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RESEARCH ARTICLE

Context-dependent aggression and ecological dominance in a Mediterranean ant community

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Abstract

Aggression plays a central role in structuring ecological communities, particularly in territorial and socially complex taxa such as ants, where conflicts within and between species are often resolved through overt aggression. Here, we combined field monitoring of ant nests over a six-month period with laboratory experiments to investigate the coexistence of three dominant ant species in an urban Mediterranean grassland: *Aphaenogaster senilis*, *Messor barbarus*, and *Tapinoma darioi*. We analysed behavioural asymmetries, dominance hierarchies, and the potential mechanisms that may facilitate coexistence. The three species were the most abundant in the study area (84% of nests), and nest surveys indicated their coexistence despite seasonal fluctuations in *A. senilis* and *T. darioi*, with some winter nests of the former taken over by the latter. Aggression was context-dependent and varied strongly among species and seasons. *A. senilis* displayed low aggression and frequent submissive behaviours; *M. barbarus* showed consistently higher aggression towards conspecifics; and *T. darioi* combined low aggression in laboratory assays with traits associated with supercoloniality, consistent with a "back-seat driver" strategy. Although native to the Mediterranean, its high occupation potential suggests that *T. darioi* may gradually reshape local communities through persistent interference. However, year-round monitoring and resource-based competition assays are required to distinguish persistent trends from seasonal dynamics. Overall, our findings highlight how behavioural plasticity, ecological context, and species-specific aggression contribute to community structure. They also underscore the importance of monitoring numerically dominant species, which can exert substantial long-term effects on community composition even when displaying low overt aggression.

Keywords Ant behaviour · Dominance hierarchy · Aggression · Mediterranean ecosystems

Introduction

Ants (Hymenoptera: Formicidae) are among the most abundant and ecologically successful animals in terrestrial ecosystems (Hölldobler and Wilson 1990). The complexity of their social organization and high habitat specialization has resulted in ants being a highly influential invertebrate group in most terrestrial habitats (Parker and Kronauer 2021; Wilson and Hölldobler 2005). The dynamics of ant species are shaped through both basic abiotic and biotic ecological processes, such as biogeographic history, climate, predation, and competition for resources (Hölldobler and Wilson 1990; Lach et al. 2009), the latter being classically considered a major factor determining ant communities' composition (Sánchez-García et al. 2022). Competition over resources can manifest itself via the interference with another ant species spatial distribution, abundance, or through resource monopolization (Cerdá et al. 2013). These mechanisms work alongside each other and are useful to describe interactions among species which can be positive, neutral or negative (aggressive) in nature (Lach et al. 20092009; Schoener 1982).

Being the numerically dominant insects in most terrestrial ecosystems, encounters between individual ants belonging to different colonies and/or species are frequent, particularly when foraging for resources. In such encounters, their interactions can be positive (e.g. grooming and trophallaxis), neutral (e.g. ignoring or antennating each

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other), or aggressive (e.g. biting and/or stinging) (Chomicki and Renner 2017). In conspecific disputes, aggression is often predicted to escalate, since individuals competing for the same resources pose the greatest threat. Nevertheless, the outcomes of these encounters vary depending on environmental fluctuations and the specific context of the interaction. This spatiotemporal variation limits competitive exclusion by dominant species (Schoener 1982), reduces costs of conflict (Andersen 2008), and ultimately promotes coexistence (Cerdá et al. 2013).

Classical ecological competition theory defines the existence of aggression hierarchies among ant species based on behavioural dominance. This hierarchical arrangement allows dominant species to monopolize resources, affecting the fitness of subordinate species (Sánchez-García et al. 2022). In these rankings, ant species are categorized based on their numerical dominance (i.e., species abundance), behavioural dominance (i.e., outcome in behavioural assays) or ecological dominance, which combines both aspects (Davidson 1998). Several studies have reevaluated the structure of these hierarchies, describing them as context-dependent competitive networks where species ranked as dominant may become subordinate whenever environmental conditions or methodologies change (Cerdá et al. 2013; Tschá and Pie 2019; Sánchez-García et al. 2022).

Understanding these dynamic hierarchies is crucial when studying specific ant communities, particularly in regions with diverse and fluctuating environments such as the Mediterranean region (Cerdá et al. 2013). In these ecosystems, the composition and behaviour of ant communities are influenced not only by interspecific competition but also by the unique adaptive traits of individual species (Santini et al. 2007).

Urban habitats can further modify ant communities' composition by simplifying ant species assemblages and facilitating the establishment of native generalist species with invasive-like characteristics such as having multiple queens or forming supercolonies (Dáttilo and MacGregor-Fors 2021). These species are commonly found within their native range but can also dominate locally disturbed or urbanized areas due to the combination of their tramp-species nature and a "back-seat driver" occupation strategy. This type of invader benefits from a decline of a native species caused by external stressors, further accelerating their displacement. In human-modified environments, such "back-seat drivers" experience relaxed ecological constraints and may reduce local ant diversity (Bauer 2012; Pohl et al. 2018; (Salyer et al. 2014). Highly competitive and behaviourally flexible taxa such as odorous ants in the genus *Tapinoma* exemplify this strategy. Examining their interactions and dominance hierarchies provides insight into the mechanisms that mediate coexistence and competitive dynamics within native ant assemblages (Cerdá et al. 2013; Stuble et al. 2017).

Despite being native to the northeastern Iberian Peninsula, *Tapinoma darioi* competes with and displaces other ant species in disturbed urban areas within its native range, including its congener *Tapinoma nigerrimum* and other closely related species (Buczkowski and Bennett 2008; Centanni et al. 2022). *T. darioi* is invasive in northern Europe, exhibiting tramp-species traits such as unicoloniality. Moreover, its extremely high worker numbers (i.e., thousands of individuals per nest) enhance its competitive abilities and facilitate both successful establishment in non-native habitats and expansion within invaded areas (Abril and Gómez 2019; Buczkowski and Bennett 2008). In spite of being highly competitive, a diverse array of native ant species has been observed coexisting with *T. darioi*. However, the impact of this dominant species on local ant fauna and the specific mechanisms underlying its coexistence with other species remain poorly understood.

