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CHARACTERISTICS OF ECOLOGICAL PREFERENCES OF ANTS (HYMENOPTERA, FORMICIDAE) BASED ON VEGETATION DATA

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Characteristics of ecological preferences of ants (Hymenoptera, Formicidae) based on vegetation data. Stukalyuk, S., Goncharenko, I., Zhyhalenko, O. & Kozyr, M. — This study aimed to identify ecological niches of ant species based on vegetation analysis and to assess their adaptation to environmental conditions using phytoindicative methods. Fieldwork was carried out in 2021 in Chernihiv Oblast, Ukraine, across a range of habitats from natural forests and meadows to agrocenoses and disturbed environments. The analysis revealed marked differences in the ecological preferences and amplitudes of ant species. *Lasius niger* and *Formica cinerea* demonstrated the broadest ecological tolerance, particularly to habitat naturalness, humidity, temperature, and soil parameters, indicating high ecological plasticity and adaptability to both natural and anthropogenic environments. In contrast, *Formica rufa* exhibited a narrower niche, associated mainly with forested habitats and more stable microclimatic conditions. Species such as *Myrmica rubra*, *Tetramorium caespitum*, and *Formica fusca* showed moderate plasticity, with varying responses to nitrogen, salinity, and soil acidity. Some species, including *Formica exsecta* and *Leptothorax muscorum*, appeared highly specialized, although limited records constrained interpretation. Phytoindication proved effective for assessing the ecological niches of ants by linking their distribution to vegetation-based environmental gradients. This approach allowed the identification of species with broad versus narrow environmental tolerances and provided insights into their adaptive strategies in heterogeneous landscapes. The findings enhance our understanding of how ant communities respond to environmental variability and demonstrate the value of phytoindication for ecological studies and biodiversity monitoring in changing ecosystems.

Key words: ants, ecological niches, phytoindication, vegetation, biotopes, adaptation.

Introduction

Ants (Hymenoptera, Formicidae) are among the most ecologically successful invertebrates, having colonised nearly all terrestrial habitats except high mountain glaciers and Antarctica (Hölldobler & Wilson, 1990). Their evolutionary success is largely attributed to ecological versatility and complex behavioural strategies that enable adaptation to both abiotic and biotic factors (Parr & Bishop, 2022). Vegetation plays a key role in shaping ant communities, influencing microclimatic conditions, nesting availability, and access to food resources (Beattie & Hughes, 2002; Zakharov, 2015). Plants serve both as habitat and trophic base, e. g., *Messor* Forel, 1890 and *Pheidole* Westwood, 1839 harvest seeds (Garrido et al., 2002; Kovář et al., 2013), while *Atta* Fabricius, 1804 and *Acromyrmex* Mayr, 1865 cultivate fungi on plant matter (Dejean et al., 2023). Myrmecochory, the dispersal of seeds by ants like *Formica polyctena* Forster, 1850, also highlights plant–ant interactions (Wolff & Debussche, 1999; Gorb & Gorb, 2003).

Vegetation structure determines habitat suitability for different ecological groups of ants (Radchenko et al., 2019), as open habitats offer higher insolation and lower humidity than forests (Hermy, 2010). Arboreal ant species such as *Camponotus vagus* (Scopoli, 1763), *Liometopum microcephalum* (Panzer, 1798), *Lasius fuliginosus* (Latreille, 1798), and *Crematogaster schmidti* Mayr, 1853 often depend on tree hollows or decaying wood (Seifert, 2018; Radchenko, 2016). Plant diversity also shapes the abundance and activity of ants through nectar, honeydew, and prey availability (Offenberg, 2001; Andrade et al., 2007).

Shifts in plant communities through succession or disturbance influence ant composition and adaptive strategies (White & Jentsch, 2004; Cross et al., 2016; Stukalyuk et al. 2020). Early successional habitats are typically colonised by *Lasius niger* (Linnaeus, 1758), *Myrmica rubra* Linnaeus, 1758, and *Tetramorium caespitum* (Linnaeus, 1758) (Demchenko, 1979). However, mature forests host species like *Formica cinerea* Mayr, 1853 and *F. exsecta* Nylander, 1846 (Demchenko, 1976; Martins et al., 2022). Ant diversity and nesting dynamics are also linked to vegetation continuity and patch complexity (Gove et al., 2009; Tavella et al., 2018).

Despite many ecological classifications (e. g., Arnoldi, 1968), specific, quantitative assessments of ants' ecological amplitudes remain scarce. Previous studies focused on only a few species (*Lasius niger*, *Formica rufa* Linnaeus, 1761, *F. polyctena*), often without integrating vegetation-based environmental gradients (Stukalyuk et al., 2023 a, b; Stukalyuk, 2025).

This study integrates myrmecology and geobotany to assess ant species' ecological preferences using phytoindicative data derived from vegetation analysis. The main aim is to evaluate how environmental factors influence ant species distribution and to quantify their adaptive potential.

Research objectives: a) to analyse the completed geobotanical descriptions; b) similarly, to analyse the ant communities in relation to the geobotanical descriptions; c) to study the parameters of ecological amplitudes for the studied ant species and to analyse the breadth of the adaptive potential of these species.

Material and Methods

Sampling

The work was carried out in 2021 (July) in Chernihiv Oblast, Ukraine. Plant and ant communities were analysed on a total of 6 sites (Fig. 1).

The study was conducted in the vicinity of the following villages: Buda and Morivsk (Chernihiv District), Krupychpole (Pryluky District), Otrohi (Kozelets District), Dziubivka and Haenky (Ichnia District). The types of biotopes and the distribution of ant species by location are presented in Tables 1 and 2 (see Results section).

11 ant species and 234 plant species were found in 12 biotopes. In total, 176 plots were studied, taking into account parameters of ants (number of species and dynamic density of ants on plots) and plants (species, projective cover).

Myrmecological methods

Each transect was conducted as a transect with 5 m spacings between the survey plots, 0 m through 50 m. A total of 14 transects were laid out in the surveyed locations. Distribution of transects by location: 3 in Haenky village (55 plots), 4 in Dziubivka (44 plots), 1 in Krupychpole (11 plots), 1 in Buda (11 plots), 2 in Morivsk (22 plots), 3 in Otrohi (33 plots). For this, a 50 m long tape with 1 m marks was used. A beacon (a peg with the transect number and distance) was installed at a distance of 5 m in each transect. For 5 minutes, all ants located inside the 0.5 m by 0.5 m plots (0.250 m^2, visual counts) were counted. The methodology is described in detail in (Czechowski et al., 2013; Stukalyuk & Akhmedov, 2022). A total of 176 plots were surveyed. Quantitative (number of individuals) and qualitative (species) data were identified. Surveys were conducted in the morning hours (9:00–12:00 local Kyiv time).

The ant species were verified using identification tags (Radchenko, 2016; Seifert, 2018), and plants were verified using Mosyakin & Fedoronchuk (1999).

