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Urbanization affects colony performance of Lasius fuliginosus (Hymenoptera; Formicidae) indirectly through tree structure and resource diversity

Stanislav Stukalyuk[1]

asmoondey@gmail.com

Institute for Evolutionary Ecology NAS Ukraine

Yaroslav Sydorenko

Mykola Kozyr[1]

Institute for Evolutionary Ecology NAS Ukraine

Research Article

Keywords: trophobiosis, arboreal ants, edge effects, microclimate, hollow-bearing trees, urban ecology, foraging networks

Posted Date: June 4th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9669958/v1

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Additional Declarations: No competing interests reported.

Abstract

Increasing urbanisation can significantly alter forest structure, microclimate and resource availability. This potentially impacts trophobiotic ants that depend on stable arboreal habitats. The role of landscape type, tree characteristics and local microclimate in the functioning of colonies of the ant *Lasius fuliginosus* remains poorly understood. In this study, we investigated the joint influence of urbanisation and tree-related factors on the colony size, foraging activity and trophobiotic efficiency of *L. fuliginosus* in Kyiv and the surrounding area in Ukraine.

The study combined two independent datasets comprising 150 colonies and 429 associated trees. The larger dataset (108 colonies and 290 trees) was used to assess patterns of variation in colony size across the natural-suburban-urban gradient (July 2021–2023). The second, more intensive dataset (July 2025, 42 colonies and 139 trees in a natural biotope) included detailed measurements of tree characteristics, trail structure, microclimate and trophobiotic activity in a deciduous forest. We analysed colony and tree parameters visited by ants using generalised linear models, generalised linear mixed models, beta regression, Random Forest models and nonparametric statistics. The foraging activity of *L. fuliginosus* colonies decreased significantly with urbanisation. Urban colonies had fewer worker ants on trails and trees, and they visited trees with smaller diameters than colonies in natural habitats. After accounting for tree diameter and species diversity, habitat type itself ceased to be a significant predictor of colony size. This suggests an indirect effect of urbanisation through the degradation of dendrocoenosis structure. The diversity of tree species used also decreased sharply with increasing proximity to urban habitats, where colonies predominantly used a single species of tree. Foraging intensity was primarily determined by microclimatic variables and tree size. Random Forest and generalised linear mixed models identified temperature, humidity, trunk diameter, moss cover and the presence of tree cavities as the main predictors of ant activity. *L. fuliginosus* activity peaked within a narrow temperature range (22–26°C) and declined at higher relative humidity (over 43%). Trophobiotic efficiency (the proportion of workers returning with a full crop) depended primarily on the species of tree and its structural condition. *Quercus robur* demonstrated significantly higher trophobiotic success and greater activity on tree trunks than other tree species. The proportion of ants returning with a full crop decreased with increasing distance from the forest edge and with an increasing proportion of dead branches in the canopy.

The results demonstrate the hierarchical organisation of environmental factors *in L. fuliginosus*. The observed effects of urbanisation on colonies appear to be mediated by changes in tree diversity and the availability of mature trees. Trophobiotic efficiency was most strongly associated with host tree species and condition. The preservation of large, mature trees (particularly *Q. robur*) and the maintenance of structurally diverse urban and suburban forests appear critical for the long-term survival of *L. fuliginosus* populations.

Introduction

Urbanisation is one of the most intense and irreversible processes of environmental transformation. Currently, more than half of the world's population lives in cities, and this proportion is expected to exceed two-thirds by 2050 (United Nations 2022; Seto et al. 2012). The expansion of urban areas is accompanied by habitat fragmentation, simplified vegetation structures, altered local microclimatic conditions and increased chemical pollution (Grimm et al., 2008). These factors exert increasing negative pressure on insect populations. According to some meta-analyses, the abundance of terrestrial insects is declining by around 9% per decade on average. Furthermore, the severity and direction of these trends can vary significantly depending on the region and functional group (van Klink et al. 2020). Urbanised landscapes are considered one of the key threats to insect biodiversity globally, primarily due to the loss of specialised habitats and resources (Sánchez-Bayo and Wyckhuys 2019; Ossola and Niemelä 2018).

Ants (Hymenoptera: Formicidae) are widely used as model organisms in the study of the ecological consequences of urbanisation. Participating in a variety of ecosystem processes such as nutrient cycling, soil structuring, seed dispersal and regulating other arthropod populations, they are considered reliable bioindicators of habitat quality (Del Toro et al. 2012; Ribas et al. 2008). Studies conducted along increasing urbanisation gradients have documented a decrease in myrmecofauna species diversity, as well as a shift in community composition towards generalist, disturbance-tolerant or invasive species (Uno et al. 2010; Tóth et al. 2019; Buczkowski and Richmond 2012). However, most of these studies are based on standardised collection methods (e.g. soil traps and bait counts), which reflect changes at the community level but do not allow us to judge the processes occurring within individual colonies.

This limitation is particularly significant given that the colony is the basic functional unit of eusocial insects. Responses to urbanisation at the colony level can differ fundamentally from those at the community level. For instance, maintaining the number of individuals in traps does not necessarily ensure the reproductive vigour or foraging efficiency of colonies. The few existing studies indicate that urbanisation can affect both colony size and foraging behaviour within the foraging area. Specifically, *Temnothorax nylanderi* urban colonies exhibited reduced aggression alongside increased foraging activity compared to forest populations (Jacquier et al. 2023). This suggests behavioural plasticity as a mechanism of adaptation to the urban environment.It remains unclear which factors determine changes in colony size along the urbanisation gradient: changes in tree composition, degradation of trophobiotic resources or microclimate transformation.

Trophobiosis plays a key role in the life cycle of ant colonies in temperate forest ecosystems. This refers to the mutually beneficial interaction between ants and aphids, whereby the ants provide the aphids with protection in exchange for carbohydrate nutrition. Urbanisation may affect trophobiosis in at least two ways. Firstly, it affects the composition and abundance of host plants. Secondly, it impacts the predator community, resulting in aphid outbreaks on urban trees (Rocha and Fellowes 2020; Korányi et al. 2021; Gaber et al. 2024). The quality of trophobiosis resources is determined by the species of host tree and its structural characteristics, such as age and crown condition (Stadler and Dixon 2005; Depa et al.

2020). In urban landscapes, therefore, the loss of large, structurally complex trees (of overmature age) may reduce trophobiotic resource availability for ants.

Lasius fuliginosus (Latreille, 1798) is a useful model for testing these hypotheses. This trophobiont ant species builds cardboard nests in tree cavities and relies heavily on aphid honeydew. It exhibits three characteristics that are sensitive to urbanisation: nesting in structurally complex trees, forming stable foraging trails and engaging in trophobiotic interactions with highly specific myrmecophilous aphids, such as those in the Stomaphis genus (Dobrzyńska 1966; Quinet and Pasteels, 1996; Depa et al. 2022). *L. fuliginosus* is a dominant species in temperate forests and exerts a pronounced structuring influence on local ant communities (Ślipiński et al. 2014; Markó et al. 2013). Despite extensive study of its biology and ecology, *L. fuliginosus* response to urbanisation remains virtually unexplored and existing data are limited to comparisons of a few populations, with little consideration given to factors acting at the tree and microclimate levels (Stukalyuk et al., 2022).

The present study aims to address these gaps. Specifically, we investigated how urbanisation and tree characteristics jointly determine the functioning of *L. fuliginosus* colonies in the Kyiv metropolitan area of Ukraine. Specifically, we assessed the following: (1) changes in colony size along the nature–suburban–urban gradient, (2) the factors that determine the intensity of foraging activity (i.e. the number of ants on trails per minute), and (3) the factors that determine trophobiotic efficiency (i.e. the proportion of workers with a full goiter). We hypothesised the following: (H1) Colony size will decrease indirectly along the urbanisation gradient, due to the loss of large, structurally complex trees rather than as a direct effect of habitat type; (H2) Foraging activity intensity will primarily be determined by microclimatic factors (temperature and humidity), which exhibit pronounced nonlinear relationships; and (H3) Trophobiotic efficiency (the proportion of foragers with full crops) will be more influenced by tree species and structural condition than by microclimate. To test these hypotheses, we employed a complementary statistical approach that combined random forest models with generalised linear mixed models.

Materials and Methods

Study area

The main study was conducted in Kyiv and the Kyiv Oblast of Ukraine in July 2025. Additional retrospective data was collected from 2021 to 2023. The region has a temperate continental climate. Data from the Kyiv weather station (Borys Sreznevsky Central Geophysical Observatory, see Table 1) from 1991 to 2025 were used as the climate norm.

Table 1. Main climate indicators for Kyiv, Ukraine (norm 1991–2020 vs July 2025)

Parameter	Norm 1991–2020	July 2025	ΔT / ΔU
T~avr~ (°C)	21.3	22.6	+1.3
T~max~ avg (°C)	26.6	33.1	+6.5
Humidity avg (%)	54	62	+8

July 2025 saw a positive temperature deviation, with an average monthly temperature of 22.6°C (ΔT = +1.3°C). Humidity was also high, with precipitation levels reaching 143% of normal at 93 mm for the month. These conditions were significantly different from the abnormally dry and hot period of 2024.

Urbanisation gradient and site description

To analyse the impact of anthropogenic environmental transformation, an urbanisation gradient comprising three types of biotope differing in landscape fragmentation and proportion of sealed surfaces was used (McKinney, 2008). *Natural* biotopes have a proportion of sealed surfaces of less than 5%. These include large forest stands with minimal anthropogenic impact. The studies were conducted in the following locations. Deciduous forest: the 700-hectare Holosiivskyi forest stand and the over-100-hectare Feofaniya tract, with dominant *Quercus robur* (main canopy), *Carpinus betulus* and *Acer platanoides* (total projective crown cover 70–90%). The understorey comprises spindle tree (*Euonymus* sp.), elderberry (*Sambucus nigra*) and young maple saplings. Forest areas related to deciduous forests were surveyed in the Botanical Garden named after Fomina (Kyiv). Mixed forests (DVRZ and Koncha-Zaspa locations) are also classified as natural. In the main layer, pine (*Pinus sylvestris*) predominates and in the second layer, oak and maple (with a total projective cover of 60–85%). The undergrowth comprises *Prunus serotina* and, less frequently, *Amorpha fruticosa* and *Quercus rubra*. Zhukov Island's floodplain forest is a relatively closed stand (projective cover 30–80%) dominated by *Q. robur*, *Populus alba*, and *P. nigra* in the main layer, which alternates with mesophytic meadow areas. Despite fragmentation, this forest type is classified as natural due to the absence of development and minimal anthropogenic impact on the stand's composition. The undergrowth is represented by *Ulmus* sp. and *Acer negundo*, and less frequently by *Amorpha fruticosa*.

Suburban biotopes (with a sealed surface area of 5–30%) are found in the peripheral zones outside city limits and consist of fragmented forested areas that transition into agricultural landscapes, such as crop fields and pastures. In the Kyiv region, they include shelterbelts (rows of trees) dominated by *Salix fragilis*, *Populus nigra* and *Quercus robur* along agricultural lands. The undergrowth is either absent or comprises *Amorpha fruticosa* and *Acer negundo*.

Urban biotopes (>50% sealed surface area) are urban landscapes with a high proportion of built-up areas. These include roadside tree alleys (one to three rows) along highways, as well as parklands in Kyiv and its satellite cities (Bucha and Irpin). The forest stand is mainly composed of linden (*Tilia cordata*), black poplar, oak, and *Robinia pseudoacacia*.

Study species and colonies identification

Lasius fuliginosus is the only European representative of the subgenus *Dendrolasius* Ruzsky, 1912 (Radchenko, 2016). This species has an Amphipalearctic distribution and is primarily found in the forest and forest-steppe zones of Ukraine, inhabiting broadleaf, mixed and floodplain forests (Radchenko, 2016; Stukalyuk et al., 2022). Colonies can be very large, containing several hundred thousand to 2.5 million workers (Dobrzyńska, 1966; Seifert, 2018). *L. fuliginosus* builds cardboard nests in the hollows of living trees, primarily at the base of the trunk or in the root zone (Seifert, 2018; Vaessen et al., 2026). It is an obligate trophobiont, with permanent foraging trails leading to protected aphid colonies that provide most of the colony's carbohydrate diet (Dobrzyńska, 1966; Depa et al., 2022). *L. fuliginosus* is an oligotherm with respect to thermal conditions (Seifert, 2018) and prefers shaded, moderately moist habitats.