The present study aims to assess the coexistence of three of the most common native ant species in the northeastern Iberian Peninsula: *Aphaenogaster senilis*, *Messor barbarus* and *T. darioi*, and to identify the behavioural mechanisms facilitating their coexistence. We monitored an urban Mediterranean grassland for six months to evaluate dominance patterns of *A. senilis* and *M. barbarus* and to assess their potential coexistence with the highly competitive *T. darioi*. In parallel, we established dominance rankings through laboratory behavioural assays to characterise interspecific differences in aggression. Based on the tramp-species attributes of *T. darioi*, we hypothesised that it would exhibit behavioural dominance and that all species would show high levels of aggression. This study provides new insight into the behavioural dynamics of the recently described *T. darioi* within its native range.

Methodology

Experimental site and studied species

The study was carried out in northeastern Spain, within the campus of the Autonomous University of Barcelona (41° 29' 59.978" N, 2° 6' 34.772" E), between October 2023 and May 2024. The study site was an urbanized Mediterranean grassland located on a steep southern slope with about 250 m^2 featuring overlapping areas of bare soil and herbaceous plants. The soil substrate had a homogenous composition throughout all the study area, exhibiting a certain degree of compaction and consolidation, and had a poorly developed edaphic profile. Vegetation was composed mainly of herbaceous species forming patches, with some areas exhibiting a more developed understory and areas of bare soil.

Before starting the experiments, all ant colonies present in the area were surveyed with their geographical coordinates recorded (Fig. 1a), their species identified using specific taxonomic keys based on body morphometrics and male genitalia (Arcos and García 2023), and approximate relative numerical abundance assessed. The three most abundant species were then chosen for the laboratory bioassay: *A. senilis*, *M. barbarus* and *T. darioi*. Approximately one hundred workers of each species were collected from three randomly selected colonies located between 2 and 35 m apart within the study area (Fig. 1b). Ants were kept for a short period of time to carry out bioassays, housed at room temperature in identical 17.8 × 9.4 cm plastic containers, each coated with Fluon™ to prevent escape and filled with a soil substrate. They were fed once a week with mealworms and a 1:3 sugar solution, and water was provided ad libitum.

The three species selected for the laboratory aggression bioassays are among the most abundant ant species in urban Mediterranean grasslands. *A. senilis* is a monomorphic and omnivorous species native to the occidental-mediterranean area (Gómez and Espadaler 1996). It has termoxerophilic preferences, with high numbers of workers per nest, and colony-fission dispersion (Agbogba 1985). *M. barbarus* is

Fig. 1 Study area (250 m²) at the Autonomous University of Barcelona, NE Spain. (A) Location and species identity of all ant nests that exhibited activity at any point during the six-month monitoring period. Nest substitutions are not shown. (B) Three nests of each of the most abundant species were randomly selected for laboratory behavioural assays. Image adapted from Google Maps

the main seed-harvester ant in Mediterranean grasslands and shrublands (Azcárate et al. 2005), where it is often numerically dominant (De Almeida et al. 2020). It has a polymorphic worker caste with behavioural adaptations (Valadares et al. 2022). Both species are monodomous (i.e., one nest per colony), monogynous (i.e., one queen per nest), and abundant in the study site (Cerdá et al. 2009; Solida et al. 2011). Conversely, *T. darioi* is exhibiting several tramp-species traits such as polydomy (i.e., multiple interconnected nests), unicoloniality (i.e., lack of aggression among nests), and polygyny (i.e., several queens per nest) (Seifert et al. 2017). Given the polydomy colony structure of *T. darioi*, nests from this species were considered to belong to the same colony within a 2-meter radius if they exhibited no aggression towards each other.

Nest monitoring

All ant nests at the field site were georeferenced and monitored biweekly during peak activity hours (12:00–16:00) (Cros et al. 1997), between October 2023 and May 2024. The survey protocol involved scraping the soil, turning over rocks, inspecting tree bases, and examining plants, fallen leaves and tree trunks. Nest size was visually estimated for one minute based on the number of individuals at the nest entrance at peak activity hours, using the following relative scale: Empty, extremely scarce (2–5 individuals), scarce (6–20), moderate abundance (21–50), abundant (51–100), very abundant (> 100).

All ant nests were documented throughout the observation period, as well as nest supersedure, noting whether the nest was empty or occupied by another species. Occupation of a previously recorded nest by another ant species was considered a nest turnover event when the new occupation persisted for a minimum of two weeks. Nests were individually marked to avoid duplication, and two workers from each newly discovered nest were collected for laboratory identification. Only nests exhibiting clear signs of ant activity were recorded; empty nests containing dead individuals at their entrance, suggesting of prior – but not current, occupation – were excluded from the dataset.

