundance varies by more than an order of magnitude (32–862), suggesting significant variability in colony size and activity levels. The median total abundance (284) suggests that most colonies are moderate in size, with very large colonies being rare. The wide interquartile range of total ant activity (221–434) suggests significant variability even among typical plots. Colony structure is flexible, with significant differences in foraging intensity and overall abundance.

The ecological niche characteristics of *L. fuliginosus* are as follows. *L. fuliginosus* is found in a moderate soil moisture range (Hd 43–54, median 48), indicating its tolerance to conditions far removed from those of extremely dry and highly waterlogged habitats (Table 2).

Of all the factors studied, temperature showed the narrowest range (Tm 56–64, median 60.5), indicating a strong preference for moderately warm microclimatic conditions. This suggests that temperature is the primary limiting factor in the distribution of *L. fuliginosus*.

Based on soil pH (Rc 53–67), *L. fuliginosus* prefers neutral and slightly acidic substrates, as highly acidic soils appear to be unfavourable. Nitrogen availability (Nt: 48–66.5) indicates a preference for habitats with a moderate trophic status; the species avoids both extremely poor and highly eutrophic soils. The light regime (Lc 39–61) reflects significant ecological flexibility: *L. fuliginosus* colonies are found in shaded areas (e. g. mesotrophic hornbeam-oak forests) and in moderately illuminated areas (e. g. riverside). The general salt regime (Sl 21–42) and continentality (Kn 35–48) fall within a relatively narrow range, whereas habitat naturalness (Nv 25–60) shows the greatest variability.

Table 1. Activity characteristics of *Lasius fuliginosus* in the foraging territory (N = 36) (number of workers per minute)

Variable	Min	P25.25.	Median.50.	P75.75.	Max
Ants on trees	16	106	145	21.5	638
Ants on trails	16	109.75	141	224.25	339
Total ant abundance	32	221	284	434	862
Number of trees	1	2	3	4	6
Number of trails	1	1	2	2.25	4

Table 2. Ranges of Didukh phytoindication scale values (min, median, max) characterising the ecological niche of *Lasius fuliginosus*

Factor_name	Factor	Min	Median	Max
Humidity	Hd	43	48	54
Soil acidity	Rc	53	57	67
Total salt regime	Sl	21	31	42
Nitrogen	Nt	48	57,5	66
Light	Lc	39	48	61
Naturalness value	Nv	25	48	60
Temperature	Tm	56	60.5	64
Continentality	Kn	35	40	48

Overall, the *L. fuliginosus* niche can be characterised as moderately broad, with clearly defined limiting factors — temperature and humidity — while edaphic parameters (e. g. acidity and nitrogen content) and illumination act as secondary gradients of habitat suitability.

Tree number and overall activity of *L. fuliginosus*. The number of foraging trees per *L. fuliginosus* colony varies greatly within each category (from one to six), indicating high heterogeneity in colony size and activity even under similar structural conditions (Fig. 1).

Pairwise Wilcoxon comparisons between plots with different numbers of trees revealed no statistically significant differences in total ant abundance; all adjusted p-values were 1.0. This suggests that increasing the number of trees per plot from 1 to 6 does not consistently impact the abundance of *L. fuliginosus* in the foraging area. Median values are comparable across almost all categories, confirming the absence of a clear monotonic relationship. Slight trends towards greater variability at intermediate tree numbers can be seen, but these are not statistically confirmed. The wide overlap of interquartile ranges between categories further indicates that the number of trees per colony alone is a weak predictor of colony size (Fig. 1).

The relationship between the total abundance of *L. fuliginosus* in a foraging area and plant species richness was evaluated using categorical and continuous approaches. When plant richness was treated as a categorical variable (see Fig. 2), a corrected pairwise Wilcoxon rank-sum test (Mann–Whitney U test) with Bonferroni adjustment revealed a statistically significant difference ($p_{(adj)} < 0.05$) exclusively between plots with low species

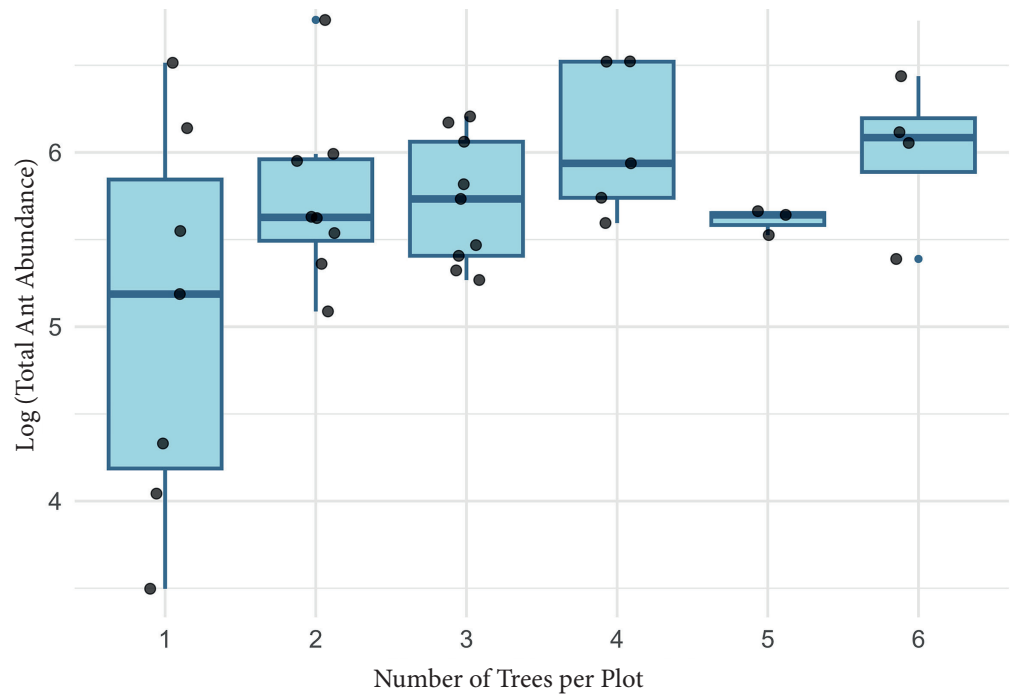


Fig. 1. Ant abundance vs. number of trees per plot

Note. Distributions present the total abundance of ants across plots. Pairwise comparisons were performed using the Wilcoxon rank-sum test (Mann–Whitney U test) with Bonferroni correction.