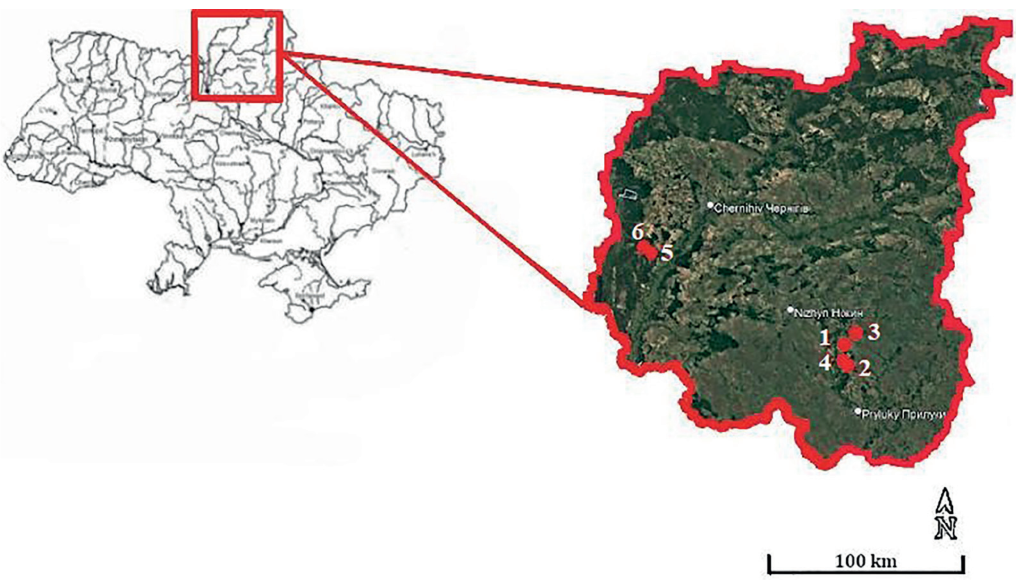

Fig. 1. The studied area in Chernihiv Oblast, Ukraine. The numbers indicate the number of plots studied at each location

Geobotanical methods

Geobotanical descriptions were carried out on the same plots where ant activity was recorded, following standard vegetation sampling methods (Mueller-Dombois & Ellenberg, 2002; Didukh et al., 2011; Goncharenko & Didukh, 2003). Plant species composition, layer structure, and cover were documented for each plot. The size of the geobotanical sample plots was 25 m^2 for herbaceous phytocenoses and between 100 m^2 to 625 m^2 for woody phytocenoses. Each geobotanical plot was arranged so that there was a sample plot in the centre, where ants were counted. We made a total of 176 geobotanical descriptions. The complete species composition of the plants and the layer structure were recorded. The projective species cover was estimated using the Braun-Blanquet scale (Braun-Blanquet, 1964).

To assess environmental conditions, we applied a phytoindication approach, which infers abiotic site parameters from the composition of plant communities. This method is well established in ecological research and widely applied across Europe (Ramensky, 1938; Ellenberg et al., 1991; Didukh, 2012). We used ecological indicator scales adapted for the flora of Ukraine (Didukh & Plyuta, 1994; Didukh, 2011), as species' environmental responses vary across biogeographic regions (Mueller-Dombois & Ellenberg, 2002; Yorkina et al., 2022).

Since different authors' scales use different scoring systems (e. g., 9-point, 120-point), we standardised all values to a unified 100-point scale for comparability (Goncharenko, 2017; Churilov et al., 2020; Goncharenko et al., 2022). In this scale, 0 points indicate the absence of a given factor, and 100 points indicate its maximum ecological presence.

The following environmental parameters were used: Hd — humidity, Rc — soil acidity (pH), Sl — total soil salinity, Nt — soil nitrogen content, Lc — light availability, Nv — degree of habitat naturalness, Tm — thermal regime (temperature), Kn — continentality of climate.

For each ant species, we calculated the mean and standard deviation of indicator values at all sites where it was found. The mean reflects the ecological optimum, while the standard deviation indicates the amplitude of ecological tolerance. This allowed for comparative evaluation of species' adaptive capacities under different environmental conditions.

Statistical analysis

The data obtained (the number of plant and ant species, the number of ants and the projected plant cover) was analysed using Past 4.13. The significance of differences in the dynamic density of a given ant species across different biotopes was assessed using the Kruskal–Wallis test, followed by Dunn's post hoc test with Bonferroni correction.

For quantitative comparisons (i. e. the number of workers of a given species per sampling event in different biotopes), only the most widespread ant species were considered (those occurring in at least three sampling plots per biotope). The data was analysed using descriptive statistics (mean, error of the mean, standard deviation) and regression analysis methods. In this case, the dependent variable was the number of ants (total as the sum of all species) or the number of ant species, and the independent variables were the number of plant species and the total projective cover. No statistical calculations were performed on the results when analysing the influence of environmental factors on ant activity. The differences are significant at $p \leq 0.05$.

Results

Distribution of ant and plant species by biotope type. In total, ants were absent on 12 out of the 176 plots. A total of 1,945 workers belonging to 15 species of ants were recorded across all biotopes (Supplementary Table S1). The highest abundance was found in overgrown psammophytic meadows, with 584 workers (30% of the entire sample; see Table 1). Large numbers of ants were also found in birch forest (265 workers, 13.6%), mixed forest (225 workers, 11.6%), and agrocenosis (229 workers, 11.8%). The lowest numbers were observed in overgrown xerophytic meadows (34 workers, 1.7%), pine forest (28 workers, 1.4%), and at the ecotone (forest edge) (51 workers, 2.6%). The latter may be explained by the fact that this biotope was surveyed only once.

Regression analysis revealed a weak but statistically significant positive relationship between the total number of ants and species richness (slope = 6.70; $p < 0.0001$; $r^2 = 0.022$; $r = 0.15$), indicating that an increase in the number of workers on a plot is accompanied by only a slight increase in species diversity. This was supported by pairwise group comparisons: the mean number of workers per plot did not differ significantly between plots with one, two, or three to five species (Kruskal–Wallis test: H (chi^2) = 4.634, Hc (tie corrected) = 4.651, p = 0.09772).

The most abundant and widespread species was *Formica cinerea*, with 886 workers (45.5%), found in 9 out of 12 biotopes. It was especially numerous in overgrown psammophytic meadows (377 workers). The Kruskal–Wallis test did not detect significant variation in the dynamic density of *F. cinerea* among biotopes (H = 6.328, Hc = 6.359, p = 0.2728), possibly due to low frequency in several habitats (only 3–5 occurrences; see Tables 1, 2–4). Even between the two biotopes where *F. cinerea* was most frequent, no significant differences were found (mesophytic meadows vs. psammophytic meadows: H = 2.146, Hc = 2.157, p = 0.1419), suggesting a relatively even distribution of this species in the most favourable environments.

The second most numerous species was *F. rufa* (279 workers, 14.3%), found in forest biotopes, especially in birch and mixed forests. The mean dynamic density of *F. rufa* workers in birch forest was 1.5 times lower than in mixed forest (8.8 ± 1.8 vs. 13.8 ± 1.8 workers per sample; Kruskal–Wallis test: H = 4.097, Hc = 4.121, p = 0.04236; Dunn's post hoc test: p = 0.04236).

Lasius niger accounted for 12.4% of the total (241 workers) and was most frequent in agrocenoses, with an average of 22.0 ± 6.1 workers per sample (Kruskal–Wallis: H = 14.07, Hc = 14.38, p = 0.0007529; Dunn's post hoc test: agrocenosis vs. mesophytic meadows: p = 0.0199; agrocenosis vs. overgrown mesophytic meadows: p = 0.0005474). There was no significant difference in *L. niger* abundance between overgrown and non-overgrown mesophytic meadows (2.9 ± 0.7 vs. 6.5 ± 2.1 workers per sample; Dunn's test: p = 0.07419), although the species tended to dominate open habitats.

Formica fusca Linnaeus, 1758 and *Lasius psammophilus* Seifert, 1992 represented 4.8% and 10%, respectively, of all workers. *L. psammophilus* was mostly found in overgrown psammophytic meadows, where its average dynamic density was three times higher than in similar meadows without pine sapling overgrowth (9.8 ± 1.5 vs.

2.8 ± 0.7 workers per sample; Kruskal–Wallis: H = 5.868, Hc = 5.906, p = 0.01509; Dunn's post hoc: p = 0.01509). This suggests that semi-open biotopes (with 0.1–7% pine sapling cover) are most favourable for this species, likely due to the constant carbohydrate source provided by aphid colonies on pine trees.