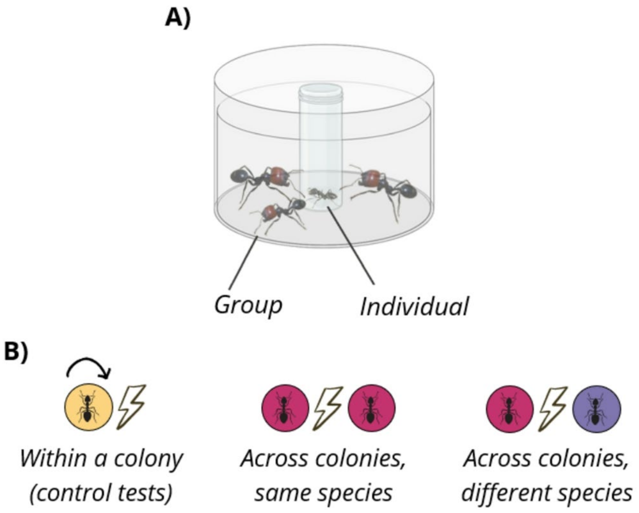

Fig. 2 (A) General experimental setup with test arena used for aggression assays demonstrating the standard protocol with one individual introduced at the centre of the arena (focal species) and a group at the periphery (contender species). (B) A full factorial behavioural assay was performed: a within-colony control, and treatment tests between colonies of the same species and between different species

Aggression bioassay

Aggression tests were conducted in a controlled laboratory environment at two distinct periods (October 2023 and March 2024) to assess seasonal variation in aggressive behaviour. The tests involved encounters between 1 ant (individual) and a group of 3 ants, simulating the effect of group size (Fig. 2). Three types of tests were performed for each colony: (1) within-colony control encounters, (2) between different conspecific colonies and, (3) between colonies of different species. Given that *M. barbarus* has two morphologically and behaviourally distinct worker castes (minors and majors, also known as soldiers), aggression assays were conducted separately for each caste, following the same protocol.

Aggression tests followed a protocol adapted from (Grangier et al. 2007). In each trial, a single ant was introduced at the centre of an arena (diameter = 8.5 cm, heigh = 11 cm) coated with Fluon™, while a group of three ants was placed at the periphery. Individual and group ants were initially separated by a tube and allowed to acclimate to the new environment for 30 s before the behavioural observations began. Each test lasted 120 s, during which the time of the first interaction, as well as all subsequent interactions, or lack thereof, were recorded every 10 s following a standardized aggression scale (Table 1). Each of the three aggression assay combinations was replicated six times per colony in both autumn and spring, and two datapoints were extracted from each trial (one for the focal species and one for the contender). In total, this resulted in 1098 tests (2196 datapoints): 306 for *A. senilis* (162 in autumn and 144 in spring), 489 for *M. barbarus* majors and minors combined (324 in autumn and 165 in spring), and 303 for *T. darioi* (162 in autumn and 141 in spring). Intraspecific tests between *M. barbarus* colonies included six replicates for each possible pairwise caste combination of major and minor workers, resulting in 72 tests per colony instead of 18. However, tests involving *M. barbarus* colony 1 could not be conducted in spring due to nest abandonment. Individual ants were randomly selected from within colonies for each test and were never reused in subsequent trials. All

Table 1 Behaviour interactions used in the laboratory bioassay with their corresponding descriptions. Behavioural interactions were classified as peaceful (antennation), neutral (indifference and freeing or not from bite and holding), submissive (avoidance and escape), or aggressive (all remaining behaviours). Only aggressive interactions were used to calculate the aggression index. The scale was adapted from Abril and Gómez 2010

Behaviour	Description	Score
Indifference	Neither aggressive nor peaceful behaviour.	Neutral
Freeing from bite and holding	Actively trying to free themselves from the opponent ant's grasp during bite and holding	Neutral
Not freeing from bite and holding	Not reacting at the opponent ant's grasp during bite and holding	Neutral
Avoidance	Changing direction or withdrawing from the opponent ant.	Submissive
Escape	Submissive behaviour, quickly moving away from the opponent.	Submissive
Antennation	Repeated tapping of the antennae on any part of the other ant's body.	Peaceful
Open mandibles	Broad opening of the mandibles as a threatening behaviour.	Aggressive
Jerking	Violent spasm without biting.	Aggressive
Gaster flexion	Raising the gaster to a vertical position as a chemical defence.	Aggressive
Biting	Quickly biting the body or the appendices of the contender ant.	Aggressive
Biting and holding	Biting any part of the rival ant and maintaining the aggression over time, escalating aggression. In some cases, it involved carrying or being dragged by the confronting ant.	Aggressive
Death	Death of the opposing ant.	Aggressive

bioassays were conducted by the same researcher, who was blind to colony identity.

Statistical analyses

All statistical analyses were conducted in R software (version 4.4.0; R Core Team, 2014). Ecological nest dynamics were analysed using a multinomial logistic regression from the *multinom* function (*nnet* package, version 7.3.19;Venables and Ripley 2002) to evaluate changes in the relative frequency of ant species' nests (response variable) over time coded as covariate. Post-hoc pairwise comparisons of species' nest proportions (i.e. the relative number of nests of each species in the study area)across the monitoring period were performed with the estimated marginal means (EMMs) from the *emmeans* package (version 1.10.7;Searle et al. 2023) applying a Tukey adjustment for multiple comparisons, and an ANOVA to evaluate overall model significance. Monthly nest turnovers events were quantified for both resident and occupier species and summarized in the supplementary materials. To assess potential effects of colony size on aggression, mean nest size was estimated for each species. Differences in worker abundance were tested using a Kruskal-Wallis and Dunn post-hoc tests, implemented via the *"FSA"* packages (version 0.9.6; Ogle 2017), with Bonferroni corrections for multiple testing.

To quantify aggression levels, we calculated an aggression index (AI) for each assay as the sum of all aggressive interactions recorded for the focal individual and the contender group. Aggression was analysed using a generalized linear mixed model (GLMM) with a negative binomial error distribution to account for overdispersion, implemented with the *glmer.nb* function from the lme4 package (version 1.1.36; Bates et al. 2014). The response variable was the aggression index. Fixed effects included focal species (species displaying the behaviour), group size (individual or group), season (autumn or spring), internest distance, and the time to first interaction (latency to the first contact during the assay). Because each assay involves a specific combination of behavioural condition (control or treatment) and contender species, these two factors were modelled jointly as an interaction term. This approach treats each condition–contender pairing as a single composite predictor, which reflects the structure of the experimental design and avoids estimating separate main effects that would not be biologically meaningful.

