



Changes in the aggressiveness of invasive red imported fire ants towards native ants: perspectives based on different latitudes and invasion status

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Abstract

How invasive species recognize novel competitors during range expansion remains poorly understood. We investigated this in the red imported fire ant (*Solenopsis invicta*, RIFA) during its northward spread in China. We assessed interspecific aggression toward three native ants using two geographic contexts: sampling native ants from different latitudes (testing *Tetramorium bicarinatum* and *Polyrhachis dives*) and comparing populations between species that occurred both within and outside their invaded range (testing *Pheidole nodus* and *Polyrhachis dives*). Results suggest aggression can be modulated by competitor identity, origin, and coexistence history. Aggression toward ground-dwelling *T. bicarinatum* decreased with increasing latitude, suggesting a “recognition lag” at the invasion front. Conversely, aggression toward arboreal *Polyrhachis dives* was higher in the non-invaded frontier than in the invaded core, indicating that the RIFA actively identifies novel threats but develops “neighborly tolerance” following coexistence. Furthermore, higher aggression toward ground-dwelling species (e.g., *Pheidole nodus*) confirmed that niche overlap may dictate competitive recognition. These findings highlight the RIFA’s behavioral plasticity; the transition from proactive threat assessment to tolerance likely facilitates successful colonizing and gaining ecological dominance in newly invaded areas.

Key words: *Solenopsis invicta*, interspecific competition, latitudinal gradient, behavioral plasticity, invasion ecology, Hymenoptera, Formicidae.

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Introduction

Competitive interactions among species are widely recognized as factors that influence the structure and dynamics of local communities (CHICK & al. 2020). Understanding the strength and direction of these interactions, especially when invasive species expand into new territories, is a crucial aspect of invasion ecology. The biotic interaction hypothesis suggests that species’ interaction intensity increases from high latitudes toward the tropics due to greater biodiversity (SCHEMSKE & al. 2009, BASKETT & al. 2020, FREEMAN & al. 2020). However, as invasive species shift their ranges northward, they encounter novel communities where the universality of such patterns and the invader’s ability to recognize new competitors remain to be validated.

Ants, as representative social insects, occupy broad ecological niches and form complex connections with various taxonomic groups (HELMS & VINSON 2002, O’DOWD & al. 2003, LEE & YANG 2022). While latitudinal varia-

tions in ant-plant mutualisms (NATHAN & al. 2025) and predation rates (JEANNE 1979) often support the biotic interaction hypothesis, interspecific interactions among ants themselves show more idiosyncratic patterns. For instance, *Temnothorax rugatulus* exhibits higher aggression at higher latitudes, contradicting the general trend (BENGSTON & DORNHAUS 2014). For a successful invader, the ability to assess and respond to competitive threats across such latitudinal gradients is critical for colony establishment and range expansion.

The adaptive flexibility hypothesis posits that invasive species possess the capacity to dynamically modulate the expression of their behavioral repertoire across different stages of invasion (WRIGHT & al. 2010). Such behavioral plasticity plays a pivotal role in the invasion process; it not only dictates the invader’s own establishment success but also shapes the adaptive potential of native species to coexist with novel threats (GRANGIER & LESTER 2012).

Furthermore, the intensity of interspecific aggression – a key behavioral trait – is often strictly modulated by the specific identity of the competitor (BERTELSMEIER & al. 2015). Consequently, the strategic regulation of behavior constitutes a critical determinant of successful biological invasions.

The red imported fire ant (*Solenopsis invicta*, hereafter RIFA) is a globally invasive species known for its low aggression threshold and high competitiveness, which has caused severe declines in native ant diversity in its introduced ranges (HOLWAY 1999, WOJCIK & al. 2001, ALLEN & al. 2004, FADAMIRO & al. 2009, ASCUNCE & al. 2011, NIE & al. 2019, XU & al. 2022). In China, RIFA is spreading northward at an alarming rate of 26.5 - 48.1 km per year (WANG & al. 2019). As of June 2025, it has reached 13 provinces, with its northernmost frontiers extending to Sichuan and Shanghai (<https://zzys.moa.gov.cn/gdxw/>). As the RIFA continues to expand into higher latitudes (WANG & al. 2023), it inevitably encounters “novel” native ant species that it has not previously interacted with. While some native ants can coexist with the RIFA through specific behavioral strategies (RAO & VINSON 2004, CALCATERRA & al. 2008, CHENG & al. 2019), it remains unclear whether the RIFA can proactively identify these potential competitors in new territories and whether its aggressive response depends on prior exposure (invaded vs. non-invaded areas).