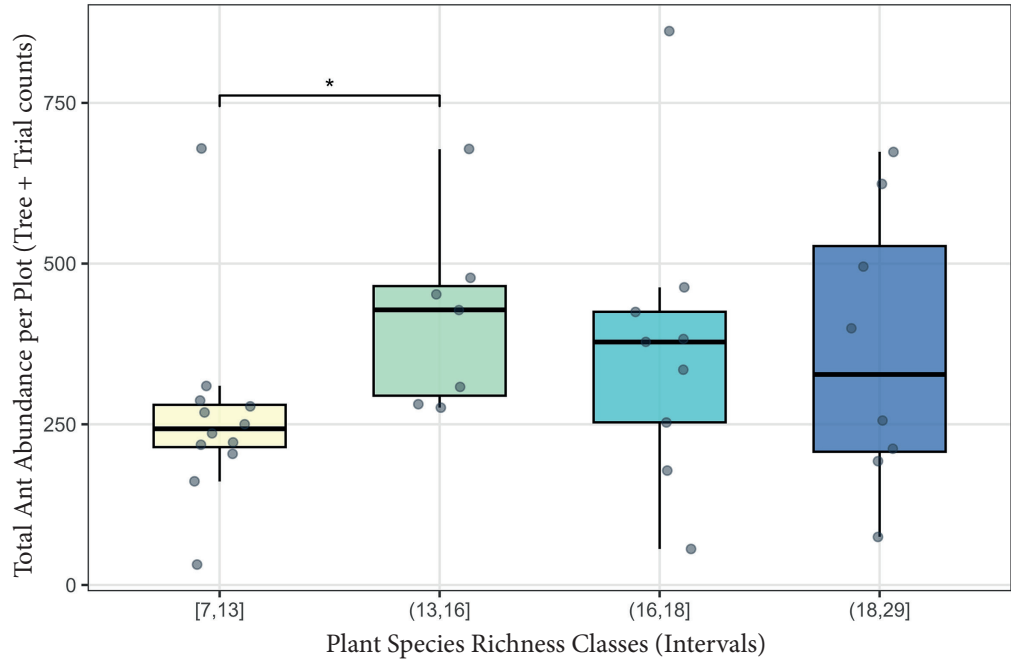


Fig. 2. Ant abundance vs. plant species richness classes per plot

Note. Boxes represent interquartile ranges of total ant abundance. Significant pairwise differences ($p_{adj} < 0.05$) evaluated by the independent Wilcoxon rank-sum test with Bonferroni correction are indicated by an asterisk (*), while non-significant comparisons are hidden.*

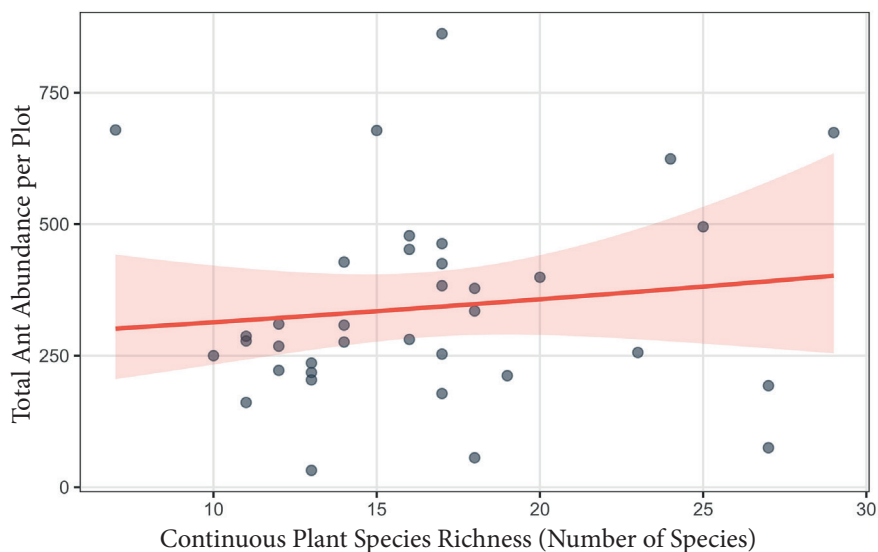


Fig. 3. Non-linear response of *Lasius fuliginosus* abundance to continuous plant species richness modeled via a Generalized Additive Model (GAM) with a quasi-Poisson error distribution. The shaded area represents the 95% confidence interval