We also included the interaction between focal species and this composite condition–contender factor to test whether species differed in their aggression patterns toward different opponents. Random intercepts were included for both focal and contender colonies to account for repeated measures and prevent pseudoreplication as well as trial IDs. Post-hoc pairwise comparisons were performed using estimated marginal means, evaluating differences among condition–contender combinations within each focal species. Tukey-adjusted p-values were used to correct for multiple comparisons, and overall model significance was assessed using Type III Wald chi-square tests. An additional GLMM was fitted with time to first interaction as the response variable, including the same fixed and random effects as the main model to test for differences in latency among species and interaction contexts.

A separated multinomial model was fitted to assess the mean estimated probabilitiesof each behavioural category (i.e. the proportion of each behaviour relative to all observed behaviours) across species pairs. The response variable was the proportion of observed behaviours, with group size (individual or group) and season as fixed effects, and internest distance and time to first interaction as covariates. Post-hoc pairwise comparisons were again conducted with the *emmeans* package and corrected for false discovery rates. All data visualizations were generated using the *ggplot2* package (version 3.5.1; Wickham 2009).

Results

Ecological dynamics

The nest survey identified 106 ant colonies across seven different species (Fig. 1A), with the three species studied in the laboratory representing over 84% of all recorded nests. These included 33 nests of *A. senilis*, 12 nests of *M. barbarus*, and 44 nests of *T. darioi*, which were significantly more abundant than the other species (Fig. 3, tables S1 & S2 show mean number of nests per month and statistical tests, respectively). The overall proportions of nests remained stable for all species except *A. senilis* and *T. darioi*, that presented a decrease and increase in their colony proportions respectively over the six-month monitoring period (ANOVA: $\chi^2_6=21.788$, $P=0.0013$, tables S1 & S2). Nest turnover was high, primarily involving the species with changes in nest proportions, being *T. darioi* occupying nests of *A. senilis* (Fig. 3, tables S3 & S4).

Nest size estimations also varied significantly among species. Across all nests surveyed, *A. senilis* showed the lowest average workers presence (12.132 ± 14.531 SD, *Total number of observations N = 292)*, whereas *M. barbarus* (37.234 ± 25.595 SD, $N=103$) and *T. darioi* (64.142 ± 44.71 SD, $N=356$) had substantially higher nest sizes (Table S5).

Behavioural assays

As a response variable, latency varied significantly among species (ANOVA: focal species, $\chi^2_3 = 25.506$, $P<0.001$; contender species, $\chi^2_3 = 35.634$, $P<0.001$). Interactions involving *T. darioi*, either as focal or contender, exhibited longer latencies (GLMM coefficients: focal *T. darioi*, Estimate = 0.697, $P<0.001$; contender *T. darioi*, Estimate = 0.395, $P<0.001$), indicating delayed engagement in encounters involving this species. No other species showed significant effects on latency.

The behavioural analyses revealed significant interspecific differences, with each species exhibiting distinct behavioural patterns of aggression. *A. senilis* displayed overall low AI values, with similar higher levels of aggression in encounters with their own species and *M. barbarus* as contenders (EMMEANS: *Estimate* = 0.159–0.178, $P>0.05$; Fig. 5, table S8). Frequently observed behaviours against *M. barbarus* workers and *T. darioi* included biting and submissive interactions like avoidance or escaping