To evaluate the RIFA’s capacity to recognize and respond to potential competitors during its northward expansion, we conducted interspecific aggression experiments using native ants from different latitudinal and invasion contexts. We hypothesized that: (1) The RIFA possesses the plasticity to adjust its aggression toward native ants across latitudinal gradients, potentially maintaining higher aggression toward potential competitors from low-latitude regions where biotic pressure is historically higher; and (2) The RIFA exhibits a “recognition lag” or altered tolerance, showing higher aggressiveness toward novel native ants from non-invaded areas compared with familiar ones in invaded areas due to the lack of long-term co-adaptation. This study aims to clarify how the RIFA’s competitive behavioral plasticity facilitates its successful colonization of new latitudinal regions.

Material and methods

Ant collection and laboratory rearing

To determine the competitive-interaction intensity of RIFA towards native ants from different latitudes, three polygyne RIFA colonies were collected in Guangzhou (23.1653° N, 113.3511° E). To confirm the behavioral uniformity of polygyne the RIFA from diverse locations, one polygyne colony was sampled from each of four additional sites situated 2 - 4 km from the primary sampling points. Individual-level aggression experiments (ten replicates per nest) revealed zero agonistic interactions between workers from these supplementary nests and the original three colonies. Additionally, to demonstrate the representativeness

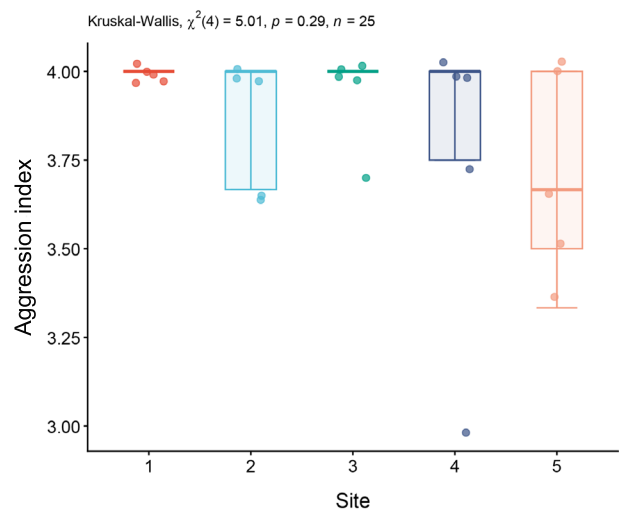


Fig. 1: Aggression index exhibited by red imported fire ant workers from five locations (Guangzhou City, but the distance between each other is 2 - 4 km) during individual-level aggression experiments (each dot in the figure represents one aggression experiment) when encountering the native competitor, *Tetramorium caespitum*, from Zhangzhou City.

of the RIFA from any single location, behavioral assays were conducted comparing the RIFA from all five sites with a standardized native competitor, *Tetramorium caespitum* (each site with five replicates). These preliminary results confirmed that the RIFA from a single site could serve as a reliable representative for the regional population (Fig. 1).