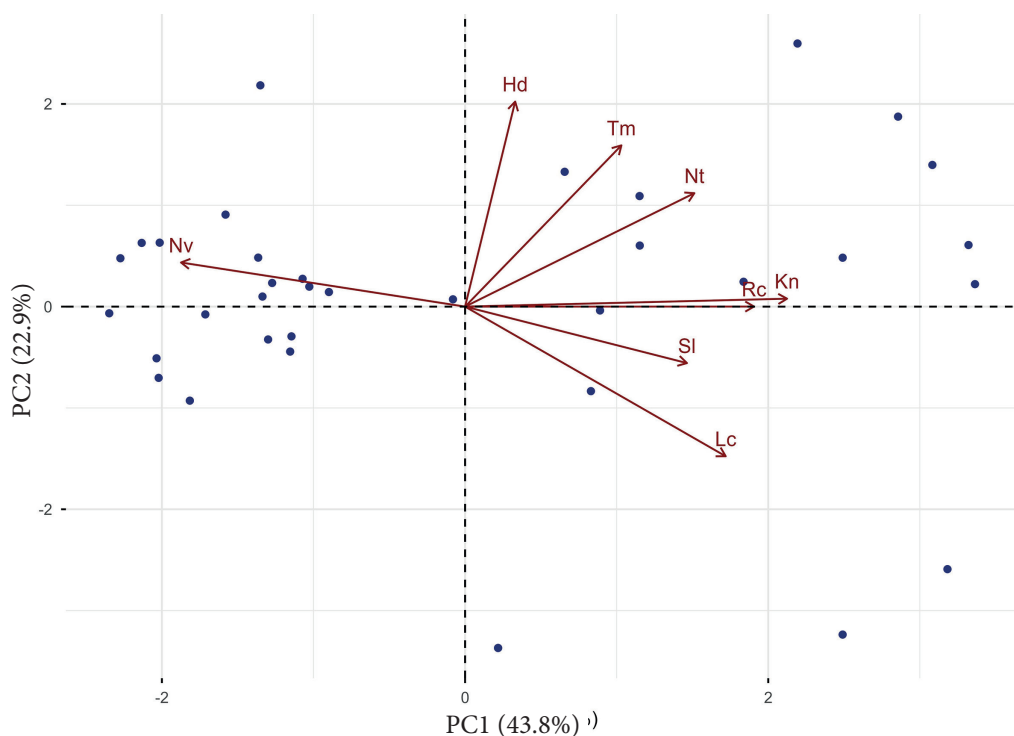


Fig. 4. PCA biplot of the ecological niche space of *Lasius fuliginosus* based on Didukh phytoindication scales. The first two dimensions explain 66.65% of the total environmental variance

richness (7–13) and those with moderately low richness (13–16), where higher ant abundance was observed.

No significant differences were detected among any other pairs of plant richness classes (see Fig. 2). To model this trend dynamically without artificial bin-

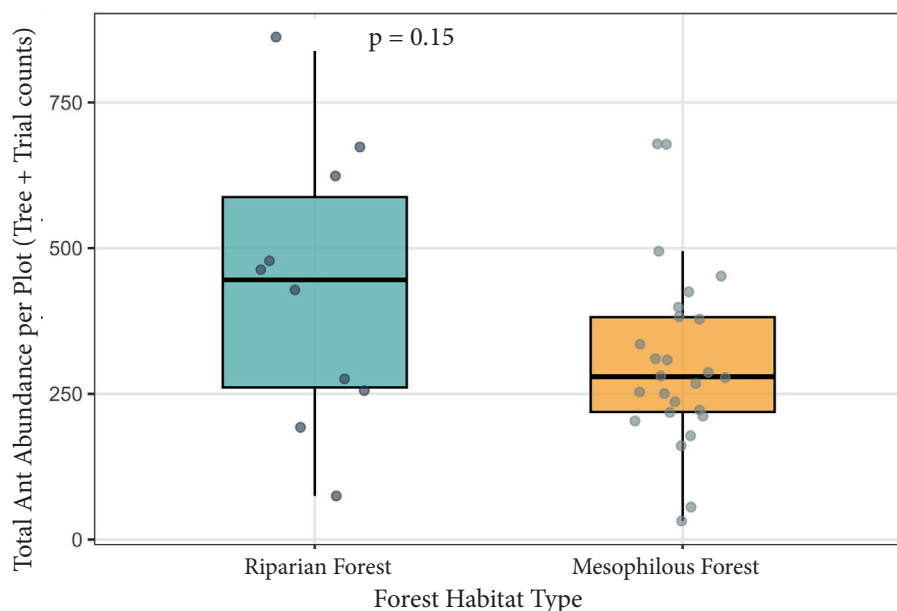


Fig. 5. *Lasius fuliginosus* foraging abundance across different forest types

Note. Medians are compared using the independent Wilcoxon rank-sum test (Mann–Whitney U test); the difference between riparian and mesophilous stands is statistically non-significant ($p = 0.1526$).

ning, a Generalised Additive Model (GAM) with a quasi-Poisson distribution was applied (Fig. 3).

The GAM trend graph confirmed that ant abundance peaks in response to moderate plant diversity and stabilises at higher richness levels.

To explore the direct predictive capacity of Didukh environmental scales on total ant abundance, a Generalised Linear Model (GLM) with a quasi-Poisson family was initially evaluated. However, the regression analysis showed that this dataset was not suitable for predictive environmental modelling: the predictors explained only 7.5% of the total deviance (Pseudo- $R^2 = 0.075$) and none of the individual factors had a statistically significant linear effect on abundance (all $p > 0.05$; e. g. Tm: $p = 0.411$; Hd: $p = 0.995$). The high dispersion parameter (106.96) reflects an aggregated, mosaic distribution of ant activity that is not linearly dependent on macroclimatic or edaphic gradients.

Consequently, rather than attempting to predict abundance via regression or machine learning models (such as Random Forest), the focus was shifted to characterising multivariate niche space. A principal component analysis (PCA) performed on the eight standardised Didukh phytoindication scales showed high efficiency: the first two principal components successfully captured 66.65% of the total environmental variance (PC1: 43.78%; PC2: 22.88%), providing a robust, low-dimensional space for ecological niche visualisation (Fig. 4).