F. fusca was most numerous in birch forest (3.6 ± 0.4 workers per sample), with a density twice as high as in pine forest (1.6 ± 0.4; Kruskal–Wallis: H = 5.793, Hc = 6.084, p = 0.01364; Dunn's test: p = 0.01364).

Myrmica scabrinodis was twice as abundant in mown mesophytic meadows compared to overgrown ones (7.9 ± 1.9 vs. 3.0 ± 0.5 workers per sample; Kruskal–Wallis: H = 4.028, Hc = 4.1, p = 0.04289; Dunn's test: p = 0.04289).

For other species, comparisons were not made due to their rarity in most biotopes.

The highest species richness was recorded in birch forest (8 species), followed by mesophytic meadows (both mown and overgrown), overgrown psammophytic meadows, and mixed forest (5 species each). The lowest diversity was found in overgrown xerophytic meadows and the ecotone, with only one species recorded in each. Xerophytic meadows, mown mesophytic meadows, and pine forest hosted only 2–3 species.

The distribution and frequency of ant species varied considerably across locations. The highest number of workers was recorded near Haenky village (803 workers) and Dziubivka (583), while the lowest was found in Morivsk (112) (Supplementary Table S2). The greatest species richness was observed in Haenky (11 species) and Otrohi (8), whereas only 2 species were identified in Morivsk.

F. cinerea was the most abundant and widespread species, dominating numerically in Haenky (377 workers) and Dziubivka (337), and also recorded in Buda, Otrohi, and Morivsk. *L. psammophilus* was also widely distributed, especially in Haenky (161 workers) and Otrohi. *F. rufa* and *F. fusca* showed more localized dominance: the former prevailed in Krupychpole and Haenky, while the latter was most abundant in Haenky and Otrohi.

The most balanced combination of abundance and species richness was found in Haenky, indicating high ecological saturation of this area. In contrast, locations such as Morivsk and Krupychpole were characterized by lower species diversity.

When comparing ant abundance and species richness with the number of samples per biotope type, the following patterns emerge. Overgrown psammophytic meadows (34 samples) yielded an average of 17.8 ± 2.6 workers and 1.38 ± 0.10 species per sample, whereas non-overgrown psammophytic meadows had 1.45 ± 0.20 species and 7.36 ± 2.78 workers per sample.

The birch forest (23 samples) had an average of 10.6 ± 1.6 workers per sample and showed the highest species richness — 2.05 ± 0.18 species per sample. In mixed forest (15 samples), the average was 15.0 ± 2.0 workers and 1.40 ± 0.13 species per sample, similar to birch forest in abundance but with slightly lower diversity.

The agrocenosis (sunflower field), based on 11 samples, yielded 20.8 ± 3.9 workers and 1.64 ± 0.20 species per sample, indicating high abundance but low species richness.

Overgrown mesophytic meadows (26 samples) had 5.8 ± 1.6 workers and 1.15 ± 0.07 species per sample, while non-overgrown mesophytic meadows (17 samples) showed 9.8 ± 1.3 workers and 1.47 ± 0.12 species per sample, suggesting greater diversity in open meadow habitats.

The overgrown xerophytic meadow, with only a single sample, produced 34 individuals and 1 species — likely due to high activity of a single dominant species (*F. cinerea*), perhaps because the plot was located near a nest.

The pine forest (11 samples) yielded only 2.5 ± 0.8 workers and 1.36 ± 0.20 species per sample, indicating low ant abundance and diversity.

The results of the statistical analysis are presented in Supplementary Table S3 (Dunn's post hoc test for abundance). Differences in ant abundance among biotopes were statistically significant (Kruskal–Wallis test: H (chi^2) = 53.35, Hc (tie corrected) = 53.57, p = 8,36E-09).

Similarly, statistical analysis revealed significant differences in ant species richness across different biotopes (Kruskal–Wallis test: H (chi^2) = 19.32, Hc (tie corrected) = 26.62, p = 0.000832; Dunn's post hoc test — see Supplementary Table S4).

Thus, agrocenoses and overgrown psammophytic meadows proved to be the most productive in terms of mean ant abundance per sample, while xerophytic meadows and birch forest showed the highest species richness per sample. This indicates different ecosystem roles of biotopes: some support high abundance of a few well-adapted ant species, while others maintain ant species diversity at moderate population densities.

Regression analysis showed no reliable relationship between the number of ants and the projected plant cover in the study plots (r^2 = 0.00035341; p = 0.80441), between the number of ants and the number of plant species in the study plots (r^2 = 0.0020852; p = 0.54731), or between the projected plant cover and the number of ant species (r^2 = 0.0023558; p = 0.52236). At the same time, a weakly expressed positive relationship was found between the number of plant species and the number of ant species (Fig. 2).

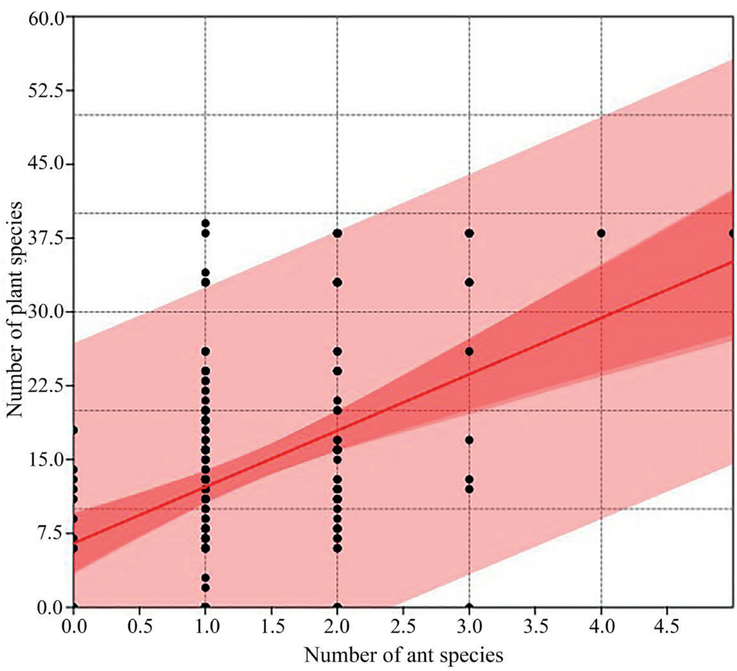

Fig. 2. Results of the regression analysis for the number of ant species and the number of plant species (r^2 = 0.15568; p = 6.01E-08)

Parameters of ecological amplitudes of the studied ant species. The final values of the magnitude of environmental factors for each of the 15 studied ant species are given in Table 1.

The following species are found in less xerophytic biotopes — *L. niger*, *F. exsecta*, *F. rufa*, *M. rubra*, *L. acervorum*, and other ant species are typical of biotopes where humidity is closer to the average. The data indicate that *L. niger* shows a relatively broad ***humidity*** amplitude (Hd: 29–61), suggesting significant ecological plasticity. *M. rubra* demonstrates a narrower but still moderate range (Hd: 46–49), indicating a preference for moderately moist environments. Among *Leptothorax* species, *L. acervorum* shows moderate ***humidity*** values and amplitude (Hd: 43–48), while *L. muscorum* displays the lowest humidity optimum (Hd: 29), indicating adaptation to drier microhabitats. The narrowest ranges are observed for *F. exsecta*, *F. cunicularia*, and

Table 1. **Magnitude of environmental factors for the studied ant species (SEM ± SD)***

