



RESEARCH ARTICLE - ANTS

Social and Spatial Organization of *Dolichoderus quadripunctatus* (Hymenoptera, Formicidae) Colonies in Forests, Urban Habitats, and Supercolonial Systems

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Abstract

Supercoloniality is characterized by vast, interconnected nest networks that lack territorial aggression, a pattern typical of many invasive ants. However, its occurrence and adaptive significance in native species remain poorly understood. Here, we examine the context-dependent shift from small, competition-limited colonies in forests to expansive supercolonies in human-modified habitats using the arboreal ant *Dolichoderus quadripunctatus* as a model. We tested three hypotheses: (H1) interspecific competition and limited inter-tree connectivity constrain abundance in closed-canopy forests and urban tree stands; (H2) internal foraging-trail networks, rather than substrate or competition, drive colony size in supercolonies and large polycalic systems; and (H3) supercolonial systems exhibit fission – fusion dynamics, enabling demographic recovery after severe crashes while maintaining the relationship between trail length and abundance. From 2024 to 2025, we surveyed 224 trees in urban and forest habitats in Ukraine, combining these data with a decade-long (2015–2025) monitoring study of one supercolony and one large polycalic settlement. Forest and urban colonies were oligodomic and limited by competition with *Lasius niger* and *L. emarginatus*, as well as by poor tree connectivity. In contrast, foraging-trail count was the dominant predictor of worker abundance in supercolonial and polycalic systems throughout the study period (rate ratios 1.93–2.41). The supercolony collapsed by over 90% between 2015 and 2024, but partially recovered in 2025; walnut trees acted as persistent refugia in this case. Thus, *D. quadripunctatus* shows that native supercoloniality can emerge through behavioral infrastructure (trail networks) when ecological constraints are relaxed, offering a rare link between classic polydomy and invasion-driven unicoloniality.

Introduction

Ant societies exhibit remarkable variation in their social organization. They range from small, monogynous and monodomous colonies to vast, polygynous supercolonies that lack nestmate recognition and territorial boundaries (Hölldobler & Wilson, 1977; Zakharov, 2015; Seifert, 2018). Supercoloniality is most evident in invasive species, such as *Linepithema humile* and *Lasius neglectus*, where reduced genetic diversity and diminished aggression enable rapid range expansion (Giraud et al., 2002; Espadaler et al., 2004; Ugelvig et al., 2008). However, in native ants, large polydomous

systems appear to be an adaptive response to stable or resource-rich environments, rather than a pathological breakdown of recognition systems (Ellis & Robinson, 2014; Zakharov, 2015; Stukalyuk et al., 2023). Therefore, understanding the ecological and behavioral drivers that allow native species to cross the threshold from localized polydomy to supercoloniality offers critical insight into the evolutionary flexibility of insect societies.

The arboreal dolichoderine ant, *Dolichoderus quadripunctatus*, is an excellent native model for such transitions. Long-term studies in Kyiv, Ukraine, have documented both typical oligodomic colonies (in 1–2 trees) and a supercolony spanning



over 130 nests across orchard rows (Stukalyuk, 2018; Stukalyuk et al., 2024). Unlike invasive supercolonies, this system remains within the species' native range and retains aggression towards distant conspecifics. This suggests a context-dependent relaxation of recognition cues rather than their complete loss. The species' trophic specialization, extensive trail networks, and ability to monopolize canopy resources through exploitative competition (Czechowski et al., 2012; Stukalyuk, 2017) further predispose it to rapid colony expansion when ecological constraints are lifted.

We used the natural gradient of colony complexity to test the following three hypotheses:

H1: In forest and urban tree stands (e.g., parks, alleys, and gardens), the abundance of *D. quadripunctatus* is primarily constrained by interspecific competition (mainly from *Lasius emarginatus*, *L. niger*), as well as limited spatial connectivity between trees. Tree diameter and microclimate play a secondary role. We therefore predicted negative correlations with competitor abundance and positive effects of inter-tree distance and urban habitat type.

(H2): In supercolonies and large polycalic settlements, internal foraging trail infrastructure would override external substrate factors and competition as the primary driver of worker numbers and spatial extent. We predicted that trail count would be the strongest predictor in GLMs across years.

(H3): Supercolonial systems exhibit fission-fusion dynamics, enabling them to partially recover after severe population crashes while maintaining the functional link between trail networks and worker abundance. We predicted significant temporal variation in nest and trail numbers, but persistent correlations between trails and abundance over a decade.

By linking ecological constraints, behavioral pre-adaptations, and long-term demographic data, this study sheds light on the conditions under which a native arboreal ant evolves a supercolony-like organization. This offers a rare counterpoint to the invasion-driven paradigm that currently dominates our understanding of unicoloniality.

Materials and Methods

Study area and sampling design

Fieldwork was conducted in June–July 2024 and 2025 in Kyiv and Kyiv Oblast, Ukraine. We compared *Dolichoderus quadripunctatus* colonies in two habitat types: deciduous forests and urban tree stands (parks, residential courtyards, gardens, and alleys). A separate decade-long dataset (2015–2025) was used for one documented supercolony (walnut–apple orchard) and one large polycalic settlement (lime alley) located within the urban area (Stukalyuk, 2018; coordinates provided in Supplementary Table S1).