To rigorously test whether the environmental niches of *L. fuliginosus* differ between the two forest stands, a non-parametric permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances was performed. This demonstrated a highly significant and distinct separation between the ecological niche configurations in riparian and mesophilous forests (PERMANOVA:

$F_{1,34} = 18.86$, $R^2 = 0.36$, $p = 0.001$). Forest type accounted for 35.7% of the total multivariate niche variance, a result that was further supported by stable, reliable non-metric multidimensional scaling (NMDS) ordination (stress = 0.0744).

In terms of actual foraging intensity, the median value for total ant abundance was higher in riparian forests (445.5 workers per minute) than in mesophilous forests (279.5 workers per minute). However, the corrected Wilcoxon rank-sum test confirmed that this difference was not statistically significant ($W = 171$, $p = 0.1526$; see Fig. 5).

This suggests that, although the two habitats represent distinct environmental niches for *L. fuliginosus*, the species exhibits similar levels of foraging activity in both types of forest.

Discussion

This study provides the first quantitative, phytoindication-based analysis of the ecological niche of *Lasius fuliginosus*. It addresses a common assumption about a single dominant ant species that is rarely tested directly: separating the question of where the species can live from how actively it forages once established. It transpires that these are two different stories. The niche itself, reconstructed from eight Didukh scales, is narrow and well-defined along its thermal and hydric axes. By contrast, the realised foraging activity is remarkably stable across two structurally and environmentally distinct forest types. This asymmetry is the paper's central result, and it is worth considering before examining the individual gradients.

Classical niche theory already anticipates this kind of decoupling. Soberón (2007) framed the distinction between the Grinnellian niche, which is condition-defined, and the Eltonian niche, which is shaped by biotic interactions and resource use. Our data map fairly cleanly onto this division: PCA and PERMANOVA describe the Grinnellian side, where the two forest types occupy essentially non-overlapping environmental space. By contrast, the Wilcoxon comparison of worker flow describes something closer to the Eltonian performance side of the niche, which did not differ. Similar decoupling between habitat suitability and realised interaction outcomes has also been observed in other ant assemblages shaped by competition and niche partitioning (Salas-López et al., 2022). This is consistent with the general expectation that abundance and activity are influenced by factors beyond the abiotic template.

Temperature produced the narrowest range of any of the eight examined scales (Tm 56–64, median 60.5), which is not so much an unexpected result as a well-founded confirmation of long-held assumptions about the species' autecology. *L. fuliginosus* is consistently described as a species of shaded forest and is considered to be oligothermic, in contrast to more thermally tolerant congeners such as *L. niger* (Seifert, 2018; Radchenko, 2016). Our data provide numerical support for this description. Temperature is also one of the more mechanistically important variables in ant ecology in general, since it constrains locomotor performance, the rate at which the brood develops and the daily rhythm of trail activity. Its role in shaping the functional composition of ants along climatic gradients has been demonstrated repeatedly

Table 3. Comparison of the ranges of phytoindication factors for *Lasius fuliginosus* (this study, N = 36) and other species of the genus *Lasius*, as well as *Formica rufa* (according to Stukalyuk et al., 2026)

Species	Hd, humidity	Rc, acidity	Sl, salt regime	Nt, nitrogen	Lc, light	Tm, temperature	Kn, continentality
<i>L. fuliginosus</i>	43–54	53–67	21–42	48–66	39–61	56–64	35–48
<i>L. niger</i>	37–51	49–64	31–44	33–63	60–74	44–67	39–48
<i>L. psammophilus</i>	33–44	43–55	24–36	30–51	64–70	47–61	35–43
<i>L. platythorax</i>	43–48	22–54	18–38	30–56	54–68	41–54	35–43
<i>F. rufa</i>	44–49	33–55	26–42	35–63	62–68	50–51	35–41

Note. The ranges for the compared species are calculated based on the mean ± SD from Stukalyuk et al. (2025). *L. fuliginosus* has a narrower niche for Tm and Hd than *L. niger*, but its temperature specialisation is comparable to that of *F. rufa*.

(Tiede et al., 2017; Uhey et al., 2020). This has a practical implication: because the thermal window is so narrow, it is plausible that colonies could be displaced or suppressed by canopy opening, edge formation or urban microclimatic warming, even in habitats that otherwise appear suitable. This is something that should be tested directly in future urban-gradient studies.

Soil moisture told a similar story (Hd 43–54, median 48). The species avoided both dry and waterlogged extremes, which is consistent with what is known about its nesting biology. Colonies build carton nests from shredded, honeydew-soaked wood that hosts characteristic fungal species. The physical cohesion of this material and the embedded fungal community presumably depend on a fairly narrow humidity range (Maschwitz & Hölldobler, 1970; Vaessen et al., 2026). The sensitivity of foraging behaviour to ambient humidity is not unique to this species either; direct behavioural responses to humidity have been documented in other species of ant (Gordon et al., 2013), which lends some generality to the pattern rather than treating it as an idiosyncrasy of *L. fuliginosus*. The same logic applies to thermoregulation in red wood ants, where nest microclimate control was shown to be central to colony performance (Stukalyuk et al., 2020).

When placed alongside other *Lasius* species and *Formica rufa*, the niche of *L. fuliginosus* appears to be narrower in a selective rather than uniform way (Table 3).