Ant Species	Hd (Humidity)	Rc (Soil acidity)	Sl (Total salt regime)	Nt (Nitrogen)	Lc (Light)	Nv (Naturalness value)	Tm (Temperature)	Kn (Continentality)
Lasius niger	44.3 ± 7.0	55.7 ± 4.4	36.7 ± 4.1	47.7 ± 6.6	66.8 ± 3.7	43.4 ± 11.1	54.1 ± 5.2	43.7 ± 4.7
Lasius psammophilus	38.5 ± 5.6	49.1 ± 6.1	30.3 ± 6.0	40.1 ± 10.6	67.0 ± 3.0	44.8 ± 5.3	53.8 ± 6.9	39.0 ± 3.6
Lasius platythorax	45.4 ± 2.9	38.2 ± 16.2	27.8 ± 10.2	42.8 ± 12.8	61.0 ± 7.4	52.2 ± 10.8	47.8 ± 6.6	38.8 ± 3.7
Formica cinerea	37.9 ± 6.9	51.8 ± 7.5	33.9 ± 6.9	42.6 ± 9.3	67.4 ± 4.7	44.7 ± 9.7	54.6 ± 6.8	44.5 ± 7.1
Formica rufibarbis	35.6 ± 5.8	48.6 ± 3.2	31.8 ± 5.0	39.9 ± 7.9	67.8 ± 2.8	42.3 ± 6.6	55.4 ± 7.9	38.8 ± 4.7
Tetramorium caespitum	37.6 ± 7.0	53.7 ± 5.8	36.7 ± 6.2	45.2 ± 11.1	67.9 ± 3.7	44.8 ± 7.4	55.4 ± 4.9	44.3 ± 6.7
Formica rufa	46.4 ± 2.1	43.8 ± 11.2	34.2 ± 7.9	49.1 ± 14.1	64.7 ± 2.9	49.3 ± 9.1	50.7 ± 0.8	38.4 ± 3.3
Formica fusca	46.6 ± 3.9	47.7 ± 10.8	36.7 ± 8.1	52.8 ± 12.9	65.2 ± 4.5	46.1 ± 8.4	50.6 ± 3.5	40.6 ± 3.8
Formica cunicularia	48.5 ± 0.7	52.5 ± 0.7	41.5 ± 0.7	61.0 ± 1.4	67	40	50	41.5 ± 0.7
Myrmica rubra	47.6 ± 1.1	48.3 ± 7.0	35.6 ± 9.3	56.0 ± 8.2	64.1 ± 4.9	45.3 ± 6.7	49.7 ± 1.2	41.7 ± 0.9
Myrmica scabrinodis	49.7 ± 10.9	54.8 ± 6.1	37.2 ± 1.8	45.0 ± 7.3	64.8 ± 3.9	44.3 ± 11.5	52.3 ± 4.5	41.2 ± 5.7
Myrmica sabuleti	43.5 ± 7.8	36.0 ± 33.9	23.5 ± 14.8	32.0 ± 7.0	57.5 ± 12.0	59.5 ± 14.8	44.5 ± 12.0	42.5 ± 2.1
Leptothorax acervorum	47.0 ± 1.9	47.4 ± 9.1	35.7 ± 8.4	54.3 ± 11.2	65.0 ± 3.8	46.6 ± 6.8	50.1 ± 1.1	40.4 ± 2.5
Leptothorax muscorum	29	62	44	33	74	61	60	55
Formica exsecta	42.6 ± 0.6	53.3 ± 2.9	35.3 ± 5.1	54.3 ± 5.8	66.3 ± 3.2	42.0 ± 7.8	54.7 ± 4.2	42.3 ± 1.5

Note. 0 is the minimum value of the factor, 100 is the maximum. * Data for *Leptothorax muscorum* are based on a single phytosociological (vegetation) survey; for *Myrmica sabuleti* and *Formica cunicularia* — on two surveys; and for *F. exsecta* — on three.

F. rufa. For the first two species this can be explained by the small number of observations, whereas *F. rufa* seems to be more demanding. All other ant species have a wide range (from 10 to 50 points), reflecting their greater adaptive potential and ability to live in biotopes with different humidity regimes.

The ***soil acidity*** factor showed less significant differences among ants compared with humidity. All species, except *F. rufa*, live in biotopes where ***acidity*** conditions are close to average. *F. rufa* is more often found in biotopes with lower acidity, i.e. on alkaline soils. Among *Lasius* species, *L. niger* has a wide range of soil acidity tolerance (Rc: 49–64), indicating ecological flexibility. For *M. rubra*, the range is narrower (Rc: 38–53), which may point to moderate specialization. *L. acervorum* (Rc: 31–53) and *L. muscorum* (Rc: 62) both show slightly above-average acidity preferences, with *L. muscorum* having the highest Rc value, suggesting a stronger association with more acidic soils.

Slight differences were found between the different ant species with regard to the ***salt regime*** factor. All species prefer biotopes with low soil ***salinity*** (optimum 31–36 points). The maximum range is found in 4 species: *F. fusca*, *L. niger* (Sl: 31–44), *M. rubra* (Sl: 22–42), *F. cinerea* (Sl: 22-51) — each showing a range of about 30–31 points. The data confirm the high plasticity of *L. niger* and *M. rubra* in relation to soil salinity. *Leptothorax muscorum* exhibits the highest value among the genus (Sl: 44), while *L. acervorum* remains within the typical low-salinity range (Sl: 22–41).

Slight differences were also found in ***nitrogen content***. *F. cinerea* prefers soils with a lower-than-average nitrogen content (optimum 42 points, e.g. on sandy soils), while the other species prefer soils with an average ***nitrogen content***. The data show that *L. niger* has a broad range of nitrogen values (Nt: 33–63), while *M. rubra* prefers slightly nitrogen-richer environments (Nt: 44–62). Among *Leptothorax*, *L. muscorum* shows the lowest nitrogen value (Nt: 33), reinforcing its association with nutrient-poor habitats, in contrast to *L. acervorum* (Nt: 33–61, mean ~54), which prefers moderately nitrogen-rich soils.

No significant differences were found with respect to ***illumination***. Most ant species were recorded in biotopes with above average ***illumination*** (*L. niger*, *F. cinerea*, *F. fusca*, *F. rufibarbis*, *T. caespitum*, *F. rufa*). The maximum amplitude was recorded for 2 species (*F. fusca* — 25 points, *F. cinerea* — 20 points). Among the *Leptothorax* species, *L. acervorum* occupies slightly shaded environments (Lc: 57–67).

Differences have been found in terms of ***naturalness*** of biotopes. *F. rufa*, *L. platythorax* are found in biotopes with a low level of anthropogenic stress (values close to the average, Nv: 40–55). The remaining species are more common in biotopes with a high level of anthropogenic pressure (Nv: 19–45). The range data reveal that *L. niger* has a particularly broad tolerance to anthropogenic impact (Nv: 17–62), suggesting a high adaptability. In contrast, *L. acervorum* (Nv: 42–58) and especially *L. muscorum* (Nv: 61) show preferences for more natural or undisturbed habitats.

As far as ***temperature*** is concerned, most ant species live in similar conditions, i.e. in biotopes with an average temperature level (which corresponds to their optimum of 50 points). The optimum of 54–55 points are observed in *F. cinerea*, *T. caespitum*, *F. rufibarbis*, and to a lesser extent in *L. niger* (Mean Tm: 54.1). The maximum amplitude is found in *L. niger* and *F. cinerea* (range of 23–39 points), the minimum in *F. rufa* and *M. rubra* (3 points), indicating more specific temperature preferences.

In terms of ***continentality***, the average values for all species are below 50 points, i.e. ants in the studied areas in the optimum prefer biotopes with milder microclimatic conditions (38÷44 points). At the same time, most species have wide amplitude, 20÷31 points (with the exception of *F. rufa*, *F. rufibarbis*, 8÷15 points).

There are significant differences in the humidity factor between ***ant species***. The mean value is lowest for *F. cinerea*, *F. rufibarbis*, *T. caespitum*, i.e. the optimum for these species is in dry conditions (Figs 3, 4).