Surveys were performed between 09:00 and 12:00 on clear days (air temperature 20–25 °C) using 10-m-wide belt transects. All trees within 5 m of the observer were inspected up to 2 m in height. When *D. quadripunctatus* was present

on a tree trunk, we recorded worker abundance (2-minute timed counts on the trunk), number of foraging trails per tree, tree species, trunk diameter at 1.6 m, inter-tree distance (both within the same colony and to the nearest tree occupied by another ant species), and shade air temperature and humidity using an SHT35 sensor (Sensirion).

The same protocol was followed for trail counts in the supercolony and polycalic settlement in 2024–2025. Historical data for 2015 originated from Stukalyuk (2018). The ants were identified in the field and, when necessary, in the laboratory, using the methods described by Radchenko (2016) and Seifert (2018).

Statistical analysis

All analyses were performed in R 4.5.1 (R Core Team, 2025). As worker counts were over-dispersed and zero-inflated, negative binomial generalized linear models (glm.nb, MASS package) were used to identify abundance predictors in (i) forest and urban tree stands ($n = 140$ observations from 224 trees) and (ii) supercolony/polycalic settlements ($n = 124$ tree-level observations across 2015–2025). The predictor sets are detailed in Tables 2 and 5. We checked for multicollinearity using variance inflation factors (package car) and removed non-significant or collinear terms to achieve minimal adequate models. For the long-term supercolony and polycalic settlement dataset, the full model for 2025 took the form: $\log(E[N]) = \beta_0 + \beta_1 \times \text{trails} + \beta_2 \times \text{tree_species} + \beta_3 \times \text{colony_type} + \beta_4 \times \text{diameter} + \beta_5 \times \text{temperature} + \beta_6 \times \text{humidity}$, where N is worker abundance per tree. Non-significant terms were retained in the full model but removed in the minimal adequate model, which identified the number of foraging trails as the sole significant continuous predictor.

Differences between habitats, tree species, and years were tested using the Kruskal-Wallis and Wilcoxon rank-sum tests (Benjamini-Hochberg correction where appropriate). Relationships between worker abundance and trail number and between *D. quadripunctatus* and competitor abundance were assessed using Spearman and Kendall correlations, respectively. Community-environment relationships were explored using canonical correspondence analysis (CCA) and visualized using non-metric multidimensional scaling (NMDS; vegan package). All figures were produced with the ggplot2 package.

Results

Support for hypothesis 1: competition and spatial constraints limit abundance in forest and urban tree stands

The species *Dolichoderus quadripunctatus* was found on 44% of the surveyed trees, forming small, oligodomic colonies (typically on one or two trees) in both deciduous forests and urban habitats such as parks, alleys, and gardens. A total of 140 colonies were found on 224 trees (Table 1, Figures 1 and S1). The abundance of workers per tree was more than twice as high in urban habitats (median 14 workers)

as in forests (median 6 workers), and urban colonies occupied trees that were, on average, closer together (2.9 meters vs 3.3 meters in forests; see Table 1).

A minimal adequate negative binomial generalized linear model (GLM) revealed three significant predictors of

worker numbers (Table 2): urban habitat (rate ratio (RR) = 1.87, $P = 0.0015$), a greater number of trees per colony (RR = 1.27, $P < 0.001$), and a shorter inter-tree distance (RR = 1.08 per meter, $P = 0.028$). Tree diameter, temperature, and humidity had no effect (Table 2, Fig S2).

Table 1. Descriptive Statistics for *Dolichoderus quadripunctatus* by Habitat.

Habitat	No. of Colonies	No. of Trees	Mean Abundance (SE)	Mean Tree Diameter, m (SE)	Mean Distance, m (SE)
Forest	68	87	6.59 (0.833)	0.571 (0.0248)	3.28 (0.15)
Urban	99	137	14.2 (1.40)	0.471 (0.0174)	2.86 (0.12)

Table 2. Coefficients of GLM for Forest and Urban Populations ($AIC = 1525.6$).

Predictor	RR	p-value	95% Confidence Interval	Note
<i>habitatUrban</i>	1.869	0.00150	1.092–2.758	Higher abundance in urban areas
<i>distance_between_trees</i>	1.076	0.02811	1.023–1.176	Positive effect
<i>trees_per_colony</i>	1.268	0.00047	1.100–1.512	Strong effect
<i>tree_diameter_m</i>	1.140	0.69718	0.586–2.983	Non-significant
<i>t</i>	1.015	0.59348	0.962–1.132	Non-significant
<i>humidity</i>	0.998	0.85738	0.973–1.020	Non-significant