Its niche is distinctly tighter than that of *L. niger* in terms of both temperature and moisture. It converges with *L. platythorax* in terms of its hydric range and its thermal specialisation is similar to that of *F. rufa*. This pattern matches the broader conclusion drawn from Chernihiv-region vegetation data, namely that phytoindication scales can reliably separate habitat generalists from forest-obligate specialists among ants (Stukalyuk et al., 2026). While the edaphic axes — acidity and nitrogen — were comparatively broad, they were still informative: the observed preference for neutral to slightly acidic, moderately nutrient-rich substrates indicate mature forest stands rather than early-successional or heavily disturbed ones. This filtering effect has also been described in ant communities in response to forest management and associated changes in stand structure (Arnan et al., 2009; Grevé et al., 2018). This naturally aligns with the vegetation composition documented in Kyiv’s

urban and peri-urban forests (Goncharenko & Yatsenko, 2020). This vegetation forms the basis for the Didukh-scale synphytoindication values employed here, which trace back to Ukrainian adaptations of the Ellenberg system and ultimately to its original formulation (Didukh & Plyuta, 1994; Didukh et al., 2011).

The response to plant species richness added a further layer of nuance, rather than simply confirming the idea that ‘more diversity means more ants’. Both the categorical comparison and the generalised additive model (GAM) converged on a threshold pattern: abundance increased only between the lowest richness class and the next one up, and then levelled off. Nonlinear, saturating or hump-shaped responses of ant assemblages to habitat complexity are well documented (Graham et al., 2009; Pihlgren et al., 2010). Furthermore, an explicitly hump-shaped richness pattern has recently been demonstrated for ants along an entirely different gradient — elevation (You et al., 2025). This suggests that such saturation is not peculiar to urban Kyiv forests, but rather a more general property of how ant assemblages respond to increasing habitat complexity. The most plausible mechanistic explanation here is trophic: moderate floristic diversity likely increases the spatial availability of aphid-bearing host plants and structural heterogeneity at understorey level. However, once the threshold of complexity is met, additional plant species may not provide further honeydew-relevant resources, which is consistent with the trophobiotic dependence of the species (Depa et al., 2022).

This trophic framework also helps to explain what would otherwise be a counterintuitive negative result: the number of foraging trees per plot had essentially no effect on total abundance (all pairwise comparisons $p = 1.0$). If the quantity of trees mattered in a simple additive way, this should not have happened. However, for a species whose colonies depend on large, mature trees with hollows, stable bark and long-established aphid colonies, the number of trees is a poor proxy for the actual resource — quality substitutes for quantity. This interpretation aligns with the broader conclusion that trophobiosis can account for a significant proportion of forest ants’ energy intake, and that vegetation quality, rather than raw tree density, influences spatial patterns of foraging investment (Brewitt et al., 2015; Lubertazzi & Tschinkel, 2003).

From a methodological perspective, the difference between the GLM and the multivariate ordination is significant and merits further discussion, as it is easy to misinterpret. The GLM explained only 7.5% of the variance and identified no significant linear predictors, which could be interpreted as a failure of the phytoindication approach. It is not. When PCA and PERMANOVA were applied to the same eight variables, they cleanly separated riparian and mesophilous plots and accounted for over a third of the total multivariate variance. These two results are not contradictory; they answer different questions: one concerns the linear predictability of abundance and the other concerns multivariate niche structure. The fact that the second method succeeds where the first method fails provides insight into how the abundance of this species is organised: it is aggregated and patchy, evidently shaped by more than one linear environmental gradient. Riparian willow-poplar stands and mesophilous oak-hornbeam stands represent different environmental templates. This parallels what has been shown for ant and invertebrate assemblages along other riparian-forest structural gradients (Johnson et al., 2014; Popescu et al., 2021; Gray et al., 2015).

Nevertheless, despite this environmental difference, the intensity of foraging did not differ significantly between the two forest types. This is arguably the study's most ecologically interesting outcome, because it means that habitat segregation and performance are not on the same axis. Once a colony's basic thermal and hydric requirements are met, it appears capable of sustaining comparable levels of activity in either setting — a form of plasticity layered on top of otherwise narrow tolerances. A conceptually similar phenomenon has been observed in ant assemblages persisting across structurally heterogeneous patches of boreal forest, where the continuity of key structural resources was more important than the uniformity of the habitat itself (Punttila, 2020). While our system is not successional in the same sense, the underlying logic — that structural and trophic continuity, rather than homogeneity, sustains performance — remains relevant.

Some of this resilience may also stem from aspects of the species' life history that are easily overlooked when the focus is solely on foraging counts. *L. fuliginosus* colonies are established through temporary social parasitism following a nuptial flight in the nests of host species within the subgenus *Chthonolasius* (Buschinger, 2009; Stukalyuk et al., 2022 c). Mixed colonies involving hosts such as *L. umbratus* can persist for extended periods before or instead of full replacement (Stukalyuk et al., 2021). This founding pathway is inherently patchy and historically contingent — a colony's presence in a given tree may be as much due to a queen successfully parasitising a host nest years earlier as to that tree's current microclimate suitability. This historical footprint could contribute to the high dispersion parameter recovered in the GLM and serves as a reminder that not all of the 'unexplained' variance in abundance is environmental noise, some of which may represent legitimate biological history that cannot be captured by a cross-sectional design.

Taking a broader view, these results reinforce the reasons why ants are considered such useful bioindicators — not just because they respond to disturbance, but also because their distribution reflects microclimate, vegetation structure, and habitat continuity over time in a way that few taxa with a faster turnover rate can (Andersen, 1997; Tiede et al., 2017; Lawes et al., 2017). This role has specifically been documented for riparian and forest ant assemblages elsewhere (Ives et al., 2011; Zina et al., 2021; Subedi et al., 2021). In this light, *L. fuliginosus* appears less like a generalist that merely tolerates a wide range of forests and more like a specialist with a narrow thermal and hydric envelope. Once inside this envelope, the species exhibits considerable flexibility in its foraging behaviour. This combination of tight environmental tolerance and plastic behavioural performance may be precisely what enables the species to remain dominant and territorially aggressive in suitable forest patches, yet be effectively absent from open, dry or heavily transformed urban habitats.