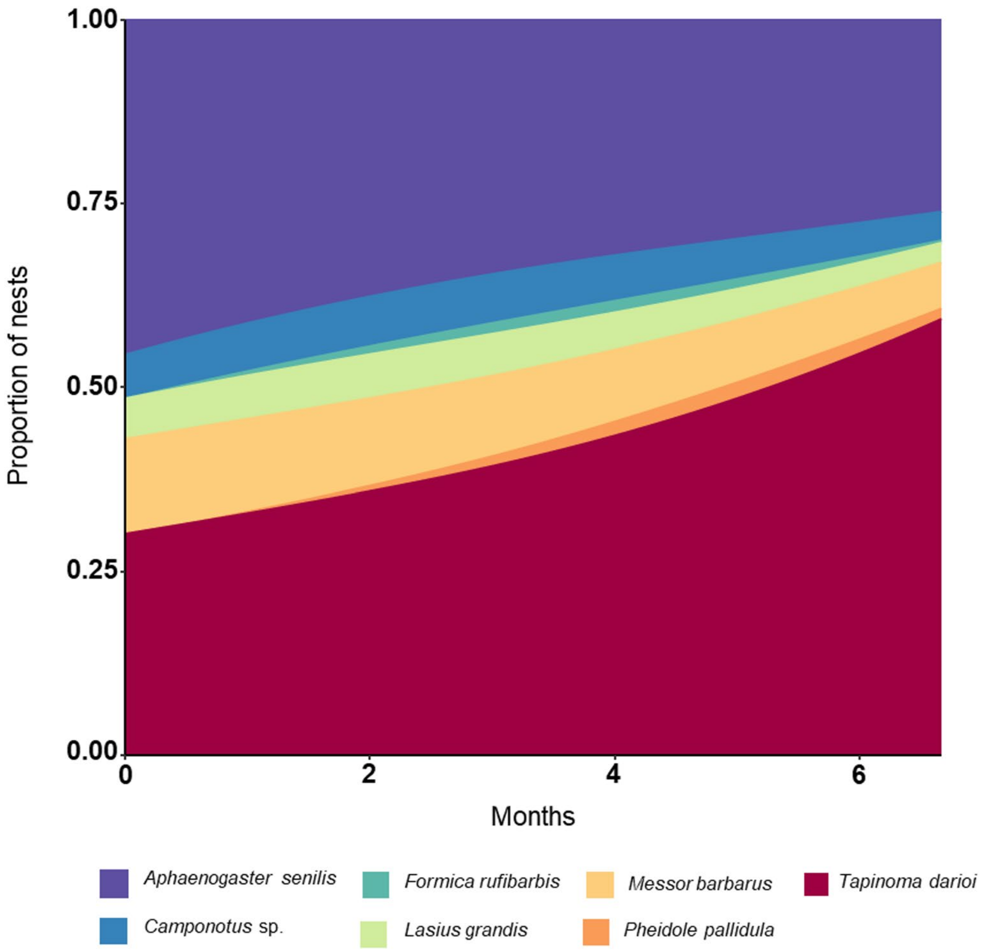

Fig. 3 Nest proportions over a six-month period in an urban mediterranean grassland. Multinomial model predictions showing the relative proportion of nests belonging to each of the seven observed species (i.e. number of nests per species relative to the total number of nests) across the monitoring period

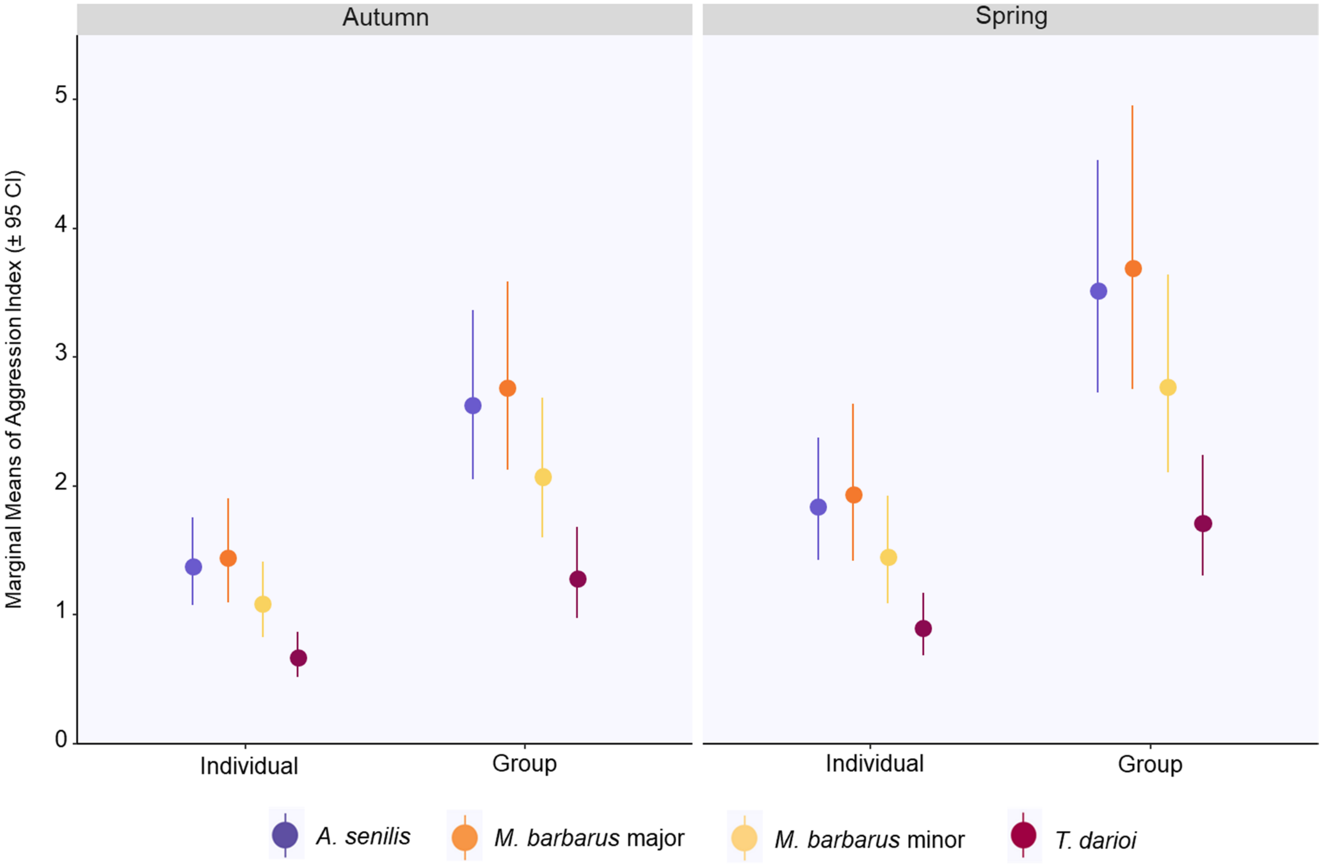

Fig. 4 Seasonality and group size influence aggression levels. Ants displayed higher aggression in spring and when tested in groups. Results of the GLMM showing the effects of seasonality and group size on the aggression index, using a negative binomial error distribution. Vertical lines represent the 95% confidence intervals

(Fig. 6, tables S9 & S10). The frequency of observed behaviours in *A. senilis* remained relatively consistent across all trials (Fig. 6 and table S10).

The two worker castes of *M. barbarus* presented behavioural differences between control and treatment conditions, whether the encounters involved the same or a different caste (Fig. 5, tables S7 & S8). Under treatment conditions, this species generally exhibited high aggression regardless of the opponent, with both castes displaying comparable aggression towards *A. senilis* and *T. darioi* (Fig. 5, table S8). However, there was a tendency of heightened aggression and high frequency of aggressive behaviours towards non-nestmate conspecifics, especially in minor workers (EMMEANS: majors, *Estimate* = 2.011, $P < 0.001$; minors, *Estimate* = 3.113, $P < 0.01$, Figs. 5 and 6, tables S8, S9 & S10). Both castes had similarities in behavioural frequency distribution towards heterospecifics, with tests frequently resulting in highly aggressive encounters (Fig. 6, tables S9 & S10).