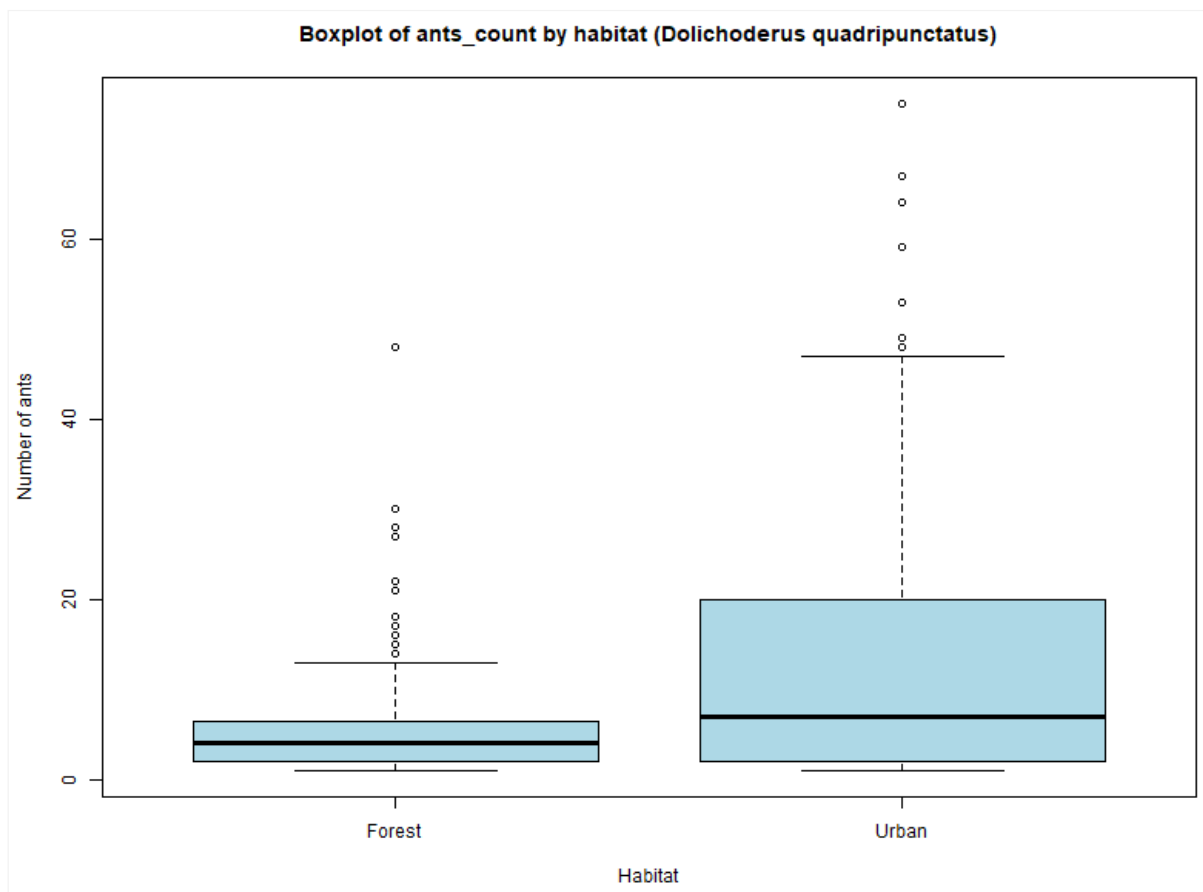


Fig 1. Abundance of *D. quadripunctatus* in Forest and Urban Habitats.

Kendall's tau correlations revealed a moderate negative association between *D. quadripunctatus* and *L. niger* ($\tau = -0.25$, $P < 0.0001$) and a weak negative association with *L. emarginatus* ($\tau = -0.10$, $P = 0.027$; Table 3).

Canonical correspondence analysis linked *D. quadripunctatus* to urban habitats and *Tilia cordata*, whereas dominant competitors (*L. niger* and *L. brunneus*) were associated with forest conditions (see Fig 2).

Table 3. Competition of *Dolichoderus quadripunctatus* with Other Ant Species.

Ant Species	Correlation Coefficient	p-value	Note
<i>Lasius niger</i>	tau = -0.248	1.371e-07	Strong competition
<i>Lasius emarginatus</i>	tau = -0.101	0.02671	Moderate competition