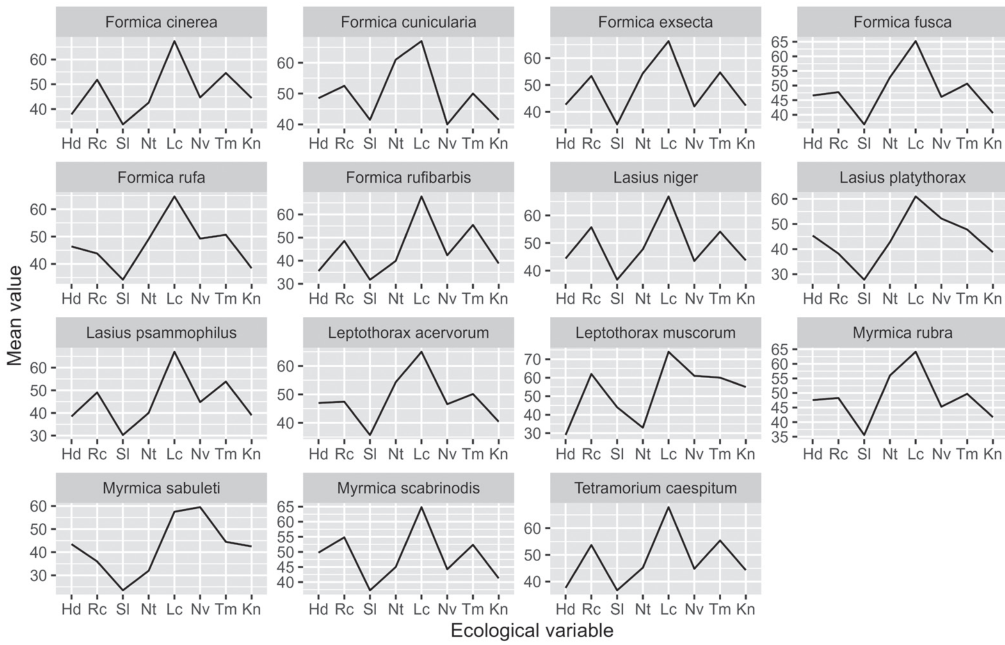

Fig. 3. Mean values (scores) of optimal habitat conditions for the studied ant species: Hd (humidity); Rc (soil acidity); Sl (total salinity); Nt (nitrogen); Lc (light); Nv (naturalness score); Tm (temperature); Kn (continentality)

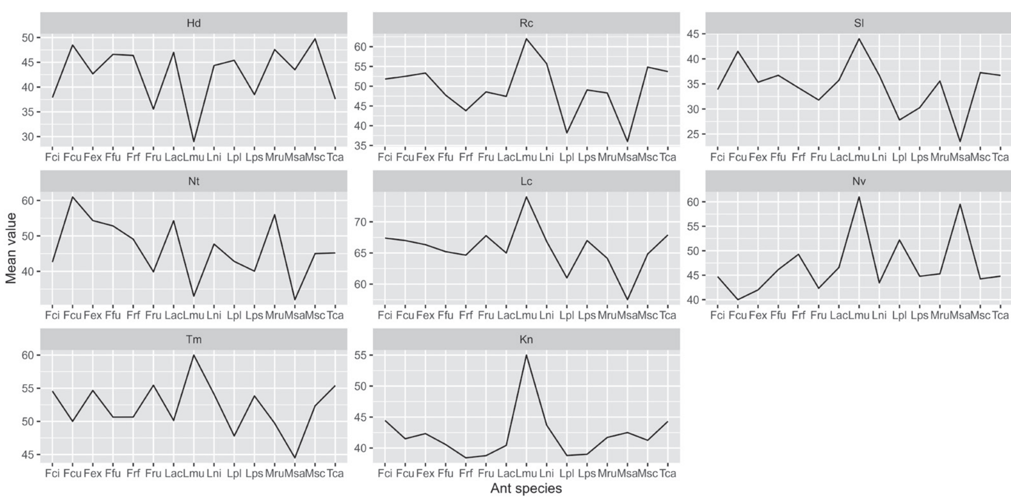

Fig. 4. Mean values of environmental factors according to ant species: *Fci — Formica cinerea; Fcu — F. cunicularia; Fex — Formica exsecta; Ffu — F. fusca: Fru — F. rufibarbis; Frf — F. rufa; Lni — Lasius niger; Lpl — L. platythorax; Lps — L. psammophilus; Lac — Leptothorax acervorum; Lmu — L. muscorum; Mru — Myrmica rubra; Msc — M. scabrinodis; Msa — M. sabuleti; Tca — Tetramorium caespitum*

F. cinerea demonstrates a broad ecological amplitude across all analyzed factors: 62 points for habitat naturalness, 39 for temperature, 37 for nitrogen content, 31 for continentality, 30 for soil acidity, 29 for salinity, 24 for moisture, and 20 for light availability. This indicates high ecological plasticity and the ability to inhabit a wide range of environments, including disturbed and urbanised areas. However, the lowest amplitude is observed for light and moisture, suggesting a relatively narrower specialization in these factors.

F. rufibarbis exhibits narrower ecological ranges compared to *L. niger* and *F. cinerea*, indicating greater ecological specialization. The highest amplitudes are recorded for temperature (24 points), nitrogen content (20), habitat naturalness (17), salinity and continentality (10 each), and light (9). This reflects the species' sensitivity to microclimatic conditions, particularly temperature and light, and a preference for less extreme environmental conditions.

F. rufa shows a broad range for several factors: 31 points for nitrogen content, 25 for soil acidity, 22 for habitat naturalness, and 17 for salinity. At the same time, it has a much narrower amplitude for continentality (8), light (7), moisture (6), and temperature (3). This suggests high sensitivity to microclimatic parameters, especially temperature, while maintaining a relatively high tolerance to soil conditions and anthropogenic disturbance.

F. fusca displays a high ecological amplitude across almost all factors: 50 points for soil acidity, 35 for nitrogen, 31 for salinity, 30 for habitat naturalness, 25 for light, 24 for temperature, 21 for continentality, and 20 for moisture. This pattern indicates broad ecological plasticity, especially regarding soil characteristics. However, its sensitivity to continentality and moisture implies partial specialization in microclimate parameters.

F. cunicularia was found at only two sites, making statistical interpretation limited. Its range across all ecological factors varies from 0 to 2 points, which likely reflects insufficient sampling rather than actual ecological narrowness. Therefore, it is premature to draw conclusions about the species' plasticity.

T. caespitum demonstrates broad ecological amplitude for most factors: 29 points for nitrogen, 25 for continentality, 24 for habitat naturalness, 21 for acidity, 19 for salinity and moisture, 13 for light, and 12 for temperature. Despite overall tolerance, the lowest amplitudes in temperature and light suggest limited adaptability to microclimatic variation. Similarity in amplitudes with *L. niger* may indicate potential competition between these species.

F. exsecta is characterized by a comparatively narrow ecological amplitude and selectivity to certain factors, possibly due to its occurrence in ecotones and low number of records (only three). The highest amplitudes are found in habitat naturalness (14 points), salinity and nitrogen (10 each), temperature (8), light (6), acidity (5), continentality (3), and moisture (1). This indicates high sensitivity to temperature and light, suggesting a preference for more stable habitats.

L. niger demonstrates high ecological plasticity and the broadest range across most environmental factors. The range reaches 45 for naturalness value (Nv), 32 for humidity (Hd), 30 for temperature (Tm), 23 for overall salinity (Sl), 21 for continentality (Kn), 15 for soil acidity (Rc), 14 for light intensity (Lc), and 13 for nitrogen content (Nt). This species shows the lowest overall specialization and is well adapted to various conditions, particularly in disturbed and anthropogenic habitats. Despite its broad amplitude, *L. niger* is relatively more specialized in terms of light and continentality compared to other factors.