Study limitations

These conclusions should be tempered by a few methodological constraints. Foraging intensity was measured as worker flow per minute rather than direct colony size or biomass, meaning it remains an indirect indicator of overall colony performance. As fieldwork was restricted to a single season (July–August 2025), seasonal and in-

terannual variation in the thermal regime, moisture, and trophobiont availability could not be captured. Some colonies were located close enough to one another that spatial autocorrelation and pseudoreplication cannot be entirely excluded. Phytoindication scales reflect environmental conditions indirectly through vegetation composition rather than continuous physical measurement. This indirectness is arguably a strength as it integrates conditions over a longer time period than a single sensor reading. Finally, temporal variation in colony social structure and worker reproduction, as documented for this species by Elst and Gadau (2018), was not accounted for here. This variation could modulate the observed abundance patterns and seems a natural direction for follow-up work, ideally combined with multi-season sampling.

This study provides the first multivariate, phytoindication-based characterisation of the ecological niche of *L. fuliginosus* in urban forests in Kyiv city. It confirms temperature and moisture as the principal limiting factors of this niche and demonstrates a non-linear, saturating response to plant species richness. Furthermore, it shows that riparian and mesophilous forests constitute genuinely distinct environmental niche spaces for the species, despite there being no difference in realised foraging activity. Overall, the results imply that niche breadth and behavioural performance should be considered distinct properties of a species' ecology, a distinction that could be valuable in many other contexts.

Conclusions

This study provides the first quantitative characterisation of the ecological niche of *Lasius fuliginosus* using multivariate phytoindication gradients. The microclimatic parameters that act as the primary environmental constraints were clearly identified: the species exhibits a specialised and narrow temperature range (T_m : 56–64 points, median: 60.5) and a well-defined soil moisture range (H_d : 43–54 points, median: 48). This allows it to successfully avoid both extreme xerophytic and waterlogged habitats.

Multivariate niche space analysis (PCA and PERMANOVA) revealed significant environmental segregation between the two macrohabitats ($F_{1,34} = 18.86$, $R^2 = 0.36$, $p = 0.001$). Riparian (willow-poplar) and mesophilous (oak-hornbeam) forests represent two distinct ecological spaces for *L. fuliginosus*. However, the species exhibits high ecological plasticity, maintaining equivalent levels of actual foraging activity across both forest types ($W = 171$, $p = 0.1526$). Nevertheless, riparian zones demonstrate higher median abundance (445.5 workers/min) and greater spatial variability than mesophilous stands (279.5 workers/min).

The structural characteristics of the vegetation influence ant foraging intensity non-linearly. The number of trees per plot (1–6) is a weak, statistically insignificant predictor of abundance ($p = 1.0$), confirming that microhabitat quality and aphid availability are more important than mere tree density. Conversely, plant species richness exhibits a distinct, hump-shaped threshold pattern modelled via a generalised additive model (GAM), whereby a significant increase in foraging activity occurs exclusively when moving from low (7–13 species) to moderately low (13–16 species) richness, after which resource saturation occurs.

These insights have direct practical applications for the management of forests and the conservation of biodiversity in the urban and suburban landscapes of the Kyiv region (e. g. the Hosiivskyi National Nature Park and Zhukiv Island). *L. fuliginosus* can be used effectively as a bioindicator in stable, moderately warm and humid forest zones under anthropogenic pressure. In order to maintain stable populations of this dominant keystone species, conservation strategies must prioritise the preservation of ancient, hollow-bearing oaks and the maintenance of structural edge mosaics within riparian ecotones. Future research should focus on multi-year longitudinal monitoring and molecular-genetic colony mapping to eliminate pseudoreplication, as well as the direct quantification of aphid colony dynamics across regional GIS climatic scales.

Acknowledgements and declaration of individual contributions. The research leading to this publication has received funding from “Funding the development of priority research fields of the Ukraine” allowance number KPKVK 6541230.

REFERENCES

- Andersen, A. N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology*, **1** (1).
- Arnan, X., Gracia, M., Comas, L. & Retana, J. 2009. Forest management conditioning ground ant community structure and composition in temperate conifer forests in the Pyrenees Mountains. *Forest Ecology and Management*, **258** (2), 51–59.
- Brewitt, K., Pinol, J., Werner, C., Beyschlag, W., Espadaler, X., Pérez Hidalgo, N. & Platner, C. 2015. Evaluating the importance of trophobiosis in a Mediterranean ant community: a stable isotope analysis. *Insectes Sociaux*, **62** (1), 81–95.
- Buschinger, A. 2009. Social parasitism among ants: a review (Hymenoptera: Formicidae). *Myrmecological News*, **12**, 219–235.
- 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**, 191–208.
- Czechowski, W., Radchenko, A. & Czechowska, W. 2002. *The Ants (Hymenoptera, Formicidae) of Poland*. Museum and Institute of Zoology, Warszawa, 1–200.
- Czechowski, W., Marko, B., Radchenko, A. & Slipinski, P. 2013. Long-term partitioning of space between two territorial species of ants (Hymenoptera: Formicidae) and their effect on subordinate species. *European Journal of Entomology*, **110** (2), 327–337.
- De Almeida, T., Blight, O., Mesléard, F., Bulot, A., Provost, E. & Dutoit, T. 2020. Harvester ants as ecological engineers for Mediterranean grassland restoration: Impacts on soil and vegetation. *Biological Conservation*, **245**, 108547.
- Depa, Ł., Vepsäläinen, K., Rutkowski, T. & Czechowski, W. 2022. Mutualism between *Lasius* ant species and *Stomaphis* aphids in relation to social parasitism among the ants. *Polish Journal of Ecology*, **70** (1), 44–55.
- Didukh, Y. P., Fitsailo, T. V., Korotchenko, I. A., Iakushenko, D. M. & Pashkevych, N. A. 2011. *Biotopes of Forest and Forest-Steppe Zones of Ukraine*. LLC MACROS, Kyiv, 1–288 [In Ukrainian].
- Didukh, Ya. P., & Plyuta, P. G. 1994. *Phytoindication of Ecosystems*. Kyiv, Naukova Dumka [In Ukrainian].
- Dobrzańska, J. 1966. The control of the territory by *Lasius fuliginosus* Latr. *Acta Biologiae Experimentalis*, **26** (2), 193–213.