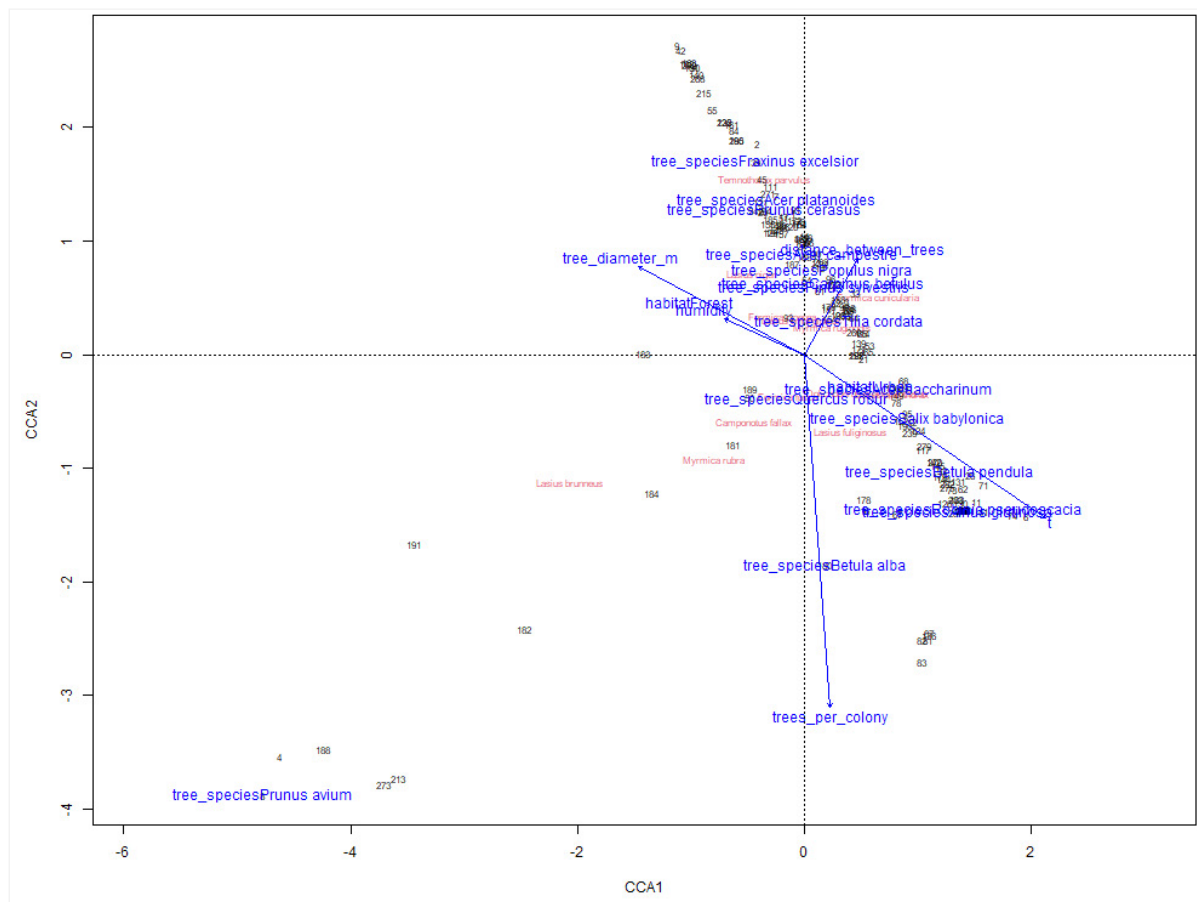


Fig 2. Canonical Correspondence Analysis of Ant Community Structure in Forest and Urban Habitats.

Non-metric multidimensional scaling confirmed clear community separation by habitat (Fig S3). Thus, H1 was fully supported: interspecific competition and limited spatial connectivity constrain abundance outside supercolonial contexts.

Support for hypothesis 2: foraging trails override substrate and competition in supercolonies and large polycalic settlements

In the long-term monitored supercolony (walnut-apple orchard) and polycalic settlement (lime alley), the number of

foraging trails per tree was the strongest predictor of worker abundance across all years (negative binomial GLM for 2025: RR = 1.93 per additional trail, $P < 10^{-13}$; see Table 4 and Fig S5).

Spearman correlations between trail count and worker numbers remained consistently high ($r = 0.76 - 0.88$, $P < 0.0001$, $R^2 = 0.57 - 0.78$) in all years and for all colony types (see Fig 3).

Tree species had only a secondary effect: *Juglans regia* supported higher densities than *Malus domestica* or

Table 4. Coefficients of the Revised GLM for 2025 ($AIC = 641.57$).

Predictor	RR	p-value	95% Confidence Interval	Note
<i>tree_diameter</i>	2.381	0.3387	0.401–14.135	Non-significant
<i>number_of_trails_per_tree</i>	1.932	1.53e-14	1.635–2.283	Highly significant
<i>tree_speciesGleditsia triacanthos</i>	0.321	0.4476	0.017–6.108	Non-significant
<i>tree_speciesJuglans regia</i>	4.759	0.0442	1.041–21.759	Significant
<i>tree_speciesMalus domestica</i>	0.0137	0.0006	0.001–0.165	Highly significant, low abundance
<i>tree_speciesOther</i>	3.160	0.1420	0.680–14.680	Non-significant
<i>tree_speciesTilia cordata</i>	2.873	0.1485	0.689–11.972	Non-significant
<i>t</i>	0.929	0.5578	0.726–1.188	Non-significant
<i>Humidity</i>	0.911	0.1762	0.796–1.042	Non-significant