T. darioi did not show significant differences in AI between control and treatment conditions during conspecific encounters (EMMEANS: *Estimate* = -14.195, $P => 0.05$; Fig. 5, table S7). Overall, this species frequently exhibited affiliative (instead of aggressive) behaviour such as antennation towards conspecifics (EMMEANS: *Estimate* = 10.644, $P < 0.001$, tables S9, S10 and S11). The aggression index remained low and consistent with those observed in conspecific interactions during interspecific tests as well (Fig. 5, table S8). In fact, *T. darioi* was significantly more likely to display submissive behaviours such as avoidance or escape when interacting with *A. senilis* or *M. barbarus* (Fig. 6, Tables S9 & S10).

Discussion

This study aimed to assess variation in aggressive interactions among species in a Mediterranean grassland ant community and to identify the ecological and behavioural mechanisms that enable their coexistence.

Of the seven species surveyed, *A. senilis*, *M. barbarus*, and *T. darioi* were the most abundant, accounting for over 84% of nests in the study area. Most ant species maintained stable nest proportions, except for *A. senilis* and *T. darioi*

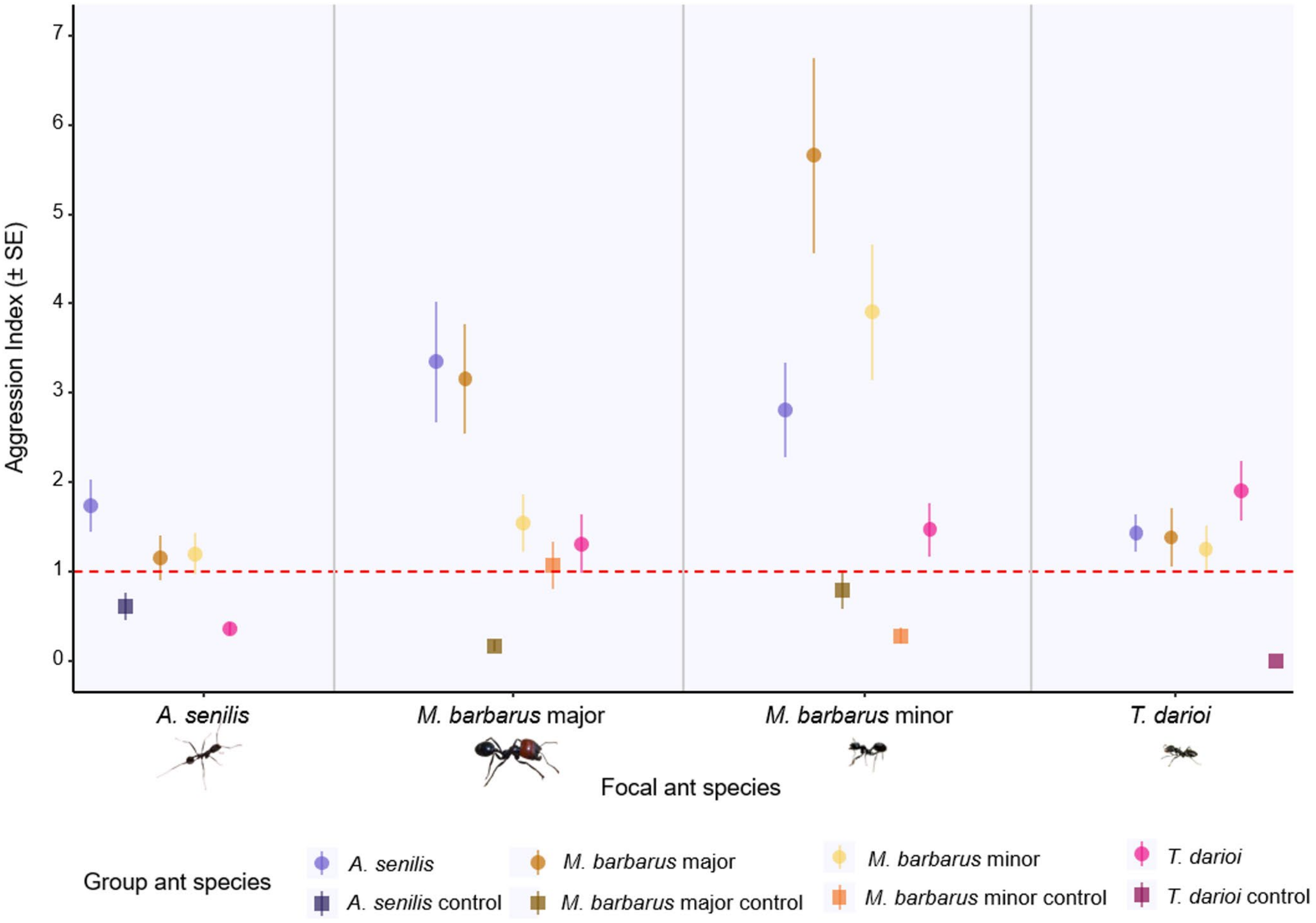

Fig. 5 Ants showed varying levels of aggression according to the contender's identity. Results from the negative binomial model show the Aggression Index of focal species when confronted with group treatments across species interactions. Overall, values below the red dotted line represent control tests with individuals from the same colony (squares), while values above this line corresponding to bioassays involving different colonies or species (circles). Vertical lines indicate 95% confidence intervals

exhibited clear seasonal fluctuations over the six-month study period. These patterns align with the high nest turnover rates in *T. darioi*, as well as its frequent occupation of *A. senilis* nests during spring. This may support the hypothesis of seasonal interference competition between these two native species, an occurrence that may be common in urbanised areas (Cerdá and Retana 1998; MacKay and MacKay 1982). Nevertheless, year-round monitoring would be required to confirm whether these patterns reflect actual competitive displacement. Ecological theory predicts that coexistence among competitors is often maintained by trade-offs such as colonization–competition or fecundity–dispersal trade-offs. Further experiments, such as bait retrieval trials (Fellers 1987; Stuble et al. 2013), would help clarify the mechanisms involved. Additional drivers, including resource availability, microhabitat variation, and intra- and interspecific interactions, are also likely to influence community structure (Levins and Culver 1971).