The colony search was conducted using the parallel linear transects. The observer examined tree trunks within a 10-metre strip on either side of the route. The survey routes were set up perpendicular to the forest edge and extended from one side of the forest to the other. To improve detection probability and reduce observer bias, each route was subsequently repeated in parallel in the return direction. Particular attention was paid to older trees. Colonies were considered separate units if the following two criteria were met: the spatial distance between adjacent colonies was at least 100 metres and there were no connecting foraging trails between them. This approach reflects the criteria for distinguishing between adjacent *L. fuliginosus* colonies in the field. In the wide sample, approximately 45 transects were completed across all study sites. Individual transects typically ranged in length from 0.8 to 2.5 km, depending on the size and accessibility of the forest patches. In the intensive sample, which focused on colony structure and trophobiotic activity, an additional 22 transects were conducted within selected localities. The mean effective route length within the intensively surveyed sites ranged from 0.5 to 2.2 km. The number of transects established per study site depended on the size and structural heterogeneity of the locality. Typically, this ranged from 2 to 8. The total distance surveyed exceeded 60 km.

Sampling and datasets

Data collection was conducted using two independent and complementary samples (a total of 150 colonies and 429 associated trees; see Table 2).

Table 2: General characteristics of the location, number of colonies and number of trees examined for two *Lasius fuliginosus* samples.

Dataset	Habitat Type	Location / Site Description	N colonies	N trees	Key Parameters Measured
Intensive Sample (2025)	Natural	Feofania, Holosiyivo, Zhukov Island, DVRZ, etc.	42	139	Foraging activity, trophobiosis, microclimate
Wide Sample (2021–2023)	Natural	Deciduous and mixed forests (Kyiv Oblast)	56	163	Colony size, nest volume, DBH, tree richness
	Suburban	Shelterbelts (poplar, willow)	26	59	Colony size, nest volume, DBH, tree richness
	Urban	City parks, roadside tree alleys	26	68	Colony size, nest volume, DBH, tree richness
Total	-	-	150	429	-

Despite a more limited set of recorded parameters (see the 'Colony and Tree Measurements' subsection), the wide sample size (n = 108, data from 2021–2023) is critical for statistically substantiating differences between habitat types (urban vs. suburban vs. natural). It enables us to identify key patterns of environmental influence. The intensive sample (n = 42, data from 2025) reveals the ecological and behavioural causes of these differences by analysing ant activity and detailed tree characteristics. Data collection within the large sample was carried out at the same time of day in July, but without microclimatic and dendrological parameter measurements.

Colony and Tree Measurements

Colony and tree parameters were recorded separately for the two samples, in accordance with different data collection objectives and protocols.

The broad comparative sample included a limited set of parameters characterising colony status along the urbanisation gradient, including the total number of foraging ants (the sum of workers recorded on the trails and trunks of all trees in the colony), the number of foraging trails, the total number of trees visited, species richness (the number of tree species used by a single colony), species identity, and trunk diameter. Diameter was measured at a height of 1.6 m using a tape measure (DBH, mm).

The intensive sample included an expanded set of 36 variables at the tree and trail levels (see Supplementary Table S1 for the full list). For each visited tree, the following were recorded: species and functional type (nest or forage); trunk diameter (m) at a height of 1.6 m; tree height; bark type; number of hollows (visual count of accessible cavities); proportion of dry branches in the crown (%); projective crown cover (%); crown condition; proportion of moss and lichen cover on the trunk (%); distance from the tree to the nearest forest edge (m); distance to the nearest neighbouring tree (m); and characteristics

of the substrate in the adjacent section of the each trail of colony (% soil; % forest litter; % logs and branches).

The host tree was identified based on a combination of features, including the presence of soil and plant material deposits (such as rotted wood and sawdust) at the base of the trunk, the convergence of all the colony's foraging trails at the tree, and the highest ant concentration on the trunk. A forage tree was identified by the absence of nesting features and a steady flow of ants along the trunk. The species richness of the dendrocenosis was calculated as the total number of tree species visited by a single colony in its foraging area at any one time.

Before constructing the regression models, collinearity testing was performed and variables with a correlation coefficient $|r| > 0.7$ or a variance inflation factor (VIF) > 5 were excluded from the analysis. Specifically, the following were excluded: tree height ($r = 0.714$ with diameter); crown condition and canopy cover ($r = 0.814$ and $r = -0.79$, respectively, with the proportion of dead branches); soil and forest litter ($r = -1.000$); lichen cover; and distance to the nest tree. Following a screening for multicollinearity (using Pearson correlations and VIF analysis), the final set of fixed explanatory predictors selected for modelling were tree type (tree_type), tree species (tree_species), trunk diameter, number of hollows, proportion of dead branches, moss cover, distance to the forest edge, air temperature and humidity. Colony ID was included separately as a random effect in GLMM analyses. Variables related to spatial reference, identifiers, trail structure or descriptive colony characteristics were excluded from the final predictive models. The maximum VIF among the retained predictors was 2.00 (temperature), which is within acceptable limits.

The distance from each tree to the nearest edge of the forest was determined using a combination of direct laser rangefinder measurements for trees at the edge of the forest and GIS-based estimation from GPS coordinates and satellite imagery for trees located deeper within forest patches.

Foraging activity and trophobiotic efficiency

Ant activity counts were conducted exclusively in clear, cloudless weather between 11:00 and 13:00 Kyiv time for both samples. The number of ants crossing a fixed counting point in both directions per minute was recorded for each foraging trail and each visited tree. For ground trails, activity was recorded at a site midway between the nest tree and the nearest forage tree. For trees, activity was recorded at a height of 1.6 metres on the trunk. Wire gates were installed above the trail surface (ground, leaf litter, tree branches and trunks) to serve as reference points for counting. In cases of high ant density, video recording was conducted, followed by frame-by-frame ant counting. Each tree and trail was counted three times at 5-minute intervals. The average of these three measurements was included in the analysis. Total colony activity was calculated as the sum of all ants recorded on the trails and trunks of all trees in the colony.

Trophobiotic efficiency was assessed as the proportion of workers with a full goiter. Among the foragers returning to the nest (down the trunk), the proportion of workers with a visible, rounded swelling of the

abdomen (consistent with a full goiter) was counted. This swelling corresponded to separated tergites and visible, lighter membranes between them. The proportion of these workers (% full goiter) in one minute constituted the trophobiotic efficiency indicator. The proportion of workers with full gasters was assessed by continuous visual scoring during the same observation interval used for traffic counts. Only clearly distended gasters were classified as “full”.

When assessing each trail by its structure, the type of substrate it passed over was indicated as a percentage of the total length of the trail. Using a relative indicator enabled us to evaluate the effectiveness of trophobiotic activity, regardless of the overall intensity of the forager flow.

Microclimate measurements

Immediately before each series of three counts, the air temperature (in °C) and the relative humidity (in%) were measured on the tree using a portable thermohygrometer with an SHT35-DIS-B2.5KS sensor (manufactured by Sensirion in Switzerland). Measurements were taken at ground level in the shade and away from direct sunlight. Therefore, the recorded values reflect the overall microclimate of the location at the time of the count. Please note that microclimatic conditions on the trunk surface and in the tree crown may differ from those measured on the ground. This limitation should be taken into account when interpreting the relationship between microclimate and ant activity on the trunks. Measurement results were recorded only after they had stabilised on the sensor. Microclimatic variables were measured during each observation session (3 counts) conducted on foraging trails and at associated trees.

Statistical analysis

All statistical calculations and data visualisation were performed using R version 4.5.2. Data preparation and graphics were carried out using the tidyverse (dplyr and ggplot2), cowplot and patchwork packages. The normality of the quantitative data distribution was tested using the Shapiro–Wilk test. As most variables did not conform to a normal distribution, non-parametric statistical methods were employed.

For the wide sample of 108 colonies, comparisons of colony parameters between the three biotope types were performed using the Kruskal–Wallis test (H), followed by pairwise comparisons using the Dunn test (FSA package) with p-value correction via Holm's method. Spearman's rank correlation coefficient (ρ) was used to analyse the relationship between the total number of workers and species richness of the trees used. A generalised linear model (GLM) with a quasi-Poisson distribution was used to estimate factors determining total colony abundance, including habitat type, mean tree diameter, total number of trees used and tree species richness as fixed predictors.

An intensive sample of 42 colonies and 139 trees was used to compare the characteristics of Quercus robur and other tree species using the Wilcoxon signed-rank test (W). Spearman's correlation was used to assess relationships between trail parameters, microclimate and worker activity. The influence of tree characteristics and microclimatic factors on worker movement intensity and trophic success was analysed using Random Forest and regression-based approaches. Random forest models (500 trees;

package 'randomForest') were constructed separately for two response variables: the number of ants on the trail per minute and the proportion of workers with a full goiter. The mtry value was selected based on minimum out-of-bag (OOB) error. The importance of the predictors was assessed using permutation importance (%IncMSE) and mean decrease in node impurity (IncNodePurity). Partial dependence plots (package pdp) were used to visualise non-linear relationships. Worker movement intensity (count data) was analysed further using a generalised linear mixed model (GLMM) with a negative binomial distribution and a random intercept effect (colony_id; package glmmTMB). The fixed effects included tree type, tree species, trunk diameter, number of hollows, percentage of dead branches, moss cover, distance to the forest edge, temperature and humidity. The proportion of workers with a full crop was analysed using beta regression (package betareg) as this variable was proportional. Before building the models, all predictors were checked for multicollinearity using Pearson's correlation coefficients and variance inflation factors (VIF). Variables exhibiting high collinearity (VIF > 5 or $|r| \approx 1$) were excluded from the final set of predictors. The statistical significance of all results was accepted at $p < 0.05$. Data are presented as mean ± SD and median values.

Results

Colony distribution and comparative analysis of parameters (wide sample)

The distribution of 108 *L. fuliginosus* colonies (wide sample) along the urbanisation gradient was uneven. 51.8% (n = 56) were found in natural habitats, while 24.1% were found in both suburban and urban habitats.

Colony-level analysis revealed statistically significant differences in key parameters of colony status (see Tables 3 and 4).

Table 3. Descriptive statistics of colony-level parameters

Biotope	n	Median Ants	Mean Ants	Median Diam, m	Median Spec. Richness
Natural	56	293.0	446.0	0.785	1.0
Suburban	26	122.5	240.0	0.769	1.0
Urban	26	116.0	141.0	0.566	1.0

Table 4. Effect of biotope on colony parameters (Kruskal-Wallis test)

Parameter	chi2	p-value	Significant differences (Dunn)
Ants	10.17	0.006	Natural > Urban
Diameter	12.79	0.002	Natural > Urban; Suburban > Urban
Spec. Richness	20.96	< 0.001	Natural > Urban/Suburban

The highest ant activity (number of ants on trails and on all trees per colony combined) and average tree diameter were observed in natural biotopes. According to the Kruskal–Wallis test, biotope significantly affects ant abundance (H_2 = 10.17, p = 0.006) and tree diameter (H_2 = 12.79, p = 0.002). Pairwise comparisons (Dunn's test) showed that urban colonies were significantly smaller than natural colonies in terms of abundance (p = 0.002) and host tree diameter (p = 0.004; see Fig. 1).

The summary box plots in Figure 1 show a consistent decrease in ant activity and tree diameter along the urbanisation gradient. There were no significant differences in the number of trees and trails per colony.