The RIFA’s aggression was first tested toward two common native species, *Polyrhachis dives* (arboreal, low niche overlap) and *Tetramorium bicarinatum* (soil-surface, high niche overlap), collected from four cities along a latitudinal gradient (Maoming, MM; Enping, EP; Lufeng, LF; Zhangzhou, ZZ). Three colonies of *T. bicarinatum* and three colonies of *Polyrhachis dives* (the sampled nests were all collected from trees) were collected from each city, respectively, resulting in a total of 24 native ant colonies. This allowed an assessment of how the RIFA responds to different regional “potential competitors” it might face during dispersal. Second, to determine whether the RIFA distinguishes between “familiar” and “novel” enemies, its aggression was compared with *Pheidole nodus* (three colonies) and *Polyrhachis dives* (three colonies) collected from a non-invaded site (Shaoyang, SY) versus an invaded site (EP). *Polyrhachis dives* and *Pheidole nodus* were selected instead of *Polyrhachis dives* and *T. bicarinatum* because during sampling in Shaoyang City, it could not be found a sufficient number of *T. bicarinatum* colonies that met the requirements for collection. Fortunately, *Pheidole nodus* colonies were abundant and of adequate scale, and they have a similar ecological niche as *T. bicarinatum* as both are ground-dwelling ant species. All the above colonies were with queens. Detailed collection information for all native ants is provided in Table 1. After collection, all ants were transported to the laboratory and reared in plastic

containers (length, width, and height were 40 cm, 30 cm, and 14 cm, respectively). To prevent escape, the inner walls of the plastic containers were coated with talcum powder. Colonies were fed a 20% sugar : water solution and frozen locusts (*Locusta migratoria*) under laboratory conditions (24 ± 2°C, 75% relative humidity (RH), and 14 : 10 h L : D) for at least 48 h before being used in subsequent experiments. All ants were identified by referring to the taxonomic keys provided by ZHOU (2001).

Individual aggression experiment

To avoid the influence of introduction sequence on aggression indices, one small RIFA worker (head widths about 0.80 mm, referring to WOOD & TSCHINKEL 1981) was first randomly selected and placed in a disposable Petri dish (6 cm diameter × 1.2 cm height) coated with Fluon. A native ant was immediately introduced, and the aggression level of the RIFA toward the native ant, along with the frequency of each aggression level, was recorded over 5 min. The introduction sequence was then reversed, and the corresponding data were recorded again for another 5 min. Regardless of the sequence, all ants were eliminated after being used once in the Petri dishes. The data from both recordings were combined into one set, meaning each set represented a total observation time of 10 min. All aggression assays were scored by a single observer who was blind to the trial being conducted.

In the experiment testing the RIFA's aggression toward native ants from different latitudes, at each latitude, three RIFA colonies were sequentially paired with six native ant colonies (two species) for individual aggression experiments, with five replicates per colony. This resulted in 90 individual aggression experiments per latitude, totaling 360 experiments across all latitudes. For the experiment testing the RIFA's aggression toward native ants from invaded and non-invaded areas, three RIFA colonies were sequentially paired with six native ant colonies from the non-invaded area and six from the invaded area, with five replicates per colony, totaling 180 individual aggression experiments.

The aggression levels of the RIFA were defined according to JELLEY & MOREAU (2023): Level -1: The RIFA exhibits immediate retreat or distinct withdrawal behavior upon physical contact or detection of the native ant. Level 0: Mutual or unilateral antennal inspection (antennation) occurs without any display of hostility, representing neutral species recognition. Level 1: The RIFA exhibits physical displays such as gaster curling or briefly mounting the dorsal surface of the native ant without initiating biting or combat. Level 2: The RIFA displays overt aggression by actively chasing, lunging at, or attempting to displace the native competitor from the immediate area. Level 3: High-intensity non-lethal combat characterized by the RIFA using its mandibles to bite, grasp, or forcefully pull the legs or antennae of the native ant. Level 4: Peak aggressive response where the RIFA maintains a firm mandibular grip while simultaneously curling its abdomen forward to deliver repeated stings and venom injection.

The aggression index was calculated using the following formula (where N represents the frequency of each aggression level):

$$\text{Aggression Index} = \frac{-1 \times N(-1) + 1 \times N(1) + 2 \times N(2) + 3 \times N(3) + 4 \times N(4)}{N(-1) + N(0) + N(1) + N(2) + N(3) + N(4)}$$

Additionally, the contact count between the RIFA and the native ants was recorded, defined as the number of encounters between the RIFA and the native ants during the 10-min observation period. The contact count is considered to be a reference indicator of the RIFA's attention toward the native ants.