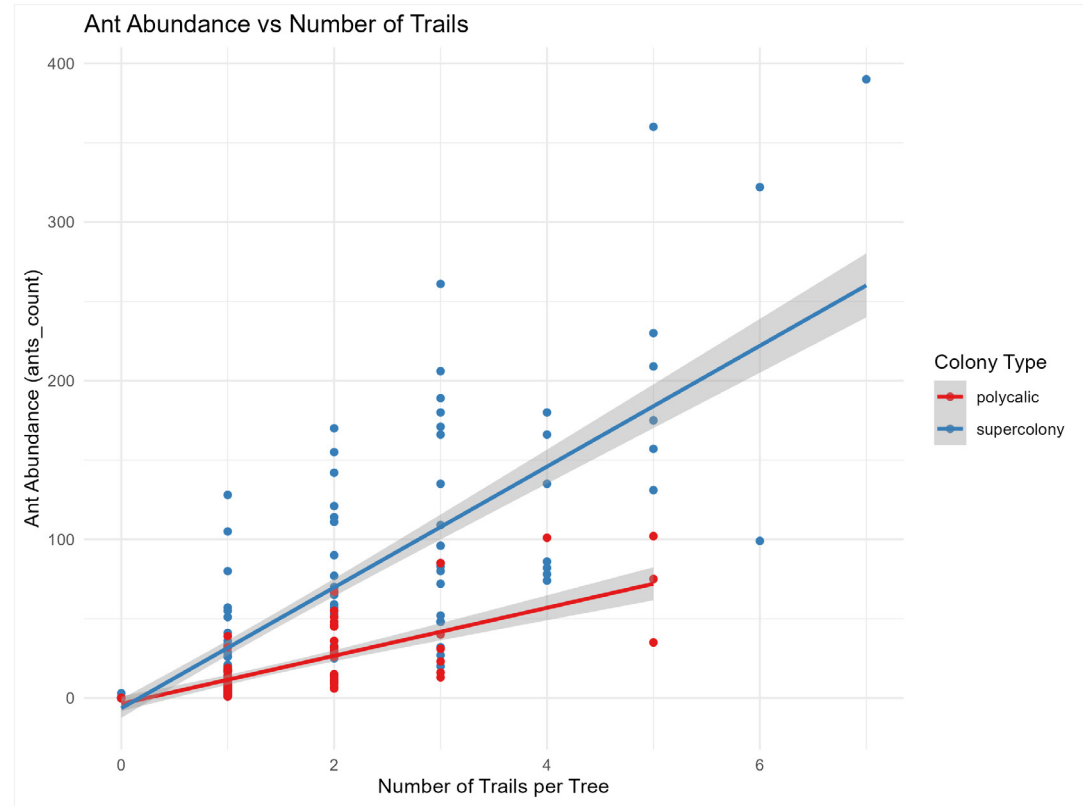


Fig 3. Relationship between Foraging Trails and *D. quadripunctatus* Abundance in Supercolony and Polycalic Settlement.

Tilia cordata (Dunn’s test, all adjusted $P < 0.0002$; see Table 5 and Fig 4), yet even on less favorable trees, worker numbers scaled tightly with trail infrastructure.

Competition from *Lasius niger* increased dramatically during the supercolony collapse (from 180 workers in 2015 to 2,331 in 2024; Fig S6), yet trail count remained the dominant driver. H2 is therefore strongly supported.

Support for hypothesis 3: fission-fusion dynamics and demographic resilience

The supercolony exhibited extreme temporal fluctuation: the number of occupied trees decreased from 71 in 2015 to 19 in 2024, followed by a partial recovery to 30 trees in 2025. Total worker abundance dropped sharply from 5603

Table 5. Results of Dunn’s Test for *tree_species*.

Comparison	Z	P.unadj	P.adj	Note
<i>Juglans regia</i> - <i>Malus domestica</i>	8.842	9.404e-19	1.975e-17	Highly significant
<i>Juglans regia</i> - <i>Tilia cordata</i>	4.252	2.118e-05	1.482e-04	Significant
<i>Malus domestica</i> - <i>Tilia cordata</i>	-4.535	5.765e-06	6.053e-05	Significant
<i>Juglans regia</i> - <i>Quercus robur</i>	2.186	0.02884	0.1514	Moderately significant
<i>Carpinus betulus</i> - <i>Tilia cordata</i>	-0.675	0.4994	1.000	Non-significant
<i>Carpinus betulus</i> - <i>Juglans regia</i>	-1.828	0.06762	0.2840	Non-significant

Table 6. Descriptive Statistics for Supercolony and Polycalic Settlement (2015–2025).

Colony Type	Year	No. of Occupied Trees	Mean Trails per Occupied Tree (SE)	Mean Abundance per Occupied Tree (SE)	Mean Abundance per All Trees (SE)
Supercolony	2015	71 (24 walnuts, 45 apples, 2 others)	3.17 (0.35)	78.9 (10.3)	78.9 (10.3)
Supercolony	2024	19 (18 walnuts, 1 other)	1.07 (0.21)	17.3 (5.3)	6.5 (2.2)
Supercolony	2025	30 (23 walnuts, 7 others)	2.53 (0.27)	56.0 (10.4)	23.3 (5.3)
Polycalic Settlement	2015	14 (limes)	1.00 (0.00)	59.4 (10.7)	13.4 (3.0)
Polycalic Settlement	2024	14 (limes; +17 surveyed neighbors)	2.07 (0.30)	34.1 (6.2)	15.4 (3.9)
Polycalic Settlement	2025	14 (limes; +33 surveyed neighbours)	5.50 (0.7)	60.8 (10.9)	18.1 (3.5)

Note: “Surveyed neighbors” refers to additional lime trees adjacent to the polycalic settlement that were inspected to assess potential colony expansion and interspecific competition with *Lasius niger*, *L. emarginatus*; these trees were not part of the core settlement.