- Ellenberg, H., Weber, H. E., Dull, R., Wirth, V., Werner, W. & Paulisen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica, Verlag Erich Goltze KG, Göttingen, 1–248.
- Elst, T. V. & Gadau, J. 2018. Temporal variation in social structure and worker reproduction in the temporary social parasite *Lasius fuliginosus* (Hymenoptera: Formicidae). *Myrmecological News*, 27, 75–85.
- Elton, C. 1927. *Animal Ecology*. London: Sidgwick & Jackson.
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity & Conservation*, 7 (9), 1221–1244.
- Goncharenko, I. V. 2017. *Phytoindication of Antropogenic Impact*. Dnipro, 1–127 [In Ukrainian].
- Goncharenko, I. V. & Yatsenko, H. M. 2020. Phytosociological study of the forest vegetation of Kyiv urban area (Ukraine). *Hacquetia*, 19 (1), 99–126.
- Goncharenko, I. V., Solomakha, I. V., Shevchyk, V. L., Dvirna, T. S., Tymochko, I. Y. & Solomakha, V. A. 2022. A phytoindication assessment of the vegetation of afforestation belts in the Middle Dnipro Region, Ukraine. *Environmental & Socio-economic Studies*, 10, 30–39. <https://doi.org/10.2478/environ-2022-0009>
- Gordon, D. M., Dektar, K. N. & Pinter-Wollman, N. 2013. Harvester ant colony variation in foraging activity and response to humidity. *PloS One*, 8 (5), e63363.
- Graham, J. H., Krzysik, A. J., Kovacic, D. A., Duda, J. J., Freeman, D. C., Emlen, J. M. & Balbach, H. E. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. *Ecological Indicators*, 9 (5), 866–877.
- Gray, C. L., Lewis, O. T., Chung, A. Y. & Fayle, T. M. 2015. Riparian reserves within oil palm plantations conserve logged forest leaf litter ant communities and maintain associated scavenging rates. *Journal of Applied Ecology*, 52 (1), 31–40.
- Grevé, M. E., Hager, J., Weisser, W. W., Schall, P., Gossner, M. M. & Feldhaar, H. 2018. Effect of forest management on temperate ant communities. *Ecosphere*, 9 (6), e02303.
- Grinnell, J. 1917. The niche-relationships of the California Thrasher. *The Auk*, 34 (4), 427–433.
- Ives, C. D., Hose, G. C., Nipperess, D. A. & Taylor, M. P. 2011. Environmental and landscape factors influencing ant and plant diversity in suburban riparian corridors. *Landscape and Urban Planning*, 103 (3–4), 372–382.
- Johnson, J. T., Adkins, J. K. & Rieske, L. K. 2014. Canopy vegetation influences ant (Hymenoptera: Formicidae) communities in headwater stream riparian zones of central Appalachia. *Journal of Insect Science*, 14 (1), 237.
- Lawes, M. J., Moore, A. M., Andersen, A. N., Preece, N. D. & Franklin, D. C. 2017. Ants as ecological indicators of rainforest restoration: Community convergence and the development of an Ant Forest Indicator Index in the Australian wet tropics. *Ecology and Evolution*, 7 (20), 8442–8455.
- Lubertazzi, D. & Tschinkel, W. 2003. Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. *Journal of Insect Science*, 3 (1), 21.
- Markó, B., Czechowski, W. & Radchenko, A. 2013. Combining competition with predation: drastic effect of *Lasius fuliginosus* (Latr.) on subordinate ant species at the northern limit of its distribution. *Annales Zoologici*, 63 (1), 107–111.
- Maschwitz, U. & Hölldobler, B. 1970. Carton-nest construction by *Lasius fuliginosus* Latr. (Hym. Formicidae). *Zeitschrift für vergleichende Physiologie*, 66 (2), 176–189. <http://doi.org/10.1007/bf00297777>
- Pihlgren, A., Lenoir, L. & Dahms, H. 2010. Ant and plant species richness in relation to grazing, fertilisation and topography. *Journal for Nature Conservation*, 18 (2), 118–125.
- Popescu, C., Oprina-Pavelescu, M., Dinu, V., Cazacu, C., Burdon, F. J., Forio, M. A. E. & Rîsnoveanu, G. 2021. Riparian vegetation structure influences terrestrial invertebrate communities in an agricultural landscape. *Water*, 13 (2), 188.
- Punntila, P. 2020. *Ant Community Structure in Successional Mosaics of Boreal Forests*. University of Helsinki, Helsinki.