Statistical analysis

Linear mixed-effect models (LMMs) were employed to analyze the aggression index (AI) of the RIFA toward two native ant species. Latitude, native species (as the target of aggression), and their interaction were included as fixed effects. To account for potential pseudoreplication and colony-level variation, the identities of the RIFA colonies and the unique nest IDs of native ants were treated as crossed random effects. The significance of fixed effects was determined using Type III analysis of variance with Satterthwaite's approximation. An analysis of estimated marginal linear trends was further performed using the emmeans package (LENTH & al. 2026) with Kenward-Roger degree-of-freedom adjustments to estimate the latitudinal slopes of the RIFA's aggression toward each native species and test whether they significantly differed.

The Kruskal-Wallis test was used for global testing, followed by Dunn's test for post-hoc pairwise comparisons, with the significance level set at 0.05. All data analyses and graph plotting were performed using the R software (version 4.5.2) (R CORE TEAM 2026).

Results

Aggressiveness of the RIFA towards native ants across different latitudes

Contact counts between the RIFA and native ants differed across latitudes. For *Tetramorium bicarinatum*, values ranged from 4.11 ± 2.43 (mean ± standard deviation) in MM to 8.89 ± 3.30 in EP. In contrast, contacts with *Polyrhachis dives* were lowest in EP (4.00 ± 2.33) and highest in ZZ (8.91 ± 4.31) (Tab. 1; Data S1, as digital supplementary material to this article, at the journal's web pages). Although some regional differences were observed, no consistent latitudinal trend was evident in the contact counts for either species (Fig. 2).

The results suggest that the aggression intensity of the RIFA toward native ants was modulated by a marginally significant interaction between latitude and the target native species ($p = 0.061$). Species-specific slope analysis further revealed that the RIFA's aggression toward *T. bicarinatum* was significantly influenced by latitude, with the aggression index decreasing as latitude increased (Fig. 3, slope = -0.456, SE = 0.185, $p = 0.0229$). In contrast, the aggression intensity of the RIFA toward *Polyrhachis*

Tab. 1: Collection information of native ant species (*Pheidole nodus*, *Polyrhachis dives*, and *Tetramorium bicarinatum*) and their interaction outcomes with the red imported fire ant. Note: Maoming, Enping, and Lufeng are all located in Guangdong province while Zhangzhou belongs to Fujian province and Shaoyang belongs to Hunan province.

Collection sites	Latitude	Longitude	Native species	Contact count (mean ± SD)	Aggression index (mean ± SD)
Maoming (MM)	21.6647	110.5432	<i>T. bicarinatum</i>	4.11 ± 2.43	2.21 ± 1.26
Maoming (MM)	21.6647	110.5432	<i>Polyrhachis dives</i>	7.07 ± 3.81	1.63 ± 1.13
Enping (EP)	22.2665	112.1633	<i>T. bicarinatum</i>	8.89 ± 3.30	1.25 ± 1.10
Enping (EP)	22.2665	112.1633	<i>Polyrhachis dives</i>	4.00 ± 2.33	0.67 ± 0.74
Enping (EP)	22.2665	112.1633	<i>Pheidole nodus</i>	4.64 ± 2.75	2.13 ± 1.02
Lufeng (LF)	23.0300	115.8373	<i>T. bicarinatum</i>	4.20 ± 1.55	2.43 ± 0.93
Lufeng (LF)	23.0300	115.8373	<i>Polyrhachis dives</i>	4.96 ± 3.03	2.16 ± 1.27
Zhangzhou (ZZ)	24.3865	117.6237	<i>T. bicarinatum</i>	7.33 ± 3.31	0.61 ± 0.82
Zhangzhou (ZZ)	24.3865	117.6237	<i>Polyrhachis dives</i>	8.91 ± 4.31	1.38 ± 0.97
Shaoyang (SY)	23.1619	113.3603	<i>Polyrhachis dives</i>	4.98 ± 2.46	1.66 ± 1.06
Shaoyang (SY)	23.1619	113.3603	<i>Pheidole nodus</i>	3.58 ± 2.20	2.26 ± 1.23