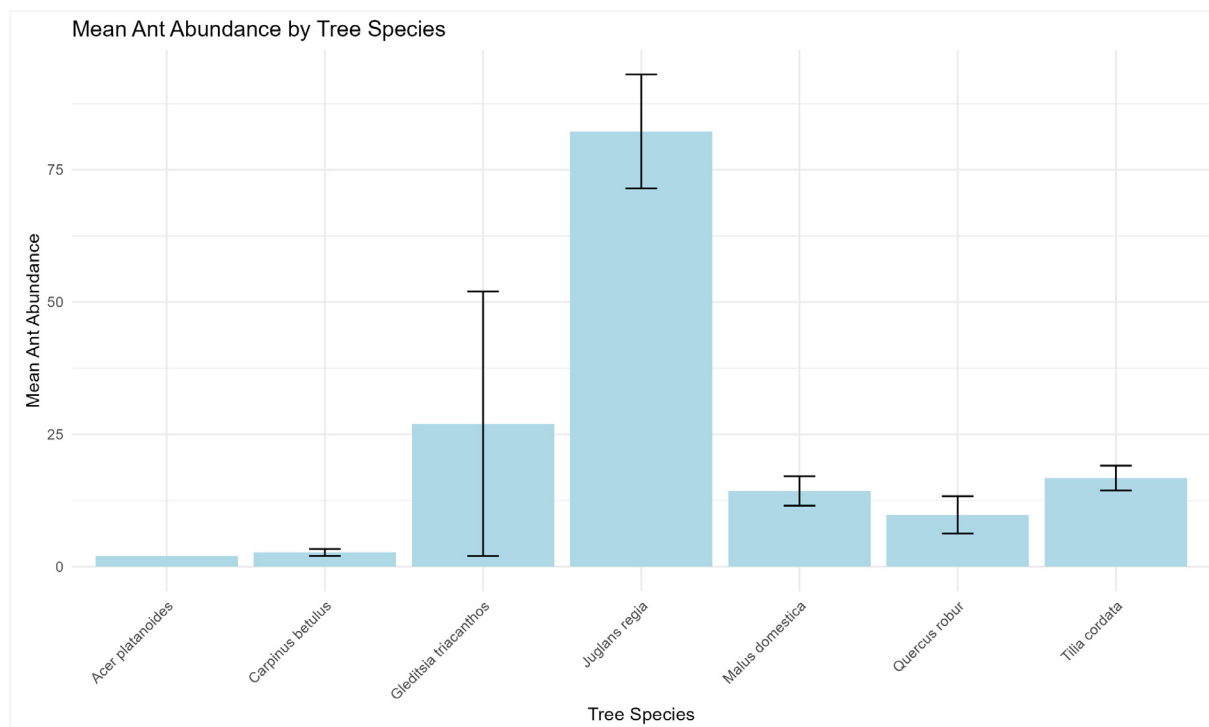


Fig 4. Abundance of *D. quadripunctatus* by Tree Species in Supercolony and Polycalic Settlement.

individuals in 2015 to 468 in 2024, and then recovered to 1793 workers in 2025. Mean abundance per all surveyed trees followed the same pattern: 78.9 (2015), 6.5 (2024), and 23.3 (2025) (Table 6, Figures 5A,B, S4A-C).

Walnut trees acted as persistent refugia throughout the crash and recovery phases. Despite this demographic

instability, the quantitative link between the number of trails and worker abundance remained strong ($r \geq 0.76$ every year; see Fig 4). The lime-alley (polycalic settlement) remained relatively stable throughout the decade, maintaining 14 trees and total worker numbers ranging from 477 to 851 (Table 6, Figure 5A,B).