L. psammophilus exhibits moderate ecological plasticity. The range is 35 for temperature (Tm), 28 for overall salinity (Sl), 21 for naturalness value (Nv), 20 for both soil acidity (Rc) and nitrogen content (Nt), 18 for humidity (Hd), 15 for continentality (Kn), and 12 for light intensity (Lc). Narrower amplitudes for light and continentality indicate certain preferences for stable microclimatic conditions, despite adaptation to various soil parameters.

L. platythorax is characterized by pronounced plasticity in soil acidity (Rc — 41), overall salinity (Sl — 28), and temperature (Tm — 35). Other indicators also vary: humidity (Hd — 6), light intensity (Lc — 18), continentality (Kn — 9), nitrogen content (Nt — 16), and naturalness value (Nv —29). Thus, *L. platythorax* occurs in a wide range of habitats, including both natural and disturbed sites, showing a preference for moderate light and stable thermal conditions.

Leptothorax acervorum predominantly inhabits less xerophytic biotopes. The range is: 28 for temperature (Tm), 22 for soil acidity (Rc), 19 for nitrogen content (Nt), 16 for naturalness value (Nv), 10 for light intensity (Lc), 8 for continentality (Kn), 5 for humidity (Hd), and 3 for overall salinity (Sl). These data indicate moderate ecological flexibility, although it is less tolerant to environmental conditions compared to species of the genera *Lasius* and *Myrmica*.

The species *L. muscorum* demonstrates extremely narrow amplitude across all factors: all values (Hd, Rc, Sl, Nt, Lc, Nv, Tm, Kn) are equal to 0, as data are presented from only one site. This indicates extreme specialization and habitation in strictly defined conditions, despite the limited sample.

Myrmica rubra demonstrates a wide ecological amplitude, indicating high adaptability. The range is: 20 for nitrogen content (Nt), 18 for temperature (Tm), 15 for soil acidity (Rc), 15 for naturalness value (Nv), 10 for light intensity (Lc), 3 for both humidity (Hd) and overall salinity (Sl), and 2 for continentality (Kn). The species is particularly sensitive to microclimatic conditions, especially humidity and temperature.

M. scabrinodis also demonstrates a broad amplitude: 46 for humidity (Hd), 42 for naturalness value (Nv), 21 for continentality (Kn), 19 for temperature (Tm), 18 for soil acidity (Rc), 16 for nitrogen content (Nt), 15 for overall salinity (Sl), and 13 for light intensity (Lc). It is less thermophilic compared to *M. rubra* but shows high tolerance to humidity and chemical soil properties.

M. sabuleti shows limited plasticity compared to other members of the *Myrmica* genus. The amplitude is: 48 for soil acidity (Rc), 35 for nitrogen content (Nt), 21 for naturalness value (Nv), 17 for light intensity (Lc), 11 for humidity (Hd), 10 for temperature (Tm), and 3 each for continentality (Kn) and overall salinity (Sl). Moderate tolerance to light and temperature may explain the mosaic distribution of this species.

The analysis of the ecological amplitudes of various ant species showed that both eurybionts and specialized species are present in the studied biocoenoses (meadow, forest, and agrocoenoses of the Chernihiv Region of Ukraine).

Specialization in temperature is demonstrated by *F. rufa*, *M. rubra*, *Leptothorax acervorum*, and *F. exsecta* (the latter also shows a narrow amplitude in light availability), while *F. rufa* is additionally specialized in humidity and light availability. *F. ru-*

fibarbis exhibits a pronounced specialization in light availability (ranging from 1 to 12 points), indicating sensitivity to microclimatic conditions.

Species with pronounced ecological plasticity and broad amplitudes for most factors (13 points and above) include *Lasius niger*, *F. cinerea*, *F. fusca*, *M. scabrinodis*, *T. caespitum*, *L. platythorax* and *L. psammophilus*. These species demonstrate high tolerance to various environmental conditions, including disturbed and urbanised areas. *Lasius niger*, in particular, stands out with the widest amplitude among all species and minimal specialization.

Moderate plasticity is observed in *M. rubra*, *M. sabuleti*, and *Leptothorax acervorum*, with each species showing certain preferences: *M. sabuleti* for soil acidity and nitrogen content, *M. rubra* for temperature and humidity, and *L. acervorum* for temperature and light availability.

F. cunicularia and *Leptothorax muscorum* were recorded in very limited numbers of sites, making reliable conclusions about their ecological amplitudes difficult. The zero or minimal values observed for all factors are likely due to insufficient sampling rather than reflecting a real narrow ecological niche.

Thus, the ant assemblages of the region consist of both widely distributed eurypagous species, well adapted to diverse and even extreme environmental conditions, and specialized species that inhabit specific biotopes (forest, meadow, ecotones) and are sensitive to particular abiotic factors, especially microclimatic conditions.

Discussion

The regression relationship we obtained between the number of ant species and the number of plant species confirmed the previously obtained data (Cardoso & Schoereder, 2014; Mohseni & Rad, 2021). Analysis of ant adaptation to various environmental factors revealed key differences. Humidity remains a significant determinant: *F. cinerea*, *F. rufibarbis*, and *T. caespitum* are better adapted to dry conditions, whereas *L. niger*, *F. exsecta*, *F. rufa*, *M. rubra*, and *Leptothorax* species prefer more humid biotopes. The narrow humidity amplitude observed for *F. exsecta* and *F. cunicularia* is likely due to limited sampling rather than true ecological specialization.

Soil acidity exerts a moderate influence. Most species inhabit moderately acidic soils, with *F. rufa* showing a marked preference for alkaline conditions. High tolerance to pH variation was recorded in *L. niger, F. fusca*, and *M. rubra*, highlighting their ecological flexibility.

Soil salinity appears to be a minor limiting factor. While all studied species favour low-salinity soils, *F. fusca*, *L. niger*, *M. rubra*, and *F. cinerea* demonstrate wide amplitudes, further confirming their broad ecological plasticity.

Nitrogen content in the soil did not produce marked species-level distinctions. *F. cinerea* shows a slight preference for nitrogen-poor soils, whereas other species are typically associated with moderate nitrogen levels, indicating low specialization along this axis.

Illumination, while initially interpreted as a less decisive factor, shows clear evidence of species-specific adaptations when considered alongside microclimatic requirements. The broadest light tolerance was observed in *L. niger*, *M. rubra*, *F. fusca*, and *F. cinerea*, whereas *F. rufa*, *F. exsecta*, *T. caespitum*, and *F. rufibarbis* exhibited a much narrower amplitude. However, rather than illumination per se, the microclimatic temperature regimes associated with light availability — especially in shaded habitats — may be the true limiting factor for thermophilic species such as *F. rufa* and *F. exsecta*. In these cases, reduced sunlight may lead to insufficient nest temperatures for colony development, potentially forcing nest relocation or even colony mortality.

In terms of their association with natural biotopes, *F. rufa* and *M. rubra* were found in less anthropogenic conditions, while *L. niger*, *F. cinerea*, and *M. rubra* demonstrated high ecological plasticity.

Our previously published data (Stukalyuk et al., 2023 a; Stukalyuk et al., 2023 b) for the 2 ant species common to this study are generally consistent (Table 2).

The method for describing the adaptive potential of ants has proven to be highly effective, since the data for 2024 (Chernihiv Region) for the main environmental factors demonstrate a significant overlap in ranges with the data for 2017–2022 (*L. niger* — Kyiv, Khmelnytskyi Region; *Formica rufa* — Kyiv Region). This suggests that the selected indicators allow a reliable assessment of the adaptive capacity of ants in different geographical conditions. For *Lasius niger*, the new 2024 data show that the ranges of key ecological factors remain largely consistent, particularly for illumination (Lc) and temperature (Tm), where values are not only overlapping but even slightly expanded. The ranges for humidity (Hd) and soil acidity (Rc) are also comparable to earlier data, indicating stability in the species' ecological preferences. However, the broader ranges observed for nitrogen content (Nt) and hemeroby (Nv/Hm) in 2024 suggest increased variability in habitat conditions, possibly reflecting greater environmental heterogeneity or anthropogenic influence in the new study area. Nevertheless, the general trends remain coherent, further confirming the robustness of the phytoindication approach.