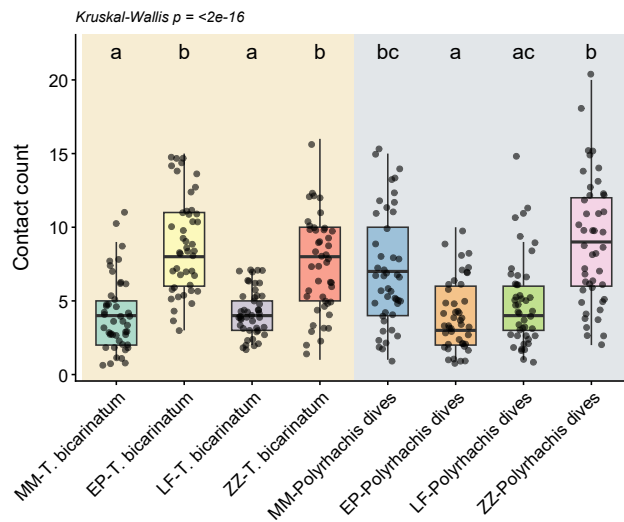


Fig. 2: Variations in contact counts between the red imported fire ant (RIFA) and native ants across different latitudes during 10-min observations (each dot in the figure represents one aggression experiment). The light brown areas represent individual aggression interactions between the RIFA and *Tetramorium bicarinatum* while the gray areas represent interactions between the RIFA and *Polyrhachis dives*. Different letters indicate significant differences ($p < 0.05$) between columns, while shared letters denote no significant difference. Note: The cities on the x-axis are arranged from low to high latitude, the letters represent abbreviations of city names; see Table 1 for details.

dives remained consistent across the latitudinal gradient (Fig. 3, slope = 0.064, SE = 0.185, $p = 0.7323$). No significant difference in aggression was detected between the two target species at the mean latitudinal level ($p = 0.542$). Random-effect analysis showed highly consistent behavioral responses across different RIFA colonies (variance = 0.0076).

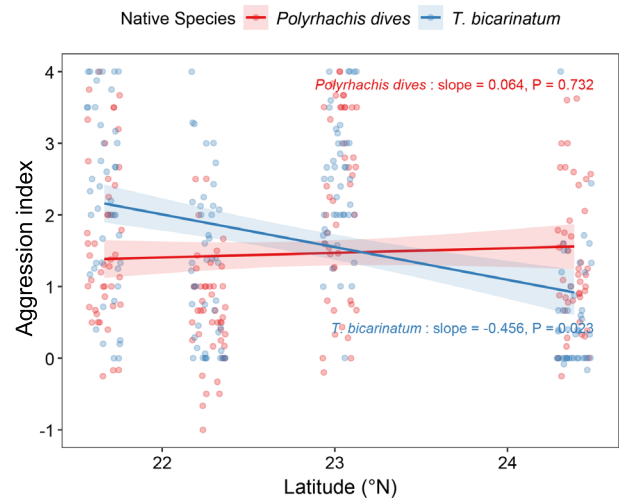


Fig. 3: Latitudinal variation in the aggression index of the red imported fire ant toward two native ant species (*Polyrhachis dives* and *Tetramorium bicarinatum*).

Aggressiveness of the RIFA toward native ants in non-invaded and invaded areas

Contact counts between the RIFA and *Pheidole nodus* did not differ significantly between the non-invaded (SY: 3.58 ± 2.20) and invaded (EP: 4.64 ± 2.75) areas. Similarly, no significant difference was observed in contact counts with *Polyrhachis dives* between SY (4.98 ± 2.46) and EP (4.00 ± 2.33) (Tab. 1; Fig. 4A). However, within the non-invaded area (SY), contact counts with the two native ant species differed significantly (Fig. 4A).

The aggression index of the RIFA toward *Pheidole nodus* was similar between the invaded (2.13 ± 1.02) and non-invaded (2.26 ± 1.23) areas. In contrast, aggression toward *Polyrhachis dives* was significantly higher in the non-invaded area (1.66 ± 1.06) than in the invaded area (0.67 ± 0.74) (Tab. 1; Fig. 4B).