Factors Determining Colony Activity

A global model (GLM, Quasipoisson) enabled us to identify the most significant factors influencing colony size (see Table 5). The mean tree diameter (p < 0.001) and tree species richness within the colony (p = 0.009) were identified as the strongest predictors. Notably, when accounting for these factors, the direct effect of the biotope (urban environment) becomes statistically insignificant (p = 0.125).

Table 5. Results of the multivariate analysis (GLM)

Predictor	Estimate	Std. Error	t-value	p-value
(Intercept)	2.904	0.586	4.952	< 0.001 ***
Mean Diameter	2.080	0.470	4.425	< 0.001 ***
Spec. Richness	0.467	0.176	2.649	0.009 **
Total Trees	0.035	0.084	0.416	0.678
Biotope (Urban)	-0.612	0.396	-1.546	0.125

Significance codes: *** p < 0.001, ** p < 0.01, * p < 0.05.

Correlation analysis confirmed positive association between worker number and the number of tree species used by the colony (Spearman rho = 0.28, p = 0.003).

A graphical analysis (Fig. 2) suggests that the association between urbanisation and colony abundance may be mediated by structural habitat characteristics. Physical environmental parameters, such as trunk diameter and tree species diversity, explained more variation in colony abundance. As the graph shows, when these variables are controlled for, the 'urban' factor itself ceases to be a significant predictor of colony decline.

Species richness and dendrocoenosis structure

The species richness of trees visited per colony decreases significantly towards urban areas ($H_2 = 20.96$, $p < 0.001$). Figure 3 illustrates the sharp transition from multi-species associations in natural habitats to mono-resource strategies in urban environments, where the median species richness value decreases to one. While oak-maple associations play a key role in forests, suburbanised areas see a shift towards *Salix fragilis*, while urbanised areas see a return to *Quercus robur* as the most stable resource.

High heterogeneity was recorded in natural biotopes, with colonies visited by up to four tree species simultaneously (see Figure 4 and Table 6).

The most stable associations include *Quercus robur* and *Acer platanoides* (nine colonies; see Table 6). In suburban and urban zones, there is a clear unification of resources: most colonies exploit only one tree species (96% of cases in urban areas). In the city, *Quercus robur* remains the main resource (15 colonies), while *Salix fragilis* dominates in the suburbs (16 colonies).

Table 6. Main tree species combinations by biotope

Biotope	Richness	Species combination	Number of colonies
Natural	1	*Quercus robur*	21
Natural	2	*Acer platanoides + Quercus robur*	9
Natural	3-4	*Different combinations (Oak, Maple, Lime, etc.)*	5
Suburban	1	*Salix fragilis*	16
Urban	1	*Quercus robur*	15
Urban	1	*Betula pendula / Robinia pseudoacacia*	5

Characteristics of host trees and differences between *Quercus robur* and other species (intensive sample)

Analysis of 139 trees visited by 42 *L. fuliginosus* colonies revealed significant differences between Q. robur and other species (see Table 7).

Table 7. Comparison of tree parameters and ant activity on *Quercus robur* and other species

Parameter	*Quercus robur* (n=72)	Other species (n=67)	Statistic (W)	p-value
Diameter, м (Mean ± SD / median)	0.76 ± 0.40 / 0.74	0.53 ± 0.34 / 0.45	3247.5	0.00043
% workers with full goiter (Mean ± SD / median)	53.6 ± 27.6 / 60	31.8 ± 26.8 / 25	3468	8.00×10^{-6}
Ants on trail / 1 min (Mean ± SD / median)	149.9 ± 114.9 / 124	153.2 ± 121.3 / 128	2411	0.998
Ants on trail / 1 min (forage vs host)	147.4 ± 119.9 / 124	159.5 ± 113.9 / 125	1985.5	0.433
Ants on trees / 1 min (Mean ± SD / median)	226.3 ± 251.1 / 171	115.4 ± 135.7 / 66	3278.5	0.00026

The trunk diameter of *Q. robur* was statistically significantly larger (Wilcoxon rank-sum test, W = 3247.5, p = 0.00043; Fig. 5A) than that of the other tree species.

The number of ants travelling along ground trails to trees per minute did not differ between *Q. robur* and other tree species (Wilcoxon rank-sum test, W = 2411, p = 0.998; Fig. 5B). No statistically significant differences were found in trail activity on host and forage trees (Wilcoxon rank-sum test, W = 1985.5, p = 0.433; Fig. 5C; Supplementary Table S3). The proportion of ants with full crops was significantly higher in oak trees (Wilcoxon rank-sum test, W = 3468, $p = 8.00 \times 10^{-6}$; Fig. 5D). Meanwhile, the number of ants moving along tree trunks was significantly higher in oak trees (Wilcoxon rank-sum test: W = 3278.5; p = 0.00026).

Trail and substrate analysis

Correlation analysis (Spearman) revealed a strong positive relationship between trail width and the number of ants on it (rho = 0.766, p < 0.001), as well as a moderate positive relationship with trail length (rho = 0.339, p = 0.012). Among the substrate types along the trail, logs and branches had the greatest positive effect (rho = 0.274, p = 0.012), while soil was negatively correlated with activity (rho = -0.345, p = 0.008; see Figure 6; Supplementary Table S2).

The proportion of forest litter did not significantly affect the outcome (rho = 0.079, p = 0.42; see Supplementary Table S1). No differences in ant activity were found between host and forage trees (median: 125 vs. 124 ants per minute; Wilcoxon rank-sum test: W = 1985.5, p = 0.433; see Supplementary Table S2).

Modelling the effect of tree characteristics and microclimate

To assess the effects of tree characteristics and microclimate on ant activity, Random Forest and GLMM models were constructed (Table 8). Random forest regression identified the leading predictors of

trophobiotic and foraging activity (Table 8 and Supplementary Table S5). For the number of ants on the trail per minute, the leading predictors were trunk diameter (%IncMSE = 15.99), temperature (14.67%) and tree species (12.61%). A graphical importance analysis (Figure 7A), based on node purity (IncNodePurity), confirms the dominant role of these factors.

For the proportion of workers with a full crop, the most important predictors based on %IncMSE were tree species (18.65%), distance to the forest edge (11.35%), and proportion of dead branches (9.18%). A similar hierarchy of factors was observed when assessed using IncNodePurity (Figure 7B). Variable importance in Random Forest models was assessed using two complementary metrics. Permutation-based importance (%IncMSE) is presented in Table 8 and reflects the increase in prediction error when a predictor is randomly permuted. Figure 7 shows variable importance based on the mean decrease in node impurity (IncNodePurity). These two measures capture different aspects of predictor contribution and may result in slightly different rankings.

Table 8. Importance of predictors in Random Forest models (%IncMSE)

Predictor	% full goiter	Ants on trail/1 min
Diameter	7.01	15.99
Temperature	5.01	14.67
Tree species	18.65	12.61
Humidity	8.24	10.27
Moss, %	7.29	7.36
Dead branches, %	9.18	5.11
Hollows, number	—	1.46
Distance to forest edge	11.35	—

Note: dashes (—) indicate that the variable was not included in the corresponding model (e.g. distance to forest edge was only used for the trophic success analysis and cavity count was only used for the traffic intensity analysis).

Nonlinear dependency analysis (PDP)

Partial dependence plots confirmed the nonlinear nature of the influence of key predictors on colony activity (see Supplementary Table S6 and Figures 8 and 9). Temperature, humidity and substrate physical parameters are critical for the overall number of workers on trails (see Fig. 8). Maximum activity was recorded within a narrow temperature range of 22–26 °C. The optimal relative humidity for intensive foraging is up to 43%; exceeding this threshold leads to a sharp exponential decline in traffic. The size of the food resource also limits activity; the number of workers on the trail correlates with trunk thickness and reaches a maximum on trees with a diameter of 0.52 m.

The influence of the edge effect stabilises at a distance of 25 m from the forest edge. This pattern is consistent with greater activity near lighter forest-edge areas.

The proportion of workers with full crops decreased with increasing proportion of dead branches, distance to the forest edge, and trunk diameter (Figure 9).

The factors determining the proportion of workers with full goiters exhibit a different pattern related to the quality of the food supply (see Fig. 9). Unlike overall abundance, maximum trophic success is observed in weakened trees (with a proportion of dry branches in the crown of 20–60%), which is characteristic of old oaks that frequently support abundant aphid colonies. Dependence on diameter exhibits a pronounced bimodal form. Peak goiter filling rates were observed in foragers exploiting either young trees (diameter <0.2 m) or overmature trees (diameter 0.9–1.0 m and above). The proportion of foragers with full crops is also sensitive to spatial location, consistently decreasing with distance deeper than 20 metres into the forest from the edge. According to the results of the beta regression analysis, tree species is the most significant predictor of trophic success. Quercus robur increases the probability of detecting foragers with full crops compared to other species (beta = 1.245, $p < 0.001$). While ant traffic density is determined by external microclimatic conditions, foraging efficiency was strongly associated with the structure and species composition of the dendrocoenosis.

A GLMM, negative binomial distribution, random intercept = colony_id) was used to analyse ant activity on the trail (AIC = 1602.5). The presence of moss ($\beta = 0.023$, $p < 0.001$) and the number of tree cavities ($\beta = 0.142$, $p = 0.021$) were found to have a significant positive effect. The proportion of dry branches had a negative effect ($\beta = -0.009$, $p = 0.001$). Tree species Salix alba significantly reduced activity ($\beta = -1.659$, $p < 0.001$). Trunk diameter showed a positive trend ($\beta = 0.290$, $p = 0.148$). The full table of coefficients is provided in Supplementary Table S4.

Differentiation of resource use within the species *Quercus robur*

A comparative analysis of oak trees used as host and forage trees revealed marked functional differences between the colonies. Host trees are characterised by significantly higher rates of wood maturity and degradation. The median diameter of host oaks was significantly greater than that of forage trees (Wilcoxon test, $W = 266$, $p < 0.001$; see Figure 10, Supplementary Table S7). However, the most critical parameter was the presence of micro-refuges. Host trees had a significantly higher number of cavities than forage trees ($W = 129.5$, $p < 0.0001$). Although host trees may be relatively young with intact bark, their use as host trees was strongly associated with the presence of internal cavities and a significant volume of old wood, which are necessary for constructing and thermoregulating cardboard nests.

Additional analysis of intensive colony sampling confirmed the identified patterns for wide sample. In forest biotopes, the average number of tree species per colony ranged from 1.8 to 2.5, reaching a maximum in old-growth park zones (Table 9).

Table 9. Tree species richness characteristics in the intensive sample (validation)

Location (Habitat type)	Mean number of tree species per colony	Maximum number of species	Number of colonies (n)
Feofania (Deciduous forest)	2.0	4	15
Holosiivskyi National Nature Park (Deciduous forest)	1.8	3	5
Zhukiv Island (Floodplain forest)	1.38	3	16
Fomin Botanical Garden (Forest patches)	4.0	4	1
DVRZ (Mixed forest)	2.5	3	2

As in the wide sample, the most stable resource combination remained the association of *Quercus robur* and *Acer platanoides* (six colonies, accounting for 14.3% of the total number of colonies), supporting the importance of these species for *L. fuliginosus*. Among single-species associations, pure oak was dominant (12 cases, accounting for 28.6% of the entire sample).

Discussion

This study demonstrated that *Lasius fuliginosus* responds to urbanisation in a multi-scale, hierarchical manner. The various functional components of colony life, such as colony size, foraging intensity and trophobiotic efficiency, are regulated by factors that are partially independent but interrelated, and that operate at different spatial scales. This finding is consistent with the multidimensional niche concept in ant ecology (Hölldobler and Wilson, 1990; Lach et al. 2010), suggesting that the effects of urbanisation require simultaneous consideration of landscape, mesoscale and local levels.

The indirect effect of urbanisation on colony abundance

Colony abundance decreased significantly along the urbanisation gradient. GLM results suggest that this effect is indirect. When tree diameter and species richness of the dendrocoenosis were included in the model, the direct effect of habitat type lost statistical significance. The results suggest that the association between urbanisation and lower colony abundance may be mediated by resource degradation, primarily by causing the loss of large, structurally complex trees and the depletion of dendrocoenosis species composition. This conclusion aligns with findings suggesting that the decline in ant and other invertebrate abundance in urban landscapes is frequently mediated by changes in vegetation composition and structure rather than the urban environment's direct impact (McKinney 2008; Buczkowski and Richmond 2012; Stukalyuk et al. 2022).