Aggression was strongly influenced by species identity (focal or contender) and by condition (control or treatment), with our behavioural assays revealing clear, species-specific differences in encounter dynamics. Previous studies have described *A. senilis* as neither dominant nor aggressive (Retana and Cerdá 1994), and our results confirm this general profile while also suggesting a more complex behavioural pattern. This species displayed consistently low aggression, especifically towards *T. darioi*, with frequent submissive behaviours such as avoidance or escaping. This could be suggesting an accurate recognition system that minimises costly conflict with *T. darioi*, especially given the interference interactions observed in the field and the associated risk of colony displacement (Batchelor and Briffa 2011; Cerdá and Retana 1998; Cerdá et al. 2009).

The harvester ant *M. barbarus* is known for its aggressive nature in Mediterranean habitats (Retana and Cerdá 1994), and our findings confirm this tendency. Both majors and minors showed high levels of aggression toward

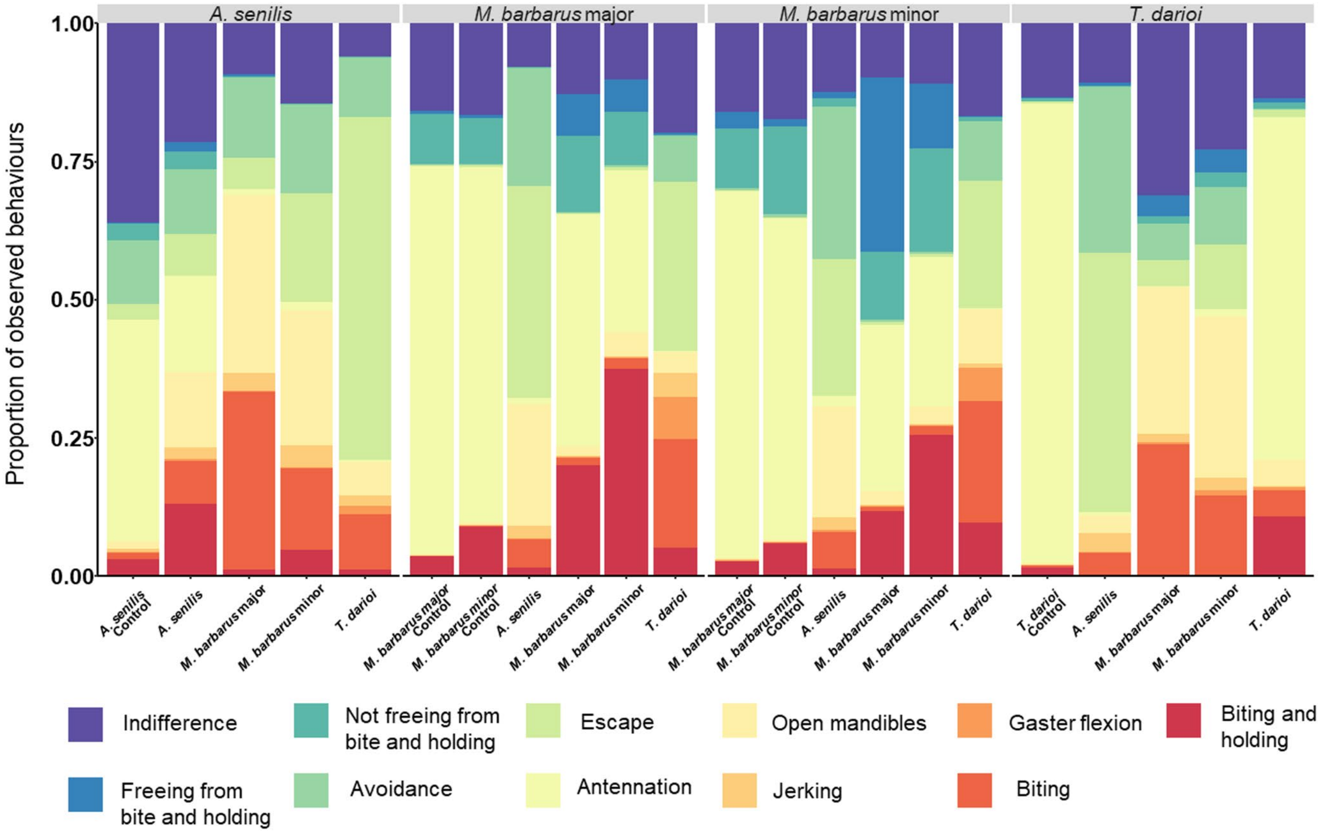

Fig. 6 Ant species exhibited distinct behavioural profiles in response to experimental conditions during conspecific and heterospecific encounters. Multinomial model results showing the mean proportion of all observed behavioural interactions across species pairs, displayed separately for control and treatment conditions. Each panel represents a focal species or caste, and bars correspond to species-by-condition combinations. Behavioural proportions are derived from model-predicted probabilities

conspecifics, with a notably higher frequency of strongly aggressive behaviours such as bite and holding (particularly pronounced in minors). Minor workers typically carry out intranidal tasks (Hölldobler and Wilson 1990) and are considered more reactive to external stimuli, which may account for their heightened aggressiveness (Valadares et al. 2022). In fact, the slightly larger minors observed may represent an intermediate (media) caste, potentially explaining the variation in observed responses (Nowbahari et al. 1999; Scharf et al. 2011; Sturgis and Gordon 2012). Further analyses linking body size to aggression are warranted to clarify these dynamics (Björkman-Chiswell et al. 2008). In interspecific encounters, *M. barbarus* displayed lower levels of aggression and submissiveness towards *T. darioi*, consistent with the idea that ants escalate aggression when strength asymmetries are small (Arnott and Elwood 2009).