For *F. rufa*, the method also showed universality: the ranges of humidity (Hd), illumination (Lc) and temperature (Tm) are almost completely consistent, and soil acidity (Rc) and nitrogen content (Nt) have moderate discrepancies, which can be explained by local soil characteristics. In general, despite the differences between the study areas, the trends remain similar, which confirms the reliability of the method. It allows an objective assessment of the adaptive potential of ants even when the geographical context changes, which is particularly important for long-term ecological and biological studies.

Known classifications of ants in relation to environmental factors consider only two of them: humidity and temperature (Arnoldi, 1968). Accordingly, by humidity

Table 2. **Comparison of phytoindication factor values for *Formica rufa*, *Lasius niger* with data from 2017–2022 (Stukalyuk et al., 2023 a; Stukalyuk et al., 2023 b)**

Factor	*L. niger* 2017-2022 (N = 36)	*L. niger* 2024 (N =20)	*F. rufa* 2020-2022 (N = 88)	*F. rufa* 2024 (N = 26)
Hd (humidity)	37.8–49.6	29.0–61.0	41.39–49.1	44.3–48.5
Rc (soil acidity)	47.4–57.9	41.9–59.7	45.1–56.5	32.6–55.0
Nt (nitrogen)	57.1–69.7	33.0–63.0	37.93–53.2	35.0–63.2
Lc (illumination)	59.5–68.5	60.0–74.6	46.11–56.8	61.8–67.6
Nv / Hm (hemeroby)	42.0–65.1	17.0–62.0	35.02–58.7	40.2–58.4
Tm (temperature)	51.7–58.4	44.0–67.0	47.56–61.3	49.9–51.5

regime, xerophiles, mesoxerophiles, mesophiles, hygro-mesophiles, hemixerophiles are distinguished. As for temperature regime, microtherms, micro-mesotherms, mesotherms, meso-macrotherms, macrotherms are distinguished (Arnoldi, 1968). In Ukraine, mesophiles and mesoxerophiles predominate, according to the temperature regime: macrotherms and meso-macrotherms (Radchenko, 2016).

It is worth noting that this K. V. Arnoldi classification covers only general trends of ants' preferences. Our analysis showed exact values of environmental factors for the studied ant species and the amplitude of the range not only for temperature and humidity factors, but also for additional environmental factors. At the same time, for the many species we studied, the number of measurements is not great enough, so further studies are needed to clarify their adaptive potential and preferences for environmental factor values.

The influence of abiotic factors on ant activity has been analysed in a number of studies. For example, high temperatures and low humidity can reduce activity (Talbot, 1934; Dlussky, 1967; Traniello, 1989; Botes et al., 2006; Mershchiev, 2010; Solida et al., 2011; Stukalyuk, 2017; Sánchez-García et al., 2022). Dominants are characterised by a narrower temperature optimum compared with subordinate ant species (Lessard et al., 2009), which may be related to the rapid degradation of their trail pheromones (Van Oudenhove et al., 2011, 2012). Subordinate species tend to have higher temperature tolerance than dominants (Wiescher et al., 2011). At extremely high air temperatures, ants practically stop their activity (Seima, 2008; Mershchiev, 2010; Zakharov & Zakharov, 2014). It is worth noting that in our study, *Formica rufa*, a dominant species, shows a clearly expressed dependence on the temperature factor, as well as on other microclimatic factors: humidity and illumination. Also, our results for *M. rubra* confirmed previously known data: this species is specialised in soil humidity and temperature (Ito, 2014). The difference between our paper and those cited above is the precise analysis of the influence of not just one factor (temperature, humidity), but several at the same time, indicating the breadth of adaptation of each ant species. This paper opens up the prospect of creating 'ecological passports' for each ant species (and other invertebrate groups), as the phytoindicator analysis provides precise values for each of the environmental factors. However, given that the ant species we studied inhabit different biotopes, including those not included in the study, further research is needed to clarify the values of the environmental factors and the breadth of the amplitude. It is known that insufficient coverage of environmental data can significantly bias the results of models or predictions (Menke et al., 2009), including different patterns when comparing ant and plant communities (Englisch et al., 2005). This is a limitation of our study.

In illuminated areas, plants that are not visited by ants have a lower biomass compared with areas where ants are present, while in shaded areas no such influence of ants has been confirmed (Kersch & Fonseca, 2005). The anthropogenic factor we studied (biotope naturalness) does not necessarily have a negative impact on biodiversity: it has been found that the number of ant species can be higher in urbanised areas than in agricultural or arid areas (Begum et al., 2021; Stukalyuk, 2025). When polluted with industrial waste, the head size of ants can decrease (Grześ et al., 2015). Ants' response to the urbanisation factor can differ between different ant species within the same genus and depends primarily on a combination of environmental factors, including climate (Gippet et al., 2017). Soil acidity, for example in wetlands, may negatively affect ant biodiversity (Bujan et al., 2015). In our study, we did not find any species specialising in this factor. The role of soil factors is more important in explaining variation in ant species composition and abundance than vegetation composition (Boulton et al., 2005). In some cases, for arboreal ant communities, interspecific competition may be a more important factor influencing their distribution than environmental factors (Camarota et al., 2016). In forested communities, precipitation has a negative effect on ant biodiversity and abundance, while in open communities it has a positive effect, i. e. abiotic factors may be more important than vegetation composition (Stukalyuk, 2017; Uhey et al., 2020). Finally, despite its obvious influence on ant activity, temperature is less important for ant biodiversity than the structural complexity of the environment determined by vegetation (Santos et al., 2022). A combination of abiotic factors (seasonality of temperature and precipitation) and vegetation parameters (productivity and vegetation type) can have a decisive influence on the structure of ant communities and their biodiversity (Arnan et al., 2014; Ramos et al., 2018). Environmental structure and spatial factors may be more important for the composition of ant communities than for plant communities (Schlunke, 2015).

Ants, such as *Messor barbarus* (Linnaeus, 1767), may themselves act as a factor accelerating successional processes, promoting vegetation restoration and returning the ecosystem to a natural state (De Almeida et al., 2020). Ant species that build mounds (*Lasius flavus* Fabricius, 1782, *Formica exsecta*) can also influence the composition of vegetation: meadows with such mounds have fewer plant species, and the vegetation on the mounds differs in species composition from the vegetation in adjacent meadows (Schütz et al., 2008; Kovář et al., 2014). Differences in vegetation on functioning anthills from surrounding areas have also been observed for red wood ants *F. rufa*, which create more fertile soils in the anthill zone (Rubashko et al., 2011*). Lasius flavus* nest mounds can accelerate the afforestation of open areas, as faster growth of spruce seedlings has been observed on their mounds. At the same time, mound volume tended to increase in partially shaded habitats, which is likely due to lower temperatures and altered microclimatic conditions rather than direct effects of illumination — especially considering that *L. flavus* is a subterranean species that rarely forages above ground (Vlasáková et al., 2009).

The set of environmental factors considered forms the niche occupied by ant species, but biotic parameters (vegetation characteristics) and ant species characteristics determine which niches are occupied by ant species (Mezger & Pfeiffer, 2011). Environmental and spatial factors can explain 62% of the variation in ant community composition (of which 45% is due to environmental factors alone) in arid biotopes, indicating the importance of studying environmental factors to understand the characteristics of ant biology (Paknia & Pfeiffer, 2014). Environmental factors can explain up to 20.4% of the functional beta-diversity of ants (Wendt et al., 2021). Therefore, to qualitatively characterise the influence of environmental factors on a given ant species, a broad coverage of the different biotopes in which it lives is necessary.