Structural characteristics of the foraging network, such as the number of trees and foraging trails per colony, showed no significant differences between habitat types. This suggests behavioural plasticity as a buffering mechanism. *L. fuliginosus* colonies can maintain spatial foraging organisation even when resource quality degrades. A similar pattern has been observed in *Temnothorax nylanderi*, whose urban colonies have been found to maintain or increase foraging activity while simultaneously decreasing aggressiveness (Jacquier et al. 2023). However, as in our case, behavioural plasticity alone may be insufficient to compensate for the loss of high-quality resources, which ultimately affects colony size (Gordon 2010; Diamond and Martin 2021).

The role of *Quercus robur* and dendrocoenosis structure

Trunk diameter and tree species richness were found to be the most significant factors determining colony activity. These findings align with the principles of habitat ecology, which state that larger and older trees are likely to provide more potential settlement sites, a consistent microclimate, and a broader foundation for trophic interactions (Southwood and Henderson 2000; Mölder et al. 2019). This is particularly relevant for *L. fuliginosus*, as constructing and maintaining cardboard nests and their thermal regime is strictly limited by the presence of sufficiently large internal cavities (Khuong et al. 2011; Brinker et al. 2019; Stukalyuk et al. 2024).

At the level of tree species, *Quercus robur* was found to have significantly higher trophobiotic activity. The proportion of workers with full crops and the number of ants on oak trunks were significantly higher than for all other tree species. The intensity of movement along ground trails did not differ between tree species. This dissociation is important for interpretation as it indicates that oak provides higher-quality resources rather than higher traffic. This pattern may reflect the presence of more resource-rich and stable colonies of myrmecophilous aphids, although these measurements were not conducted. Oaks are known to be among the most productive host trees for specialist aphids in temperate Europe (Stadler and Dixon 2005; Depa et al. 2020). The obligate mutualism of *L. fuliginosus* with *Stomaphis aphids*, which are primarily associated with oak, creates a stable, high-calorie carbohydrate base (Depa et al. 2022). The constancy of such trophic links has been documented in studies of the spatial specialisation of the foraging behaviour of *L. fuliginosus* (Dobrzyńska 1966; Quinet and Pasteels 1996; Quinet et al. 1997).

The bimodal relationship between trophobiotic efficiency and trunk diameter (with peak values in young and overmature trees and a depression at intermediate diameters) can be explained as follows. There may be differences in tree stress, with young trees with thin bark actively forming surface phloem tissue that is accessible to aphids. In contrast, overmature oaks with 20–60% dry branches in the crown are chronically weakened. According to the host stress hypothesis, this may increase phloem nutrient availability, consequently increasing the productivity of aphid colonies (Koricheva et al. 1998; Stadler and Dixon 2005). Trees of intermediate age and diameter that are in good physiological condition are likely to be less attractive to specialised myrmecophilous aphids.

Microclimate as a regulator of foraging traffic

Microclimatic variables (temperature and humidity) were the leading predictors of foraging activity intensity in both the Random Forest and GLMM models. The highest levels of activity were observed within a temperature range of 22–26°C. Exceeding a relative humidity threshold of ~43% was accompanied by a sharp, exponential decline in foraging traffic. These non-linear relationships are consistent with known thermal efficiency curves in ants. Activity is limited by a species-specific temperature range (Porter and Tschinkel 1993; Diamond et al. 2012) and by excess humidity along environmental gradients (Kaspari and Weiser 2000).

Another study demonstrated active thermoregulation in *L. fuliginosus* nests in spring, enabling colonies to remain active at low external temperatures (Stukalyuk et al. 2024). This is consistent with the narrowness of the observed temperature optimum and suggests that high foraging activity occurs only within a strictly defined thermohygric window. Changes to the microclimatic regime, including those associated with the urban heat island effect or increased drought in urbanised areas, may influence colony foraging activity, even when suitable trees remain available.

Tree structural characteristics and ant activity: GLMM results

A generalised linear mixed model identified several tree structural characteristics that were independently associated with foraging activity. The positive effects of moss cover (β = 0.023) and the number of tree cavities (β = 0.142) are consistent with the concept of microstructural habitat complexity. Moss cover may contribute to moisture and temperature buffering on the trunk surface, creating a more stable microclimate, while tree cavities likely provide nesting or shelter opportunities during periods of adverse conditions. The negative effect of the proportion of dead branches on traffic and the positive effect of moderate desiccation (20–60% of the crown) on trophobiotic efficiency reflect subtle physiological differences. Chronic tree weakening may increase resource quality for aphids, while critical tree condition reduces the overall attractiveness of the trunk as a route. The negative association of Salix alba with activity (β = −1.659) suggests that not all tree species visited by *L. fuliginosus* are equally valuable as food resources, with willow likely supporting less stable or less diverse associations of myrmecophilous aphids.

Trophobiotic success and the edge effect

The decrease in the proportion of workers carrying a full crop at distances greater than 20 metres from the forest edge is consistent with the general logic of the edge effect in forest ecology. Ecotone zones are typically characterised by higher light levels, which may enhance photosynthetic activity and phloem productivity. This is also consistent with data showing that, in urban landscapes, reduced predation pressure on aphids (due to a reduction in the coccinellid and other aphid-eating insect community) can lead to aphid population outbreaks specifically at forest edges and in park areas (Korányi et al. 2021). Gaber et al. (2024), however, found increased aggressive behaviour in urban ants defending aphids in a similar system (*Lasius niger* + aphids on *Tanacetum vulgare*), interpreting this as a compensatory response to reduced resource reliability. By contrast, our data document a decrease in trophobiotic

efficiency deeper in the forest, suggesting that highly productive carbohydrate sources may be concentrated in ecotone zones.

Comparing Random Forest and GLMM: complementarity of approaches

The discrepancy in predictor ranking between Random Forest (%IncMSE) and GLMM reflects fundamental differences in what each method measures rather than contradiction between them. Random Forest is optimised for prediction and is adept at identifying non-linear relationships and interactions between predictors; this explains why temperature and stem diameter were identified as variables with broad non-linear effects. GLMM, in contrast, estimates the independent contribution of each predictor while controlling for the others. This allowed the identification of more specific, yet statistically robust, effects of structural characteristics (wood hollows and moss). The use of complementary methods is increasingly recommended in ecological studies of complex systems (Lach et al. 2010).

Hierarchical Model of Habitat Selection and Conservation Value

Overall, the results support a three-level hierarchical model of system organisation. At the landscape level, urbanisation is associated with changes in the availability of suitable trees and the overall composition of the dendrocoenosis. At the mesoscale, the composition of tree species and the distance to the forest edge influence the quality of trophobiotic resources. At the local level, microclimatic conditions and trunk microstructure are associated with variation in foraging traffic intensity. This three-level organisation is consistent with the modern understanding of multiscale habitat selection in insects (Del Toro et al. 2012).

By combining the modelling results, we can formulate an integrated functional profile of the optimal habitat for *L. fuliginosus* at the level of the individual tree (see Supplementary Tables S8–S9). Nest and forage trees have different ecological requirements, reflecting their distinct roles in colony organisation. The optimal nesting tree is a large, old-growth *Quercus robur* with a trunk diameter of 0.7–1.2 m, multiple cavities, high moss coverage and a moderate proportion (20–60%) of dead branches in the crown, located within 20–30 m of the forest edge. In contrast, an optimal host tree does not necessarily have to have cavities; the determining factor here is the abundance of myrmecophilous aphids in the crown, which is higher on medium- and large-diameter trees in a warm, relatively dry microclimate. This distinction has direct practical significance. Effective protection of *L. fuliginosus* colonies in urbanised landscapes is likely to depend on the preservation of large oaks as a nesting substrate, as well as the maintenance of a structurally diverse environment including trees of different ages and conditions, which are capable of providing a stable trophobiotic base.

The differentiation of the functions of nest and forage trees within the *Q. robur* species reflects the colonies' high level of functional specialisation. Host trees are strictly limited by the presence of large cavities, whereas forage trees can be relatively young if productive aphid colonies are present. This distinction is important for conservation purposes. Conserving large, old-growth oaks is essential

primarily as a nesting resource, whereas maintaining the trophobiotic base requires preserving trees of diverse ages and conditions, including weakened specimens with moderate crown decline. Similar conclusions about the critical role of structurally complex, old-growth trees in maintaining forest entomofauna have been reached in studies on the management of oak forests in Central Europe (Mölder et al. 2019). From the perspective of urban green space management, the results suggest that the removal of 'physiologically weakened' trees with moderate crown decline would be inappropriate, as these trees were associated with the highest trophobiotic activity in our dataset and could be crucial for the survival of *L. fuliginosus* colonies in conditions where resources are limited.

Limitations and future prospects

This study has a number of limitations that must be acknowledged. The primary intensive sampling data were collected during a single field season and within a single metropolitan area, which limits the study's generalisability across time and geography. The observational design precludes direct inference of causal relationships. As trophobiotic efficacy was estimated based on standardised proportional observations rather than individual-level counts, the beta regression models did not explicitly weight observations according to the number of returning workers. A key variable - aphid abundance and composition on trees was not directly measured despite being the primary mechanistic link between tree characteristics and trophobiotic efficacy (Stadler and Dixon 2005; Depa et al. 2020). Future research should integrate the direct quantitative characterisation of aphid communities at the tree level, comparative analysis across multiple metropolitan areas and experimental manipulation of tree availability and microclimate. Cross-species comparisons with other arboreal *Lasius* species, such as *L. emarginatus* and *L. brunneus*, would enable us to determine whether the observed dependence on *Q. robur* is specific to *L. fuliginosus* or indicative of a broader pattern among temperate arboreal ants.

Conclusions

This study suggests that the response of *Lasius fuliginosus* to urbanisation is largely indirect, and may be mediated through resource degradation rather than direct physiological stress in the urban environment. Colony activity was most strongly associated with tree diameter and species richness of the dendrocoenosis, while the significance of habitat type was lost when these variables were included in the model. Colony trophobiotic efficiency was strongly linked to tree species: *Quercus robur* was associated with a significantly higher proportion of workers with full crops and a greater number of ants on trunks than all other species combined. In contrast, foraging traffic intensity was most strongly associated with microclimatic factors (temperature and humidity), which exhibited pronounced nonlinear relationships. Additionally, trunk structural characteristics (e.g. hollows and moss) made an independent contribution. The functional specialisation of nest and forage trees within the *Q. robur* species is clearly evident. The former are limited by the presence of internal cavities and the volume of old wood, while the latter are limited by the availability of trophobiotic resources. Taken together, the results support a three-level hierarchical model: urbanisation acts at the landscape level through the composition and structure of the dendrocenosis, tree species and condition determine trophobiotic efficiency at the mesoscale, and

microclimatic conditions regulate foraging activity locally. From a practical perspective, the obtained data support the preservation of large old-growth trees, especially *Q. robur*, and maintaining structurally diverse stands, including physiologically weakened specimens, as these are key elements of the urban environment likely important for the long-term persistence of *L. fuliginosus* colonies.

Declarations

Acknowledgments:

This work was supported by the Programme “Support for the development of priority areas of scientific research in Ukraine”, KPKVK 6541230 (for S. Stukalyuk).

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Funding

This work was supported by the Programme “Support for the development of priority areas of scientific research in Ukraine”, KPKVK 6541230 (for S. Stukalyuk). No additional funding was received to assist with the preparation of this manuscript or for conducting the study.

Ethics approval

This study did not require ethics approval as it involved observational field research on invertebrates (ants) without any invasive procedures, manipulation of animals, or collection of specimens.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Authors’ contributions

Stanislav Stukalyuk: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing & editing, Visualization, Project administration.