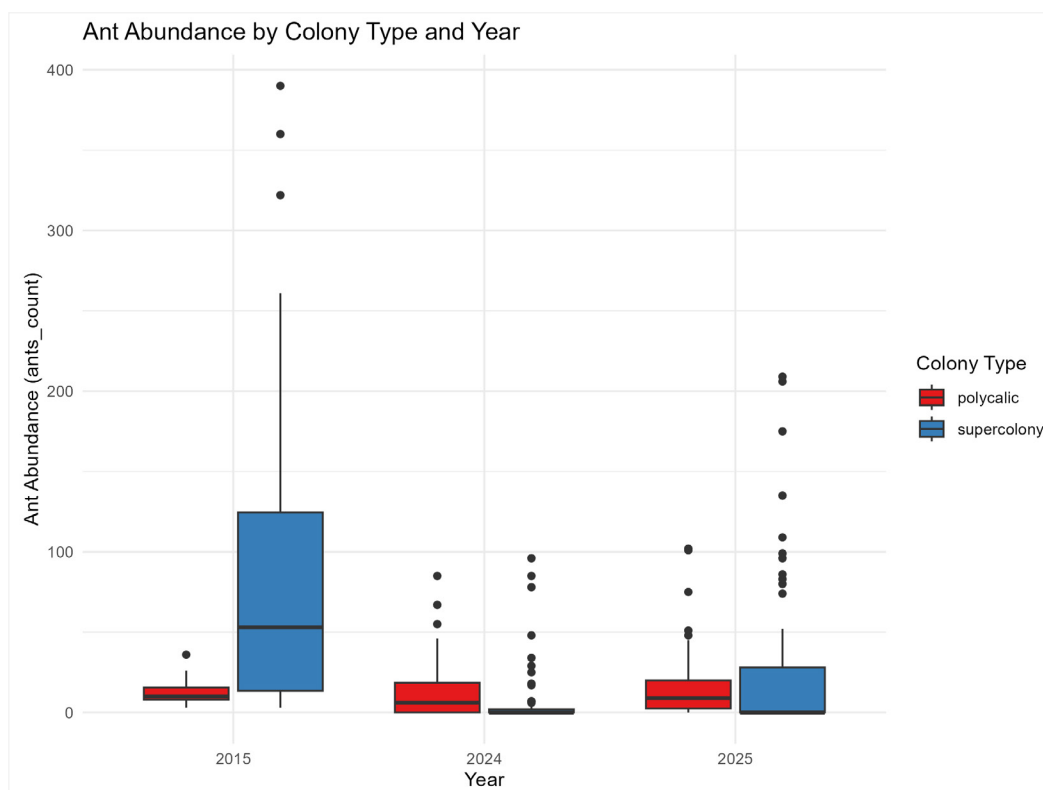


Fig 5. Abundance of *D. quadripunctatus* by year and colony type in the supercolony and polycalic settlement. (A) Total worker abundance per colony. (B) Mean abundance per all surveyed trees (including unoccupied trees), reflecting overall colony density across the study plot. Error bars in (B) represent ± 1 SE.

Wilcoxon tests confirmed highly significant differences between years in the supercolony (all $P < 0.03$), but not in the polycalic settlement (Fig S6). These patterns demonstrate classic fission–fusion dynamics and fully support hypothesis 3 (H3): supercolonial systems can withstand severe bottlenecks and reorganize rapidly around behavioral infrastructure (trails) rather than at fixed nest sites.

Discussion

Our findings reveal a striking habitat gradient in the organization of *Dolichoderus quadripunctatus* colonies, ranging from small, competition-constrained settlements in forests and urban areas to expansive supercolonies in orchards. This highlights context-dependent escalation towards unicoloniality in a native species. This supports our hypotheses: H1, where interspecific competition and spatial constraints dominated non-supercolonial abundance; H2, where trails overrode substrates in large settlements; and H3, which demonstrated fission–fusion resilience over a decade. Below, we contextualize these patterns across both native and invasive systems, emphasizing the unique traits of *D. quadripunctatus* and their implications for social evolution.

Supercoloniality in invasive species such as *Linepithema humile* enables transcontinental dominance through unicoloniality, which involves genetic homogeneity and the absence of aggression, yielding billions of workers across thousands of kilometers (Moffett, 2012; Vogel et al., 2010). By contrast, native systems such as the *Formica rufa* group of supercolonies (e.g., *F. exsecta* with 3,347 nests/22 ha; Markó, 2009) are ecologically bounded. Aggression between subunits maintains stability in resource-rich forests (Holzer et al., 2008). *D. quadripunctatus* bridges this gap: its supercolony (134 nests and 5,603 workers in 2015) rivals that of *Formica*, but it lacks genetic uniformity and retains subordinate traits in forests (e.g., negative $\tau = -0.25$ with *L. niger*; see Table 3). Unlike the expansion of *L. humile* from bottlenecks (Tsutsui et al., 2000), the polydomy of *D. quadripunctatus* pre-adapts it for fusion without invasion, with trails ($r = 0.76\text{--}0.88$; Fig 3) serving as ‘social glue’ similar to the networks of *Anoplolepis gracilipes* (Abbott, 2005; Drescher et al., 2010). A particularly close parallel can be seen with the arboreal invasive species *Crematogaster subdentata*, which forms true supercolonies in its native Central Asian range (foraging area up to 600 m², with 5–7 nests per tree), using the same strategies as *D. quadripunctatus*, such as bark nesting and intensive trophobiosis (Stukalyuk et al., 2021; Stukalyuk, 2015). Both species monopolize the canopy through exploitative rather than competitive means. However, *C. subdentata* supercolonies are markedly more aggressive, showing almost complete loss of nestmate recognition, even between distant subunits. In contrast, *D. quadripunctatus* exhibits intraspecific aggression outside the orchard and undergoes reversible fission–fusion (supercolony → polycalic subunits in 2024 → partial supercolony recovery in 2025; see Table 6 and Fig S4A–C).

Therefore, while *C. subdentata* represents the invasive endpoint of arboreal dolichoderine supercoloniality, *D. quadripunctatus* shows that a similar demographic and spatial escalation can be achieved in a native species without genetic purging or irreversible unicoloniality. However, its arboreal niche limits its ability to dominate at ground level, distinguishing it from the mound-based territoriality of *Formica* (Robinson, 2014).