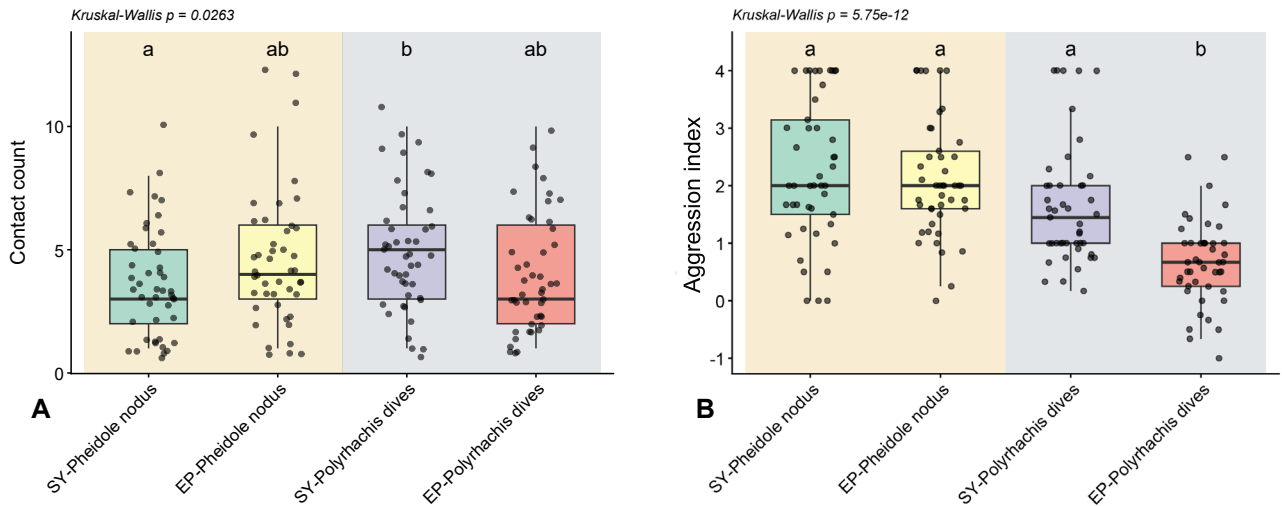


Fig. 4: Variations in contact counts (A) and aggression index (B) between the red imported fire ant (RIFA) and native ants from non-invaded (SY, Shaoyang City) and invaded (EP, Enping City) areas during 10-min observations (each dot in the figure represents one aggression experiment). The light brown areas represent individual aggression interactions between the RIFA and *Pheidole nodus* while the gray areas represent interactions between the RIFA and *Polyrhachis dives*. Different letters indicate significant differences ($p < 0.05$) between columns, while shared letters denote no significant difference. SD = standard deviation.

Discussion

Ants exhibit significant ecological and behavioral variation along latitudinal gradients. For instance, *Libinia dubia* shows reduced chemical defenses at higher latitudes due to decreased predation pressure (STACHOWICZ & HAY 2000), and life-history strategies often shift with latitude to adapt to varying environmental constraints (BLANCKENHORN & FAIRBAIRN 1995). Our results demonstrate that the RIFA's aggressiveness is not a fixed trait but a plastic response that depends on the species identity and geographic origin of native competitors. This suggests that as the RIFA spreads northward into higher latitudes, its ability to identify and respond to “novel” potential competitors will be asymmetric, leading to a predictable but non-uniform restructuring of local community compositions.

The consistent, low aggressiveness of the RIFA toward *Polyrhachis dives* across latitudes indicates a uniform recognition template for this arboreal species. In contrast, the significant decrease in aggression toward *Tetramorium bicarinatum* at higher latitudes suggests that the RIFA may perceive higher-latitude populations as a lower competitive threat or that there is a geographic divergence in the cues the RIFA uses to recognize this species as a competitor. Such a pattern implies that in the initial stages of northward colonization, the RIFA might exhibit a “behavioral delay” or insufficient aggressiveness in recognizing higher-latitude native ants as enemies, potentially reducing initial biotic resistance (CARTHEY & BANKS 2014). However, the overall relatively low aggression toward these native species could also suggest that the RIFA's initial establishment in new latitudinal zones might be easier than expected if environmental filters are overcome. As the RIFA continues its expansion, these behavioral interactions may further shift through phenotypic

plasticity or rapid evolution to optimize the recognition of local competitors.