Yaroslav Sydorenko: Investigation, Data curation, Visualization.

Mykola Kozyr: Investigation, Resources, Writing & editing.

All authors read and approved the final manuscript.

References

1. Bonser AL, Wright PJ, Bament S, Chukwu UO (1998) Optimal patch use by foraging workers of Lasius fuliginosus, L. niger and Myrmica ruginodis. Ecol Entomol 23(1):15–21
2. Brinker P, Weig A, Rambold G, Feldhaar H, Tragust S (2019) Microbial community composition of nest-carton and adjoining soil of the ant Lasius fuliginosus and the role of host secretions in structuring microbial communities. Fungal Ecol 38:44–53
3. Buczkowski G, Richmond DS (2012) The effect of urbanization on ant abundance and diversity: A temporal examination of factors affecting biodiversity. J Insect Conserv 16(2):191–199. https://doi.org/10.1007/s10841-011-9405-4
4. Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices. Myrmecological News 17:133–146
5. Depa Ł, Mróz E, Orczewska A, Szawaryn K (2020) Evolution of trophobiosis — the origin and evolution of ant-aphid relationships. Biol Rev 95(6):1574–1589. https://doi.org/10.1111/brv.12629
6. Depa Ł, Węgierek P, Wieczorek K, Kanturski M (2022) Mutualism between Lasius ants and Stomaphis aphids — a case of trophobiosis with a social parasite. Pol J Ecol 70(1):44–55. https://doi.org/10.3161/15052249PJE2022.70.1.004
7. Detrain C, Deneubourg JL (2008) Collective decision-making and foraging patterns in ants and honeybees. Insectes Sociaux 55(1):1–10. https://doi.org/10.1007/s00040-007-0971-6
8. Diamond SE, Martin RA (2021) Evolution in cities. Annu Rev Ecol Evol Syst 52:519–540. https://doi.org/10.1146/annurev-ecolsys-012021-021402
9. Diamond SE, Sorger DM, Hulcr J, Pelini SL, Toro D, Hirsch I, Oberg C, E., Dunn RR (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Glob Change Biol 18(1):448–456. https://doi.org/10.1111/j.1365-2486.2011.02542.x
10. Dobrzańska J (1966) The control of the territory by Lasius fuliginosus Latr. Acta Biologiae Exp 26(2):193–213
11. Gaber H, Ruland F, Jeschke JM, Bernard-Verdier M (2024) Behavioural changes in the city: The common black garden ant defends aphids more aggressively in urban environments. Ecol Evol 14:e11639. https://doi.org/10.1002/ece3.11639
12. Gordon DM (2010) Ant encounters: Interaction networks and colony behavior. Princeton University Press
13. Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319(5864):756–760. https://doi.org/10.1126/science.1150195

14. Hölldobler B, Wilson EO (1990) The ants. Harvard University Press
15. Jacquier L, Molet M, Doums C (2023) Urban colonies are less aggressive but forage more than their forest counterparts in the ant Temnothorax nylanderi. Anim Behav 199:11–21. https://doi.org/10.1016/j.anbehav.2023.02.004
16. Kaspari M, Weiser MD (2000) Ant activity along moisture gradients in a Neotropical forest. Ecology, 81(8), 2203–2211. https://doi.org/10.1890/0012-9658(2000)081[0207:AAAMGI]2.0.CO;2
17. Khuong A, Theraulaz G, Jost C, Perna A, Gautrais J (2011) A computational model of ant nest morphogenesis. In ECAL 2011: Proceedings of the 11th European Conference on Artificial Life (pp. 404–411)
18. Korányi D, Szigeti V, Mezőfi L, Kondorosy E, Markó V (2021) Urbanization alters the abundance and composition of predator communities and leads to aphid outbreaks on urban trees. Urban Ecosyst 24(3):571–586. https://doi.org/10.1007/s11252-020-01061-8
19. Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: A meta-analysis. Ann Rev Entomol 43:195–216. https://doi.org/10.1146/annurev.ento.43.1.195
20. Lach L, Parr CL, Abbott KL (eds) (2010) Ant ecology. Oxford University Press
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. Ann Zool 63(1):107–111
22. McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst 11(2):161–176. https://doi.org/10.1007/s11252-007-0045-4
23. Mölder A, Meyer P, Nagel R-V (2019) Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (Quercus robur, Q. petraea) forests: An overview. For Ecol Manag 437:324–339. https://doi.org/10.1016/j.foreco.2019.01.006
24. Ossola A, Niemelä J (2018) Urban biodiversity: Patterns, processes and implications for conservation. Ann N Y Acad Sci 1429(1):1–12. https://doi.org/10.1111/nyas.13666
25. Porter SD, Tschinkel WR (1993) Fire ant thermal preferences: Behavioral control of growth and metabolism. Behav Ecol Sociobiol 32(5):321–329. https://doi.org/10.1007/BF00183789
26. Quinet Y, Pasteels JM (1996) Spatial specialization of the foragers and foraging strategy in Lasius fuliginosus (Hymenoptera: Formicidae). Insectes Sociaux 43:333–346
27. Quinet Y, de Biseau JC, Pasteels JM (1997) Food recruitment as a component of the trunk-trail foraging behaviour of Lasius fuliginosus (Hymenoptera: Formicidae). Behav Process 40(1):75–83
28. Ribas CR, Schoereder JH, Pic M, Soares SM (2008) Ants as indicators of the conservation value of Brazilian Cerrado. Biodivers Conserv 17(13):3233–3244
29. Rocha EA, Fellowes MDE (2020) Urbanisation alters ecological interactions: Ant mutualists increase and specialist insect predators decrease on an urban gradient. Sci Rep 10:6406. https://doi.org/10.1038/s41598-020-63562-y

30. Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: A review of its drivers. Biol Conserv 232:8–27. https://doi.org/10.1016/j.biocon.2019.01.020
31. Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences, 109(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109
32. Ślipiński P, Markó B, Rzeszowski K, Babik H, Czechowski W (2014) Lasius fuliginosus shapes local ant assemblages. North-Western J Zool 10(2):404–412
33. Southwood TRE, Henderson PA (2000) Ecological methods, 3rd edn. Blackwell Science
34. Stadler B, Dixon AFG (2005) Ecology and evolution of aphid–ant interactions. Annu Rev Ecol Evol Syst 36:345–372. https://doi.org/10.1146/annurev.ecolsys.36.091704.175531
35. Stukalyuk S (2015) Structure of ant assemblages in broad-leaved forests of Kyiv. Entomol Rev 95(3):370–387. https://doi.org/10.1134/S0013873815030126
36. Stukalyuk S (2017) Interactions of dominant ant species in broadleaf forests. Entomol Rev 97(6):747–767. https://doi.org/10.1134/S0013873817060061
37. Stukalyuk S, Akhmedov A, Gilev A, Reshetov A, Radchenko Y, Kosiuk N (2022) Effect of urban habitats on colony size of ants (Hymenoptera, Formicidae). Turkish J Zool 46(1):1–14. https://doi.org/10.55730/1300-0179.3057
38. Stukalyuk SV, Radchenko Y, Balabukh V (2024) Active thermoregulation in Lasius fuliginosus nests in spring (Hymenoptera: Formicidae). Fragmenta Entomologica 57(2):271–286. https://doi.org/10.13133/2284-4880/1047
39. Tóth E, Móra A, Csabai Z, Horváth R, Markó B (2019) Urbanization increases the proportion of generalist ants in ant communities. Insect Conserv Divers 12(5):402–411
40. Tschinkel WR (2011) The organization of foraging in ant colonies. J Insect Sci 11(26):1–26. https://doi.org/10.1673/031.011.2601
41. United Nations, Department of Economic and Social Affairs, Population Division (2022) World urbanization prospects: The 2022 revision. United Nations
42. Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosyst 13(4):425–441. https://doi.org/10.1007/s11252-010-0136-5
43. van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368(6489):417–420. https://doi.org/10.1126/science.aax9931
44. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated count data. R J 9(2):378–400. https://doi.org/10.32614/RJ-2017-066
45. Cribari-Neto F, Zeileis A (2010) Beta regression in R. J Stat Softw 34(2):1–24. https://doi.org/10.18637/jss.v034.i02
46. Liaw A, Wiener M (2002) Classification and regression by randomForest. R News 2(3):18–22

Figures

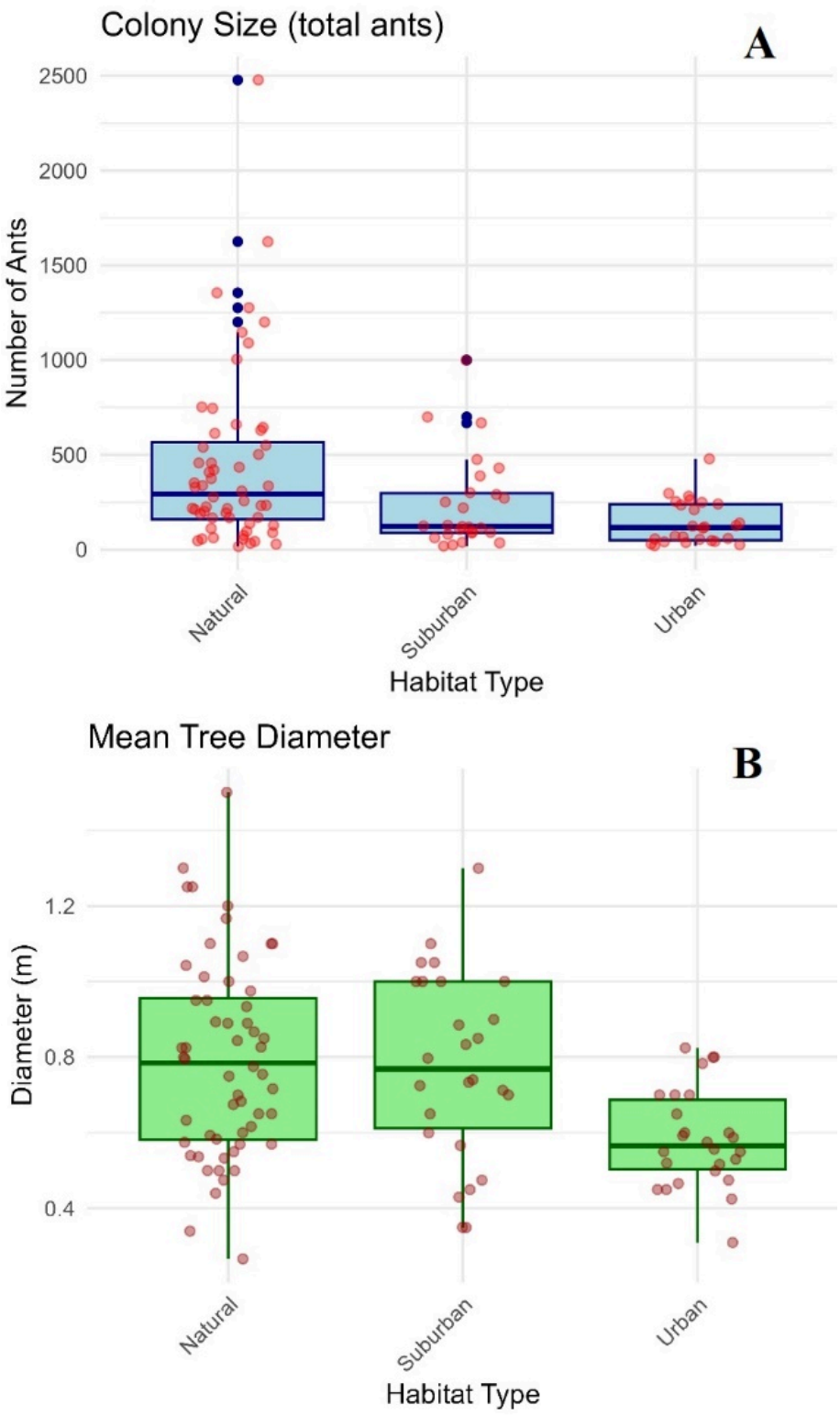


Figure 1

Distribution of *Lasius fuliginosus* colony parameters along the urbanisation gradient (A: overall ant activity; B: tree diameter)