Polycalic settlements, which Zakharov (2015) describes as intermediate polydomy, likely precede supercoloniality. In these settlements, multiple discrete nests exchange workers without full fusion, which buffers stress (Czechowski & Vepsäläinen, 2009). In *Lasius niger*, a polydomous species without true supercolonies (Stukalyuk, 2025), polycaly enhances resilience through budding but lacks the trail-driven escalation observed in *D. quadripunctatus*. Our data support this transitional role: the supercolony fissioned into polycalic subunits in 2024 (with a decline of over 90%, affecting 19 trees; see Table 6), yet refugial walnuts (with multi-nest persistence; see Fig S4A–C) enabled refusion by 2025 (with 30 trees and 1,793 workers). This mirrors *Formica lugubris* complexes, in which polycaly precedes supercolony formation under low competition (Cherix & Bourne, 1980). However, *D. quadripunctatus* trails accelerate recovery, unlike *L. niger*, which exhibits ground-based budding (Stukalyuk, 2025). Thus, polycaly acts as a ‘stepping stone’, with the connectivity provided by *D. quadripunctatus* arboreal trails being absent in *Lasius*.

The stability of the *D. quadripunctatus* supercolony – its persistence for decades despite crashes – stems from the orchard conditions: a contiguous canopy and predictable trophobionts (e.g., aphids on *Juglans regia*, $RR = 4.76$, $P = 0.044$; see Table 4), as well as minimal interference from ground-nesting ants (e.g., dominance of *L. emarginatus* absent; see Table 3). This is similar to the resilience of the *Formica rufa* group in stable forests, where mounds mitigate the effects of climate stress (Gösswald, 1989; Erard et al., 2016). However, it contrasts with the behavior of the invasive species *Anoplolepis gracilipes*, which thrives in disturbed tropical regions due to unchecked polydomy (O’Dowd et al., 2003). Favorable factors, such as reduced competition ($\tau = -0.10$ with *L. emarginatus*; see Table 3) and walnut refugia (see Fig S4), mirror the formation of supercolonies by *F. polyctena* in open woodlands (Sorger et al., 2025). However, *D. quadripunctatus* trail fidelity ($r = 0.76\text{--}0.88$; see Fig 3) provides a unique form of arboreal stability.

Our work advances the field of sociobiology by quantifying native supercoloniality. Trails (H2) and fission–fusion (H3) in *D. quadripunctatus* enable escalation without the pathology observed in *L. humile* (Helanterä et al., 2009), thereby bridging the gap between *Formica* polydomy (Lindström et al., 1996) and Dolichoderine invasives (Buczkowski, 2012). In contrast to the urban supercolonies of *Tapinoma sessile* (Buczkowski & Bennett, 2008), the collapse and recovery of our system in 2024 emphasize the transitional role of polycaly – subunits reforming via refugia – as opposed to the stable complexes of *F. lemani* (Novgorodova & Taranenko, 2024).

Limitations include pre-2024 microclimate gaps and the rarity of tree samples, which could potentially mask interactions (e.g., *Tilia* in CCA; see Fig 2). Future genetics (Czechowski et al., 2023) and trophobiont assays could clarify dispersal and indirect effects.

The abundance of *D. quadripunctatus* reflects competition and spatial limits in forests, but escalation is driven by trails within supercolonies, with polycaly acting as an adaptive intermediate. This resilient yet subordinate native model contrasts with invasive species and informs conservation amid urban fragmentation (Markó, 2009; Giraud et al., 2002).

Conclusions

The species *Dolichoderus quadripunctatus* exhibits a remarkable continuum of colony organization within its native range. This ranges from small, competition-limited settlements in forests and urban tree stands to expansive supercolonies in orchards. Outside of supercolonial contexts, worker abundance is primarily constrained by interspecific competition with *Lasius niger* and *L. emarginatus* (Kendall's tau = -0.25 and -0.10), as well as by limited connectivity between trees. In contrast, tree diameter and microclimate play negligible roles. In contrast, supercolonies and large polycalic systems are predominantly governed by internal foraging-trail infrastructure (negative binomial GLM rate ratio = 1.93 per additional trail, explaining 57-78% of the variance), with the tree species (*Juglans regia*) having only a secondary effect. Decade-long monitoring (2015-2025) revealed extreme yet reversible demographic fluctuations: a collapse of over 90% in 2024 was followed by a rapid partial recovery in 2025, driven by persistent walnut refugia and fission-fusion dynamics. Therefore, supercoloniality can emerge and persist in the native range through behavioral pre-adaptation (i.e., trail networks) rather than genetic purging or irreversible loss of nestmate recognition, offering a rare counter-example to the invasion-driven paradigm that has dominated the field for the past two decades.

Declaration of conflict of interest

The authors declare no conflicts of interest.

Authors' Contribution

S. S.: conceptualization; methodology; formal analysis; data curation; writing-original draft; writing-review & editing; visualization; project administration.

Y. S.: investigation; resources; writing-review & editing.

Data availability

The datasets generated and analysed during the current study are available in the Zenodo repository:
<https://doi.org/10.5281/zenodo.21100700>

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