A critical question in invasion biology is whether invaders can distinguish between “familiar” enemies in established zones and “novel” potential competitors in non-invaded areas. While studies on *Wasmannia auropunctata* suggest that native ants in invaded areas develop stronger competitive responses over time (LE BRETON & al. 2007), our findings regarding the RIFA reveal a different strategic flexibility. Although the RIFA's aggression toward *Pheidole nodus* was unaffected by invasion status, its aggression toward *Polyrhachis dives* was significantly higher in non-invaded areas than in invaded areas (Fig. 4B). This higher aggression toward “novel” populations suggests that the RIFA proactively identifies potential competitors in new territories, but this intense response may transition into “tolerance” or habituation after prolonged coexistence – a finding consistent with our second hypothesis. This “recognition-to-tolerance” transition may be a key mechanism allowing the RIFA to stabilize its presence in diverse native communities after the initial invasion phase (TRIGOS-PERAL & al. 2021).

The precision of the RIFA's recognition mechanism also appears to be modulated by niche overlap. Invasive ants often display heightened aggression toward native species that represent a significant ecological threat (CREMER & al. 2006, CHONG & LEE 2010). In our study, the RIFA exhibited higher aggression toward the ground-dwelling *Pheidole nodus* (Myrmicinae) than toward the arboreal *Polyrhachis dives* (Formicinae) (Tab. 1). This supports the idea that the RIFA prioritizes the identification of competitors with high niche overlap. Field observations confirm that both the RIFA and *Pheidole nodus* prefer foraging on the ground and frequent similar urban habitats, such as sidewalks and

building foundations (SKVARLA & al. 2024). In contrast, the spatial segregation between the ground-nesting RIFA and the arboreal-nesting *Polyrhachis dives* (ROBSON & al. 2015) may reduce the frequency of lethal encounters, eventually facilitating a form of “neighborly tolerance” in invaded ranges.

This behavioral modulation is likely rooted in the way ants learn and update their nestmate and competitor recognition templates (ERRARD & HEFETZ 1997). In ant communities, interactions often fluctuate between the “evil neighbor effect” (BEY & al. 2025) and the “dear enemy effect” (LANGEN & al. 2000). While the relationship between the RIFA and *Polyrhachis dives* in invaded areas leans toward the “dear enemy effect,” we speculate this is an indirect result of limited niche overlap reducing the necessity for constant conflict. Notably, the RIFA’s strong territoriality suggests they may initially treat all “novel” native ants as “evil neighbors” upon first contact in new latitudes. However, this effect in the RIFA may not rely on associative learning as their massive colony size and competitive dominance mean they rarely encounter formidable opponents that could “teach” them avoidance. Instead, their strategy appears to be one of proactive aggression toward new potential threats, followed by a refined tolerance once the local community structure has been suppressed or stabilized.

Conclusion

In conclusion, our study provides evidence that the red imported fire ant (*Solenopsis invicta*) possesses a plastic behavioral mechanism for identifying and responding to potential competitors during its northward expansion. Rather than exhibiting a static level of aggression, the RIFA adjusts its competitive intensity based on the ecological niche and the “familiarity” of native ants. The discovery that the RIFA displays higher aggression toward native populations in non-invaded areas than in invaded ones suggests a proactive strategy for securing resources when encountering novel competitors. As the RIFA spreads to higher latitudes, its interactions with native communities are characterized by a niche-dependent recognition process: prioritizing high-intensity conflict with ground-dwelling competitors while maintaining a lower but consistent pressure on arboreal species. This behavioral flexibility – transitioning from proactive identification to long-term tolerance – likely mitigates the costs of constant conflict and facilitates the RIFA’s establishment in diverse ecosystems. These insights into the behavioral ecology of the RIFA emphasize that its range expansion is not merely a process of dispersal but a complex behavioral adaptation to the varying competitive landscapes across latitudinal gradients. Future research should focus on the chemical and molecular basis of these recognition templates to further unravel the success of the RIFA as a global invader.

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Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All the related data can be found in the attached “raw data” excel file.

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