T. darioi is a supercolonial species that appears particularly well adapted to urban habitats, gradually expanding through multiple invasion phases (Salyer et al. 2014). Although high aggression is typically associated with interspecific nest occupation, *T. darioi*, like other *Tapinoma* species, may follow a “back-seat driver” strategy, displacing native species via persistent occupation, high numbers and potential resource monopolization rather than overt aggression (Bauer 2012; MacKay and MacKay 1982). In our study, while *T. darioi* showed low aggression in behavioural tests, it increased its nest occupancy through time, suggesting ecological and possibly numerical dominance (Leonetti et al. 2019).

Although overall aggression was low, *T. darioi* displayed higher aggression towards other *T. darioi* nests, a pattern observed in supercolonial species such as *Formica pressilabris* that may be linked to limited genetic and resource flow within supercolonies (Hakala et al., 2020), or by the presence of adjacent supercolonies within the study area. This species also showed clear nestmate discrimination, with increased antennation toward conspecifics. Interestingly, it exhibited more antennation between nestmates than non-nestmates, contrary to patterns observed in other supercolonial ants (Björkman-Chiswell et al. 2008; Sturgis and Gordon 2012). This indicates an ability to distinguish its own nest from others, suggesting a nuanced tactile communication system (Hölldobler and Wilson 1990). Given its supercolonial structure and parallels to the global invasive

Linepithema humile (Leonetti et al. 2019), field studies would be valuable to assess its full dominance potential.

Aggression increased in group settings, but this increase was modest relative to the number of individuals present, indicating that groups produced more total aggression without showing higher per-capita aggression. Determining the behavioural contributions of individuals versus groups more precisely would require targeted one-to-one assays, which represent an interesting direction for future research. Ants that began interacting earlier exhibited higher levels of aggression, a pattern driven by the greater opportunity for interactions within the assay rather than behavioural differences per se. Accounting for latency in the model therefore prevented confounding and allowed species and seasonal effects to be interpreted more reliably. When considering latency as a response factor, we observe that interactions involving *T. darioi* were consistently delayed, regardless of whether it acted as focal or contender, whereas no other species showed significant effects on latency. The relatively low aggression of *T. darioi*, together with its reliance on numerical dominance, may explain these longer latencies in interactions with *A. senilis* and *M. barbarus*, suggesting a reduced propensity for rapid escalation during encounters. Seasonal differences were clear, with aggression being higher in spring than in autumn. This variation in aggressive behaviours may reflect an adaptative response to resource availability (Katzerke et al. 2006). Heightened aggression in spring has been previously observed in other ant species, such as *Formica exsecta* (Katzerke et al. 2006) and *L. humile* (Suarez et al. 2002), in which the presence of developing brood likely increases colony food requirements in spring, when resources may still be scarce (Solida et al. 2011). While the results from controlled laboratory bioassays offer key insights, they may not capture the complexity of field dynamics, where mass recruitment and large-scale interactions often determine outcomes (Lach et al., 2009).

Overall, our findings highlight the flexible and context-dependent nature of aggressive interactions among three common ant species in urban Mediterranean grassland. Through detailed behavioural assays, we revealed a hierarchy in which *A. senilis* emerges as behaviourally subordinate, whereas *M. barbarus* and *T. darioi* appear codominant. Despite the nest turnover in *A. senilis* by *T. darioi*, the species overall coexistence likely reflects an interplay between numerical dominance and behavioural plasticity, modulating aggression according to season and opponent identity. Notably, *T. darioi* displayed traits typical of species with a great occupation potential. Its supercolonial structure, high nest density and nest occupation without extreme aggression in laboratory tests, positions it as a classic “back-seat driver” invader. In disturbed or urban habitats, these advantages may facilitate the exclusion of both native dominant and subordinate species. This may support the hypothesis that *T. darioi*’s displaces other species through competitive interference, although year-round field studies integrating resource monopolization are needed to rule out that these patterns are natural seasonal fluctuations. Given ongoing human-driven changes to Mediterranean landscapes, the potential for *T. darioi* to expand and reshape community structure is considerable. Its success reflects broader patterns observed in other invasive or disturbance-adapted ants, where numerical dominance, social organization, and behavioural flexibility facilitate gradual yet consequential shifts in community composition (Holway 1999). Impacts in such cases often emerge not through abrupt competitive exclusion, but through the progressive erosion of native species’ ecological roles and interaction networks, changes that may be cryptic until well advanced (Strayer et al. 2006). As such, *T. darioi* may serve as a compelling model for understanding how “back-seat driver” invaders modify ecosystems over time, highlighting the interplay between subtle behavioural mechanisms and long-term community restructuring (Holway et al. 2002; Strayer et al. 2006).

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Data availability The original datasets as well as the R script used to analyse the data are publicly available on CORA Data Repository (González-Lleida et. al., 2026).

Declarations

Conflict of interests The authors have no competing interests to declare in any material discussed in this article.

Ethical approval In accordance with European (Directive 2010/63/EU), Spanish (Real Decreto 1386/2018), and Catalan (Decret 214/1997) regulations, experiments involving insects are exempt from requiring ethical committee approval. Nevertheless, samplings were carried out efficiently to minimize damage to the nests, and the colonies maintained in the laboratory were regularly monitored to ensure they remained in optimal conditions.

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