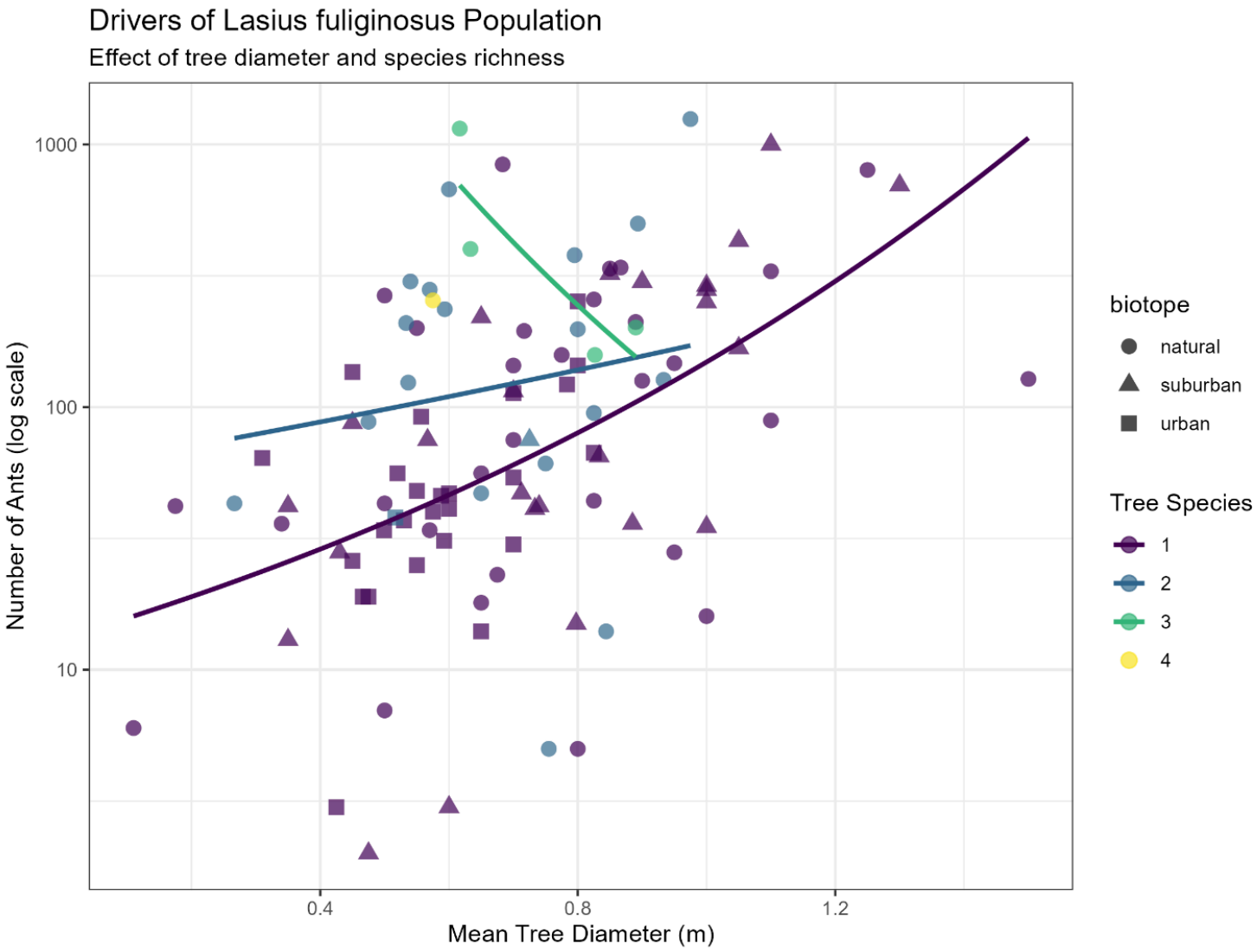


Figure 2

Contribution of biotope structural characteristics to the total abundance of *Lasius fuliginosus* colonies (GLM modelling results)

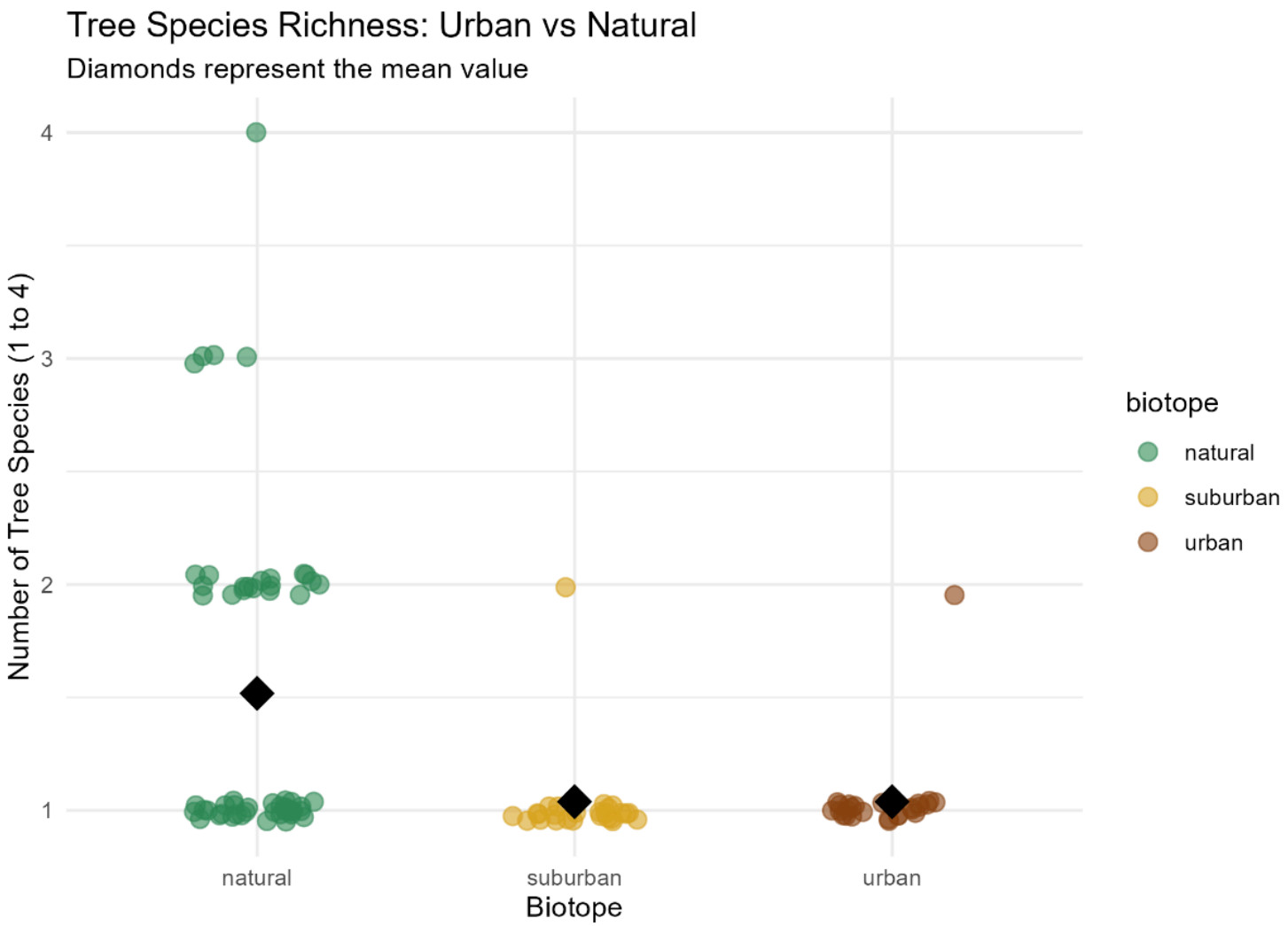


Figure 3

Species richness of host trees in Lasius fuliginosus colonies along the urbanisation gradient