Conclusions

The study confirmed efficiency of the phytoindicator method in characterising ecological amplitudes of different ant species. This method revealed significant differences between species in a number of key environmental factors such as humidity, soil acidity, salinity, nitrogen content, illumination, temperature and continentality. Main advantages of the phytoindicator method in the study of ants are:

Accuracy in determining the optimal habitat conditions of species. The phytoindication method confirmed that *F. cinerea*, *F. rufibarbis*, and *T. caespitum* prefer dry biotopes, while *F. rufa*, *M. rubra*, and *L. niger* are associated with more humid conditions. Although these ecological preferences have long been known from field observations, the application of the phytoindication method provides a quantitative assessment of each species' ecological amplitude — expressed in specific values (ranging from 0 to 100) — which allows for more precise comparisons across environmental gradients. This demonstrates the value of the method not only in confirming known trends but also in identifying indicator species for different ecosystem types with greater ecological accuracy.

Identification of ecological amplitude ranges. The study showed that some species, such as *F. exsecta*, have narrow ecological amplitudes, indicating their high specialisation. At the same time, species such as *L. niger* and *M. rubra* have a wide range, reflecting their high ecological plasticity and ability to live in a variety of conditions.

Determination of species adaptation to different environmental conditions. The phytoindication method showed that *F. rufa* is more abundant in biotopes with low soil acidity, while *L. niger*, *F. fusca* and *M. rubra* are able to live in a wide range of acidity, confirming their adaptive capacity.

Identifying the relationship between anthropogenic impact and species distribution. The study showed that *F. rufa* and *M. rubra* prefer biotopes with a low level of anthropogenic impact, while other species, such as *L. niger* and *F. cinerea*, can be found in biotopes with a high level of anthropogenic impact.

Comprehensive characterisation of species habitat conditions. The phytoindication method allowed not only description of individual environmental factors, but also comparative analysis of the combination of these factors, identifying patterns in the distribution of ants in relation to a set of environmental conditions. The phytoindication method is therefore highly informative and applicable to the study of ant ecology. Its use allows not only to classify species according to their environmental preferences, but also to predict their distribution under changing environmental conditions, which is particularly important in the context of biodiversity monitoring and ecosystem conservation.

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Supplementary Table S1. **Dynamic density and occurrence of the studied ant species across biotopes***

Category	Birch forest (23 samples)	Xerophytic meadows (3 samples)	Overgrown xerophytic meadows (1 sample)	Mesophytic meadows (17 samples)	Mown mesophytic meadows (11 samples)	Overgrown mesophytic meadows (35 samples)	Mixed forest (18 samples)	Psammophytic meadows (11 samples)	Overgrown psammophytic meadows (34 samples)	Field (sunflower agrocenosis) (11 samples)	Pine forest (11 samples)	Forest edge (ecotone) (1 sample)
Formica cinerea	23 (1)	46 (3)	34 (1)	92 (13)		78 (4)	69 (3)	52 (7)	377 (17)	64 (6)		51 (1)
Formica cunicularia Latreille, 1798	2 (2)											
Formica fusca	73 (20)					2 (1)	4 (3)				15 (8)	
Formica rufa	133 (15)						146 (11)					
Lasius niger				46 (7)	3 (2)	38 (13)				154 (7)		
Tetramorium caespitum	2 (1)			4 (1)				5 (2)	2 (1)	11 (5)		
Formica exsecta				23 (3)								
Formica rufibarbis Fabricius, 1793								10 (2)	26 (9)			
Lasius platythorax Seifert, 1991	22 (2)										12 (6)	
Lasius psammophilus		2 (1)						14 (5)	178 (18)			
Leptothorax acervorum (Fabricius, 1793)	5 (5)						2 (2)					
Leptothorax muscorum (Nylander, 1846)						1 (1)						
Myrmica rubra	5 (5)						4 (2)					
Myrmica sabuleti Meinert, 1861									1 (1)		1 (1)	
Myrmica scabrinodis				1 (1)	79 (10)	33 (11)						
Sum	265	48	34	166	82	152	225	81	584	229	28	51
Number of ant species	8	2	1	5	2	5	5	4	5	3	3	1

* Occurrence is given in parentheses (number of plots where the species was recorded) following the dynamic density value.

Supplementary Table S2. **Distribution and frequency of ant species across different locations**

Category	Buda	Dziubivka	Krupychpole	Morivsk	Otrohi	Haenky
Formica cinereal	156 (6)	337 (28)			16 (5)	377 (17)
Formica cunicularia						2 (2)
Formica fusca		2 (1)	4 (3)		15 (8)	73 (20)
Formica rufa			146 (11)			133 (15)
Lasius niger		192 (13)		33 (11)	16 (5)	
Tetramorium caespitum	5 (2)	15 (6)				4 (2)
Formica exsecta		23 (3)				
Formica rufibarbis					16 (3)	20 (8)
Lasius platythorax					12 (6)	22 (2)
Lasius psammophilus		2 (1)			31 (6)	161 (17)
Leptothorax acervorum	1 (1)		1 (1)			5 (5)
Leptothorax muscorum		1 (1)				
Myrmica rubra	4 (2)					5 (5)
Myrmica sabuleti					1 (1)	1 (1)
Myrmica scabrinodis		11 (3)		79 (10)	23 (10)	
Sum	166	583	151	112	130	803
Number of species	4	8	4	2	8	11

Supplementary Table S3. **Results of Dunn's post hoc test with Bonferroni correction for pairwise comparisons of ant abundance across different biotope types**

Category	Birch forest	Mesophytic meadows	Mown mesophytic meadows	Overgrown mesophytic meadows	Mixed forest	Psammophytic meadows	Overgrown psammophytic meadows	Field (sunflower agrocenosis)	Pine forest
Birch forest		1	1	0.1512	1	1	1	1	**0.02008**
Mesophytic meadows	1		1	0.4318	1	1	1	1	0.05356
Mown mesophytic meadows	1	1		1	0.7488	1	0.7537	0.1248	1
Overgrown mesophytic meadows	0.1512	0.4318	1		**0.002373**	1	**0.000224**	**0.000232**	1
Mixed forest	1	1	0.7488	0.002373		0.2727	1	1	**0.000423**
Psammophytic meadows	1	1	1	1	0.2727		0.2352	**0.04051**	1
Overgrown psammophytic meadows	1	1	0.7537	**0.000224**	1	0.2352		1	**0.000104**
Field (sunflower agrocenosis)	1	1	0.1248	**0.000232**	1	**0.04051**	1		**4.42E-05**
Pine forest	**0.02008**	0.05356	1	1	**0.000423**	1	0.000104	4.42E-05	

Note. Statistically significant differences are highlighted in bold here and in Table 4.

Supplementary Table S4. **Results of Dunn's post hoc test with Bonferroni correction for pairwise comparisons of ant species richness across different biotope types**

Category	Birch forest	Mesophytic meadows	Mown mesophytic meadows	Overgrown mesophytic meadows	Mixed forest	Psammophytic meadows	Overgrown psammophytic meadows	Field (sunflower agrocenosis)	Pine forest
Birch forest		1	**0.004876**	**0.000302**	0.4889	0.902	**0.02539**	1	0.2461
Mesophytic meadows	1		1	1	1	1	1	1	1
Mown mesophytic meadows	**0.004876**	1		1	1	1	1	1	1
Overgrown mesophytic meadows	**0.000302**	1	1		1	1	1	0.9008	1
Mixed forest	0.4889	1	1	1		1	1	1	1
Psammophytic meadows	0.902	1	1	1	1		1	1	1
Overgrown psammophytic meadows	**0.02539**	1	1	1	1	1		1	1
Field (sunflower agrocenosis)	1	1	1	0.9008	1	1	1		1
Pine forest	0.2461	1	1	1	1	1	1	1	