- R Core Team. 2026. R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Radchenko, A. 2005. A review of the ants of the genus *Lasius* Fabricius, 1804, subgenus *Dendrolasius* Ruzsky, 1912 (Hymenoptera: Formicidae) from East Palaearctic. *Annales Zoologici* (Warsaw), **55** (1), 83–94.
- Radchenko, A. G. 2016. *Ants (Hymenoptera, Formicidae) of Ukraine*. Institute of Zoology, Kyiv, 1–495 [In Russian].
- Rocha, F. P., Bogar, T. A., Weemaels, A. I., Hu, J., Liang, M., Park, C. & Guénard, B. 2024. Two sides of the same coin? Ants are ecosystem engineers and providers of ecosystem services. *Myrmecological News*.
- Salas-López, A., Violle, C., Munoz, F., Menzel, F. & Orivel, J. 2022. Effects of habitat and competition on niche partitioning and community structure in neotropical ants. *Frontiers in Ecology and Evolution*, **10**, 863080.
- Sanders, D. & van Veen, F. F. 2011. Ecosystem engineering and predation: The multi-trophic impact of two ant species. *Journal of Animal Ecology*, **80** (3), 569–576.
- Seifert, B. 2018. *Ants of Northern and Central Europe*. Lutra Verlags-und Vertriebsgesellschaft, Tauer, 1–408.
- Ślipiński, P., Marko, B., Rzeszowski, K., Babik, H. & Czechowski, W. 2014. *Lasius fuliginosus* (Hymenoptera: Formicidae) shapes local ant assemblages. *North-Western Journal of Zoology*, **10** (2).
- Soberón, J. 2007. Grinnellian and Eltonian niches and species distribution modeling. *Ecological Informatics*, **2** (2), 111–123.
- Stukalyuk, S. V. 2017. Interactions of three dominant ant species, *Lasius emarginatus* (Ol.), *Formica rufa* L., and *Lasius fuliginosus* (Latr.) (Hymenoptera, Formicidae) among themselves and with subordinate species in broadleaf forests. Communication 1. *Entomological Review*, **97**, 747–767.
- Stukalyuk, S., Radchenko, Y., Netsvetov, M. & Gilev, A. 2020. Effect of mound size on intranest thermoregulation in the red wood ants *Formica rufa* and *F. polycetena* (Hymenoptera, Formicidae). *Turkish Journal of Zoology*, **44** (3), 266–280.
- Stukalyuk, S., Radchenko, Y., Gonchar, O., Akhmedov, A., Stelia, V., Reshetov, A. & Shymanskyi, A. 2021. Mixed colonies of *Lasius umbratus* and *Lasius fuliginosus* (Hymenoptera, Formicidae): when superparasitism may potentially develop into coexistence: a case study in Ukraine and Moldova. *Halteres*, **12**, 1–15.
- Stukalyuk, S., Akhmedov, A., Gilev, A., Reshetov, A., Radchenko, Y. & Kosiuk, N. 2022 a. Effect of urban habitats on colony size of ants (Hymenoptera, Formicidae) In memory of Professor A. A. Zakharov (Russian Academy of Sciences, Moscow). *Turkish Journal of Zoology*, **46** (2), 194–206.
- Stukalyuk, S., Akhmedov, A. & Kosiuk, N. 2022 b. Trail activity of ants (Hymenoptera, Formicidae) at different habitat structure. *Serangga*, **27** (3), 143–161.
- Stukalyuk, S., Akhmedov, A., Stelia, V., Shymanskyi, A. & Netsvetov, M. 2022 c. Nuptial flight in ants (Hymenoptera: Formicidae). *Serangga*, **27** (1), 152–179.
- Stukalyuk, S., Kozyr, M. & Goncharenko, I. 2024. Habitat analysis of *Formica rufa* and *Formica polycetena* (Hymenoptera: Formicidae) preferences in Kyiv City, Ukraine according to vegetation. *Serangga*, **29** (1), 29–48.
- Stukalyuk, S., Goncharenko, I., Zhyhalenko, O., & Kozyr, M. 2026. Characteristics of ecological preferences of ants (Hymenoptera, Formicidae) based on vegetation data. *Zoodiversity*, **60** (1), 16–39.
- Subedi, I. P., Budha, P. B., Kunwar, R. M., Charmakar, S., Ulak, S., Pradhan, D. K. & Animon, I. 2021. Diversity and distribution of forest ants (Hymenoptera: Formicidae) in Nepal: Implications for sustainable forest management. *Insects*, **12** (12), 1128.
- Tiede, Y., Schlautmann, J., Donoso, D. A., Wallis, C. I., Bendix, J., Brandl, R. & Farwig, N. 2017. Ants as indicators of environmental change and ecosystem processes. *Ecological Indicators*, **83**, 527–537.

- Uhey, D. A., Hofstetter, R. W., Remke, M., Vissa, S. & Haubensak, K. A. 2020. Climate and vegetation structure shape ant communities along elevational gradients on the Colorado Plateau. *Ecology and Evolution*, **10** (15), 8313–8322.
- Uno, S., Cotton, J. & Philpott, S. M. 2010. Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosystems*, **13** (4), 425–441.
- Vaessen, L., Russ, K., Kirchmair, M., Neuhauser, S., Schlick-Steiner, B. C. & Steiner, F. M. 2026. How carton-nest fungi of the ant *Lasius fuliginosus* interact with each other and with the root-rot fungus *Armillaria mellea*. *Mycologia*, 118(1), 1–9. <https://doi.org/10.1080/00275514.2025.2568230>
- You, S. J., Xu, Z. H. & Zhang, X. M. 2025. Testing a Hump-Shaped Pattern with Increasing Elevation for Ant Species Richness in Daliang Mountain, Sichuan, China. *Diversity*, **17** (5), 308.
- Zakharov, A. A. 2015. *Ants of Forest Communities, Their Life Cycle and Role in Forests*. KMK Scientific Press, Moscow, 1–404 [In Russian].
- Zina, V., Ordeix, M., Franco, J. C., Ferreira, M. T. & Fernandes, M. R. 2021. Ants as bioindicators of riparian ecological health in Catalanian rivers. *Forests*, **12**, 625.

Received April 26 2026

Accepted 28 October 2026