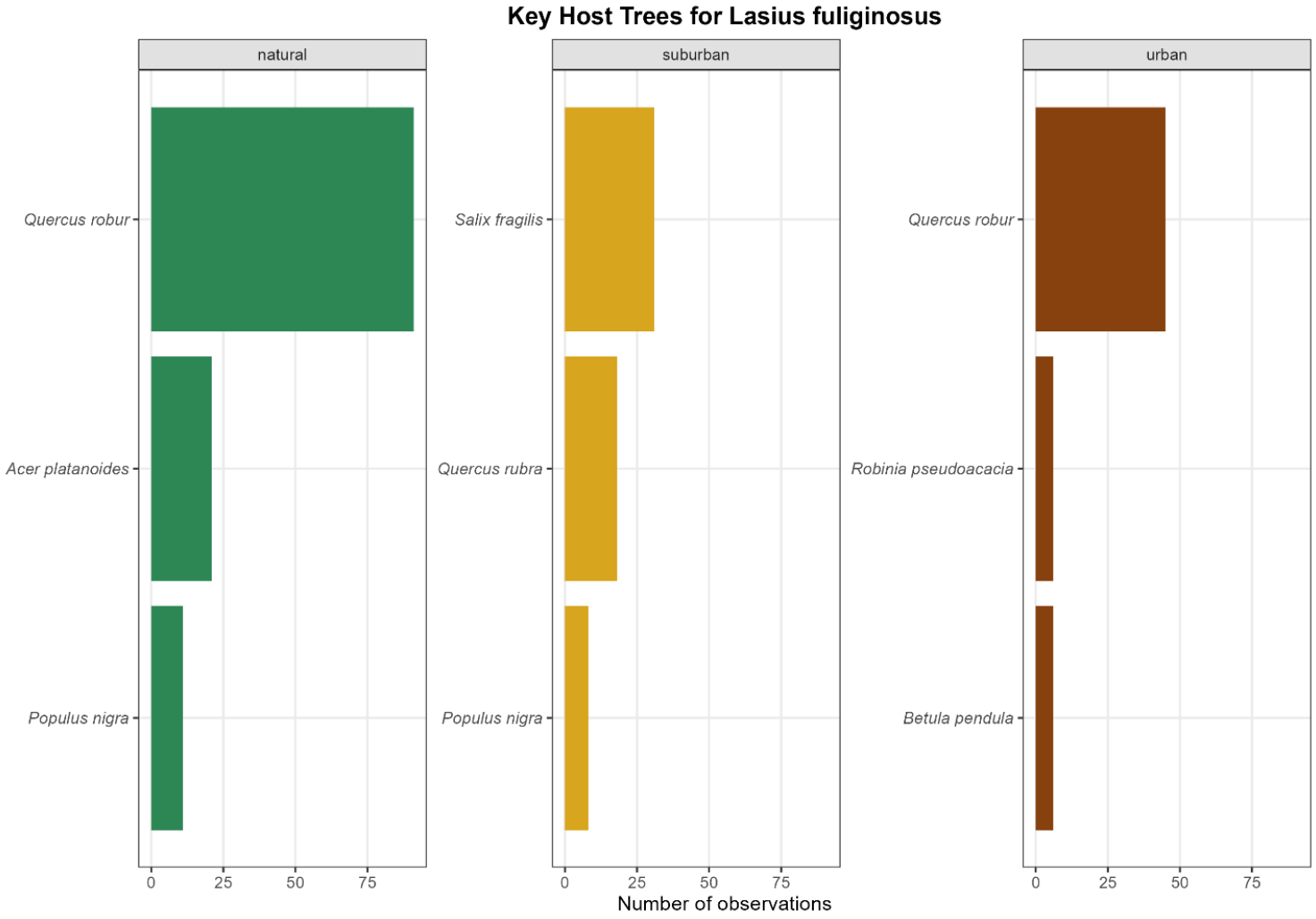


Figure 4

Main tree species and combinations exploited by colonies in various biotopes

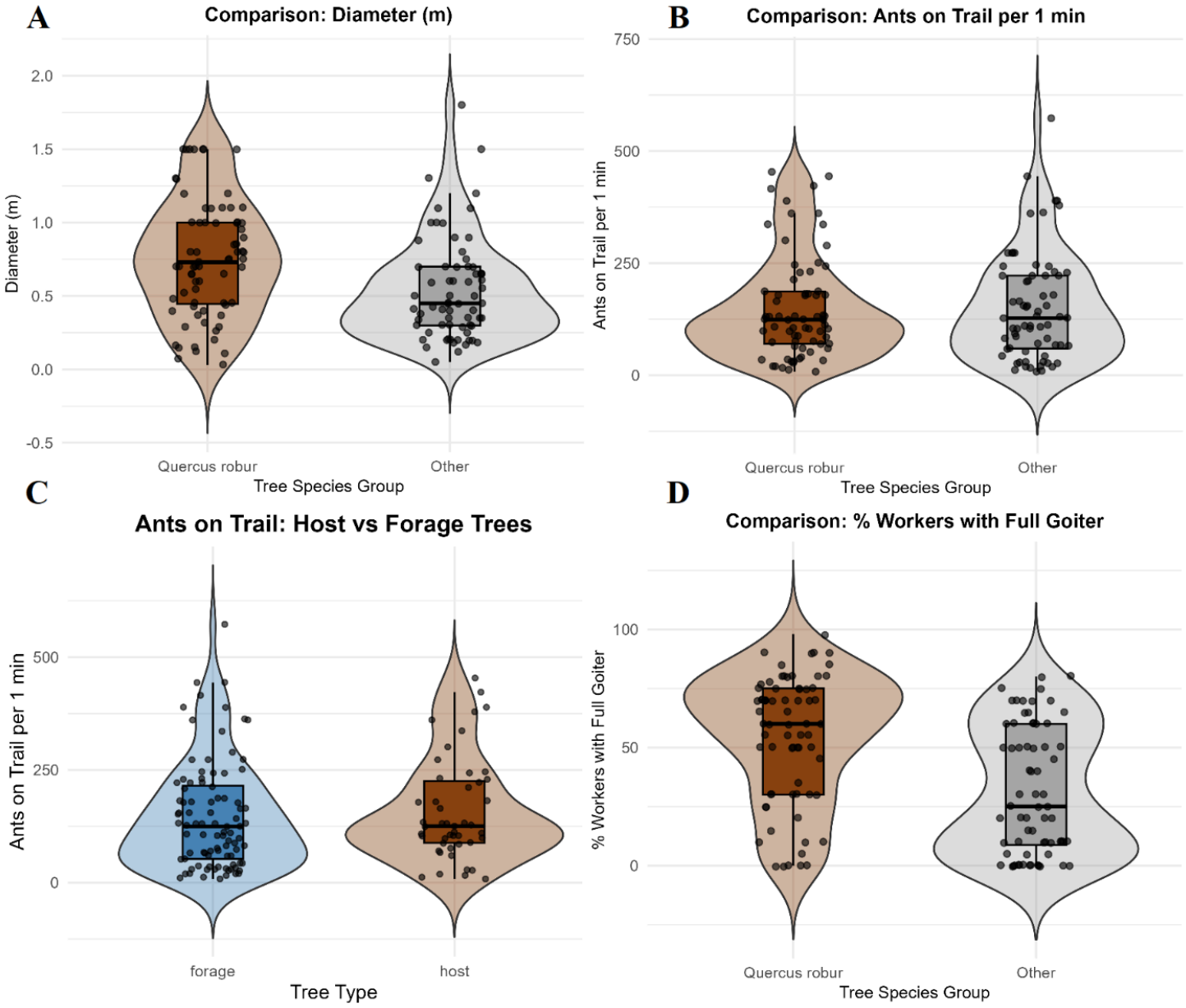


Figure 5

Trunk diameter comparison in *Quercus robur* and other tree species (A); ant trail activity (B); ant trail activity along the trunks of host and forage trees (C); and the percentage of ants with full crops on the trunks of oaks and other tree species (D) (violin plots).

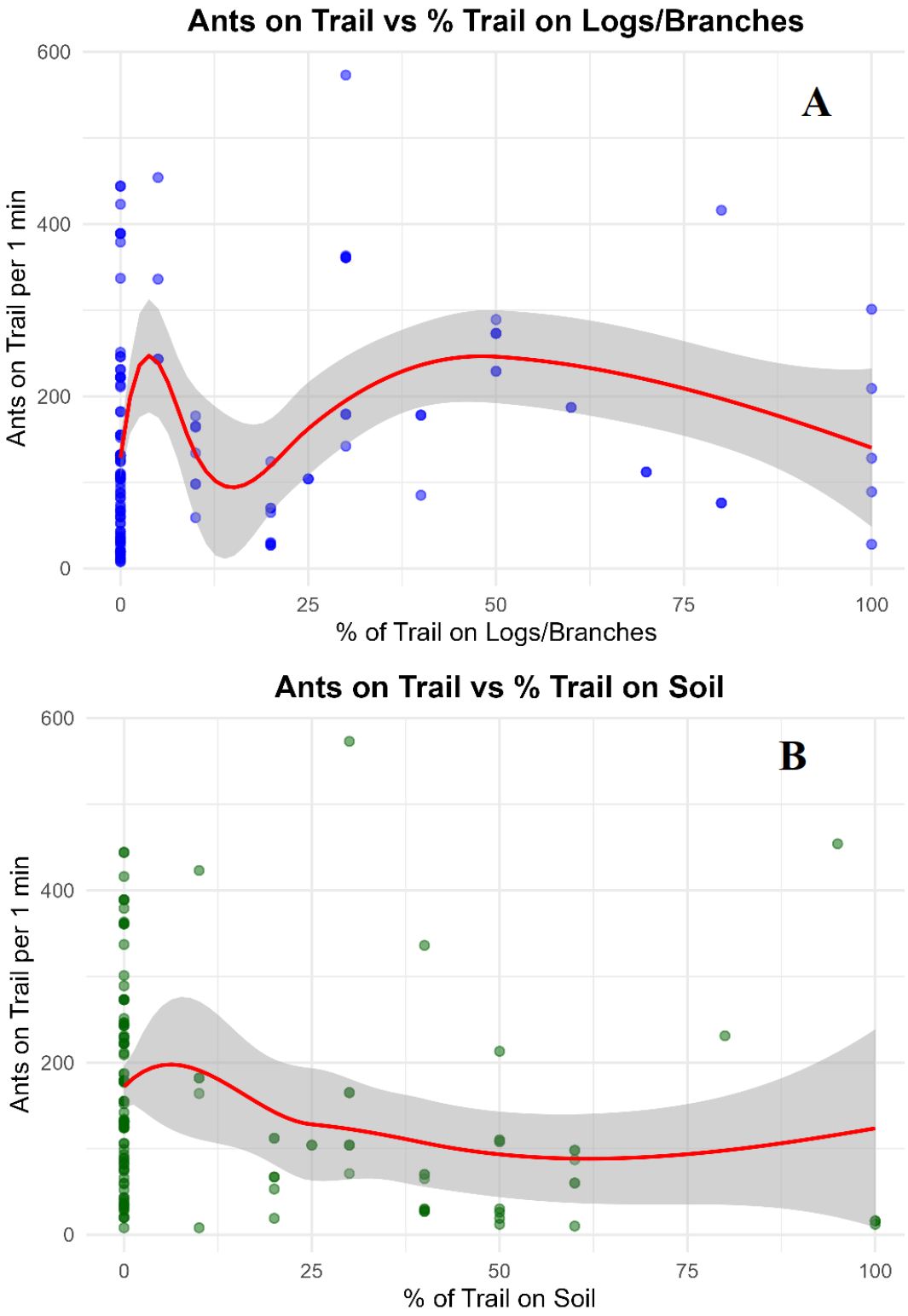


Figure 6

Effect of trail physical characteristics and substrate type on worker movement intensity in *L. fuliginosus*. A: Substrate type: logs and branches. B: Substrate type: soil without litter

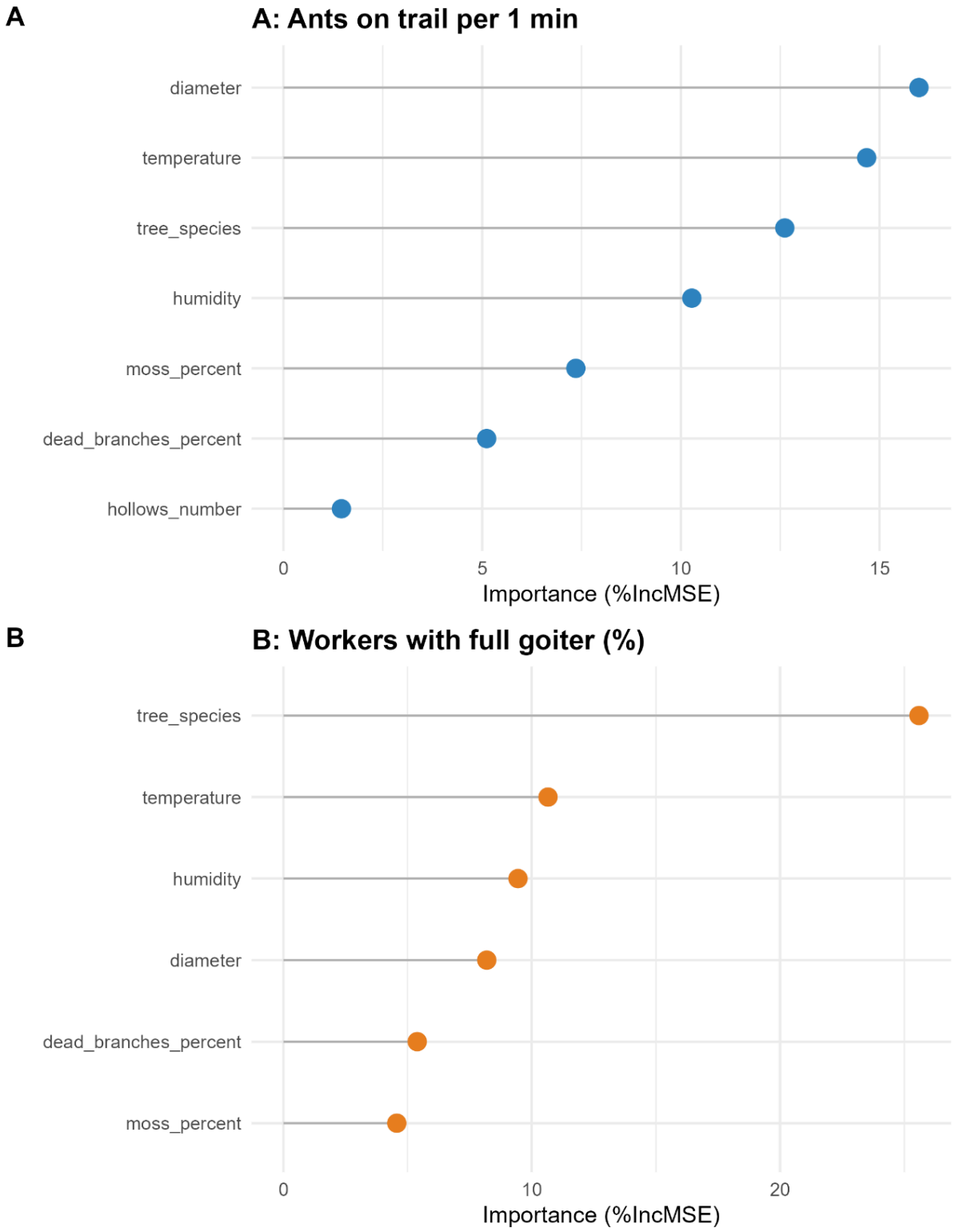


Figure 7

Predictor importance in Random Forest models for *L. fuliginosus* activity: (A) Number of ants on the trail per minute; (B) Proportion of workers with a full crop. Importance was assessed using the percentage increase in mean square error (%IncMSE). Higher values indicate a greater contribution to the model's predictive ability.

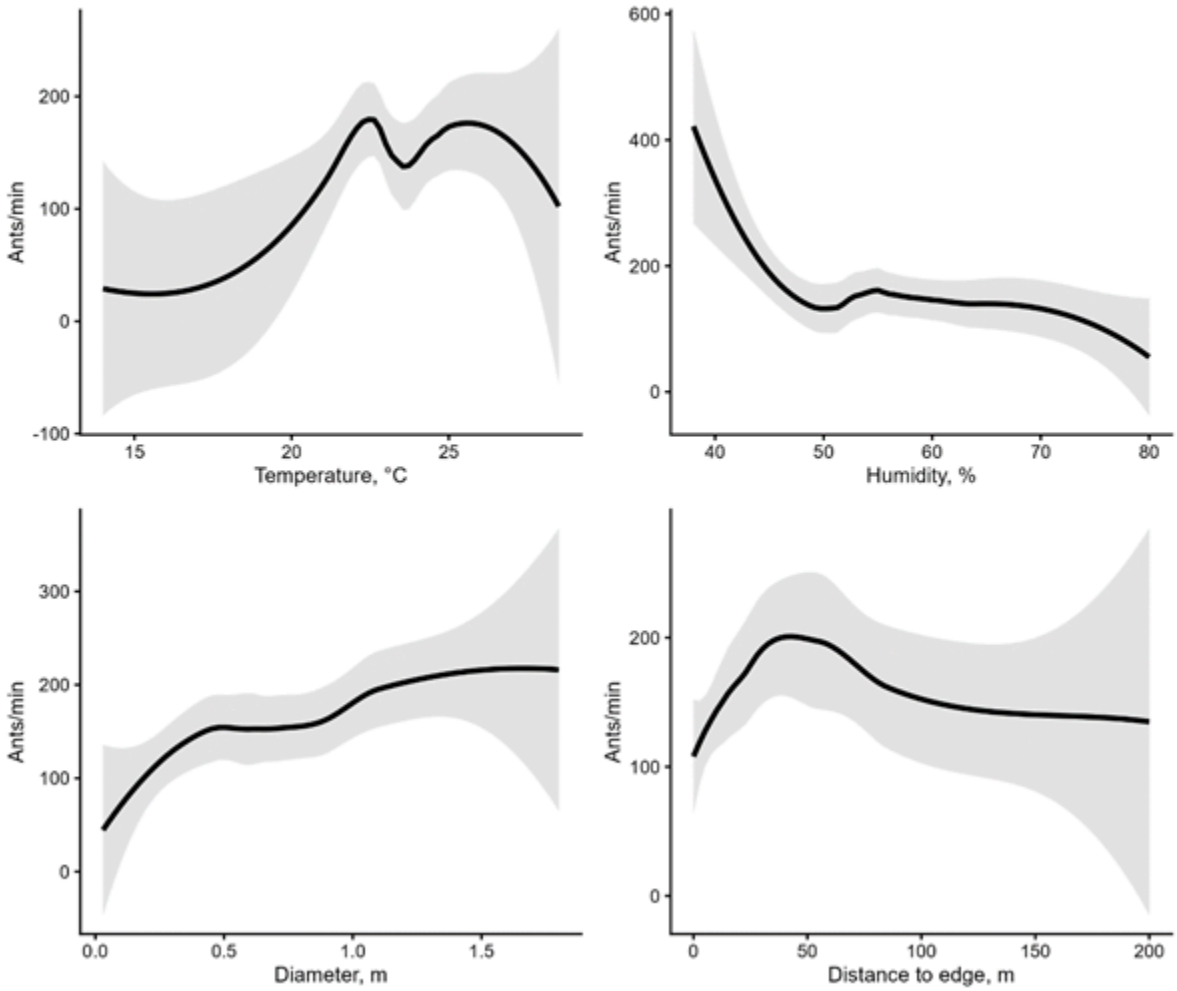


Figure 8

Partial dependence plots of the main predictors for the number of ants on trail per minute in the Random Forest model

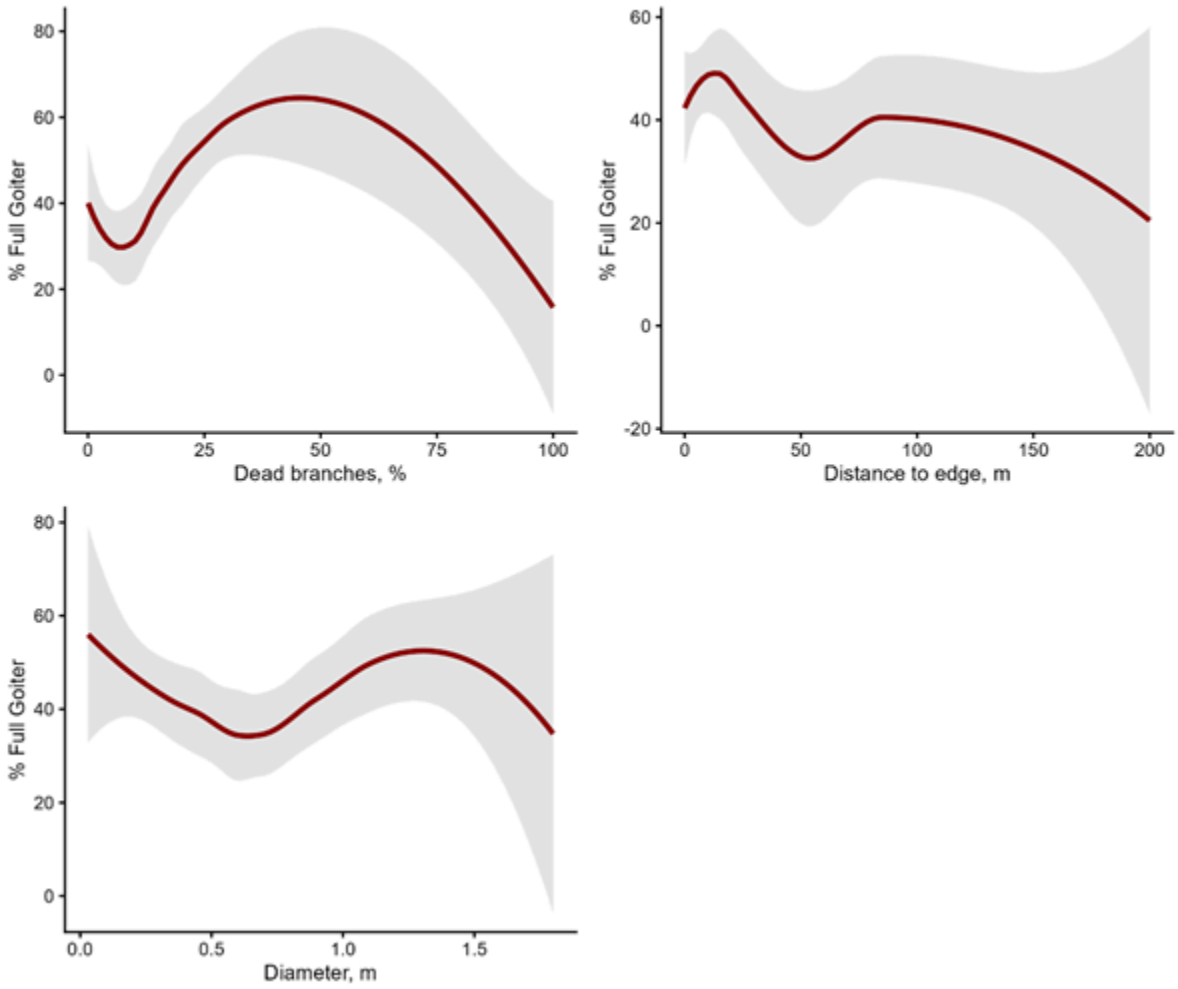


Figure 9

Partial dependence plots of the main predictors of the proportion of workers with full goiters in the Random Forest model

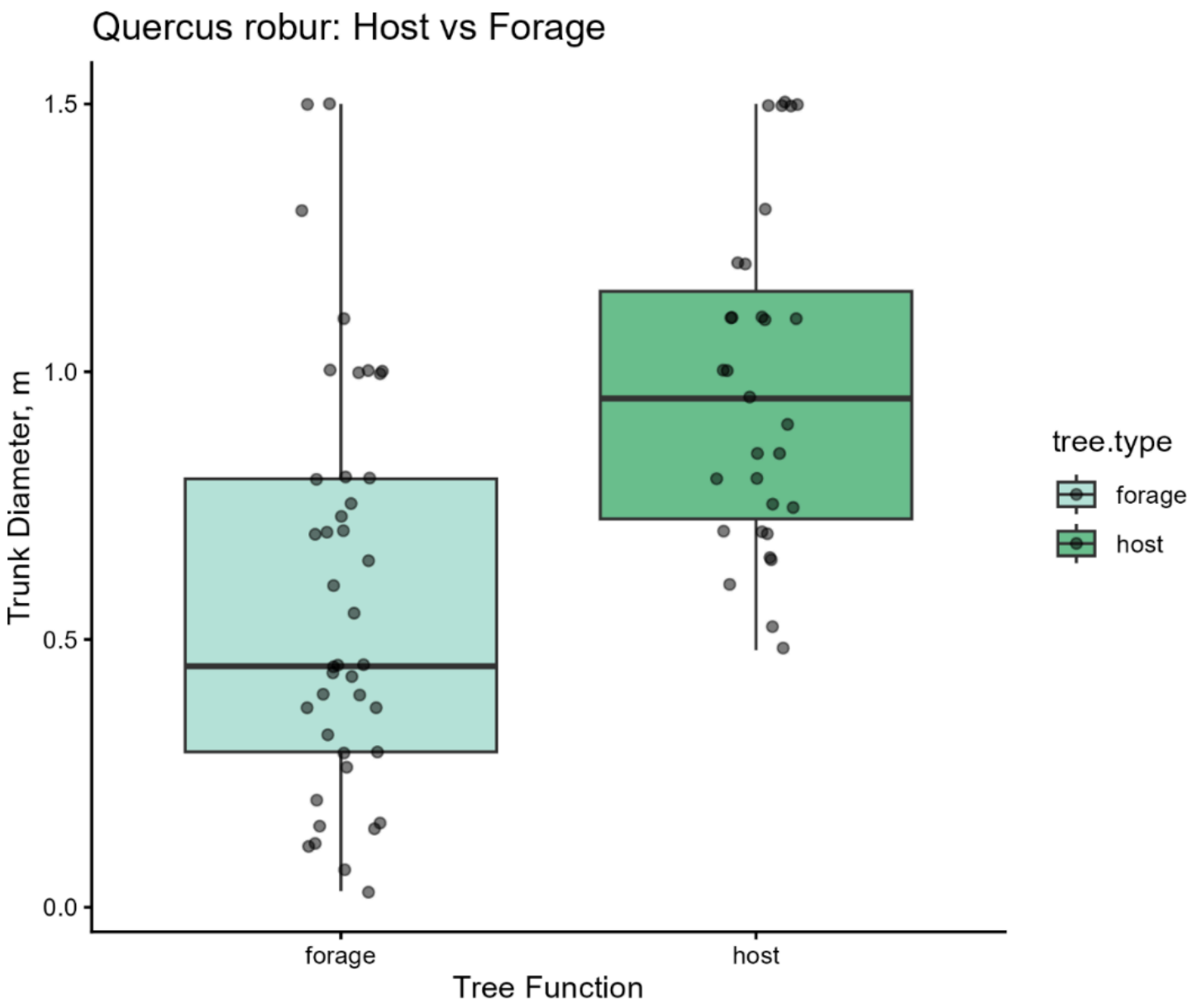


Figure 10

Comparison of trunk diameter and number of hollows between host and forage trees of *Quercus robur*. Significant differences ($p < 0.001$) reflect the high selectivity of *L. fuliginosus* in choosing nesting sites

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementFinal.docx