Functional traits drive the competitive assembly of ant communities and impact colony performance in competition mesocosms

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ABSTRACT

1. Studies along broad spatial and habitat gradients evidence that organisms' traits can influence community assembly through their impact on dispersal and environmental filtering. However, the role of traits in structuring local faunal communities within habitats remains poorly understood. In particular, the often-assumed role of traits in affecting the outcome of competition among animal species is rarely tested.
2. We coupled a field study with a mesocosm experiment to explore how ant species' traits shaped competition and community structure, leveraging a small mangrove ecosystem which conceivably imposed minimal dispersal- and environmental filtering effects on ant community assembly.
3. We first surveyed the ant communities inhabiting 115 mangrove trees using >2000 carbohydrate and protein baits, and directly measured multiple morphological, physiological (critical thermal maximum) and dietary (stable isotope trophic position) traits of all ant species. We then coupled co-occurrence network analyses with meta-analytical models to uncover the trait-based mechanisms structuring species co-occurrences in the field. Finally, in a mesocosm experiment, we reared 100 colonies of eight ant species from the mangrove over 30 days under different competition

treatments to investigate trait-mediated effects of competition on ant colony performance.

4. Patterns of ant species co-occurrences and bait recruitment indicated strong competition for limited protein-rich resources. Accordingly, dissimilarities in three traits – eye size, pronotum width and antennal scape length – consistently explained species co-occurrences, suggesting that the communities were competitively assembled by a partitioning of resource acquisition strategies among species. Species co-occurrences were also to a lesser extent explained by similarities in critical thermal limits, suggesting mild environmental filtering.
5. In the mesocosm experiment, increasing hierarchical differences in eye size and pronotum width between neighbouring ant colonies exacerbated interspecific competitive effects on colony survival and growth.
6. Our results empirically demonstrate that traits linked to resource acquisition influence competition outcomes and community structure in ants. Importantly, they also suggest that the effects of species trait differences on competition are context-dependent: whereas dissimilarities in species' traits facilitated resource partitioning in the mangrove, hierarchical differences in trait values distinguished species' competitive abilities for shared resources in the mesocosms.

KEYWORDS

Biodiversity, experiment, hierarchy, limiting similarity, mangrove, tropical

INTRODUCTION

A predictive understanding of how species are organised in space and time is the ‘Holy Grail’ of community ecology (Funk et al., 2016). The advent of trait-based ecology (McGill et al., 2006) has arguably brought ecologists closer to achieving this goal, by revealing how assembly processes such as dispersal- and environmental filtering mechanistically select on phenotypic properties of organisms (i.e. ‘functional traits’) to determine community composition across broad spatial extents spanning landscapes and even macroecological gradients (Funk et al., 2016; Lammana et al., 2014; Bruelheide et al., 2018; Wong et al., 2019). Still, much remains unclear about how traits facilitate assembly processes which operate within local communities at fine spatial scales, where the effects of dispersal sorting and environmental heterogeneity are reduced.

Interspecific competition is a dominant process structuring local faunal communities, but how trait differences between co-occurring species influence this process is poorly understood. Contrary to the effects of dispersal- and environmental filtering, competition is expected to result in local communities comprising species with substantially dissimilar trait values, as competitive exclusion occurs among species with similar traits, in line with the theory of limiting similarity and niche partitioning (McArthur & Levins, 1967; Adler et al., 2013). Accordingly, the effect of competition in driving the assembly of a local community is often inferred from a pattern of dissimilarity in the community’s multidimensional trait space, as measured by aggregative metrics such as functional divergence and overdispersion (Kraft et al., 2008; Levine et al., 2024). However, such multidimensional and aggregative community-level approaches may overlook opportunities to understand the disproportionate effects that individual traits may have on competitive interactions, and how these vary across different species within communities. Furthermore, coexistence theory (Chesson, 2000) suggests that rather than purely arising from (directionless) limiting trait similarity and niche partitioning, community structure under competition may also arise from a ‘limiting dissimilarity’ in competitive abilities (Ågren & Fagerström, 1984), where, for a given degree of niche partitioning, hierarchical (i.e. directional) differences in trait values distinguish species’ competitive abilities for a shared resource, and only species that are not too different in competitive abilities can coexist (Herben & Goldberg, 2014). Most crucially, as many studies of community trait patterns are observational, there is a need to test experimentally the mechanisms assumed to underpin competition structuring (D’Andrea & Ostling, 2016), such as the effects of traits on competitive interactions between co-occurring species, and the associated costs to individual performance in terms of survival and growth.

Arboreal ant communities occupying discrete but interconnected habitats, such as trees in forests or plantations are ideal model systems for exploring the influence of functional traits on interspecific competition and community assembly. A rich literature suggests that interspecific competition in general, and particularly interactions between dominant and subordinate species, strongly structures arboreal ant communities (Room, 1971; Majer et al., 1994; Ribas & Schoereder, 2004; Pfeiffer et al., 2008; Hoenle et al., 2025; but see Sanders et al., 2007). This is because key resources such as carbohydrates and proteins essential for the maintenance, growth and reproduction of ant colonies, as well as nest sites, are often limited and unevenly distributed in canopy habitats (Davidson, 1997). Traditionally, the effect of competition in structuring ant communities has been inferred from segregated patterns of species co-occurrences at the community level (e.g. Sanders et al., 2007), but there are significant limitations to this approach. One is that various non-competitive processes can also generate segregated patterns in species co-occurrences (see Blanchet et al., 2020). Another is that community-level patterns may fail to capture the asymmetric nature of interactions at the fine ecological scales where competition unfolds, such as between pairs of species (Araújo & Rozenfeld, 2014). There is hence an opportunity to advance understanding of the mechanistic basis of competition in ant communities by coupling trait-based approaches which can systematically quantify species' phenotypic differences with network-level co-occurrence analyses which can account for asymmetric interactions under a hypothesis-driven framework (Wong et al., 2021). Moreover, there is a need to ascertain the 'functionality' of multiple ant traits that have been presumed to influence interspecific competition. These include body size (Fayle et al., 2015) and other morphological measurements (Wong et al., 2021), diet (Blüthgen et al., 2004), and thermal tolerance (Bestelmeyer, 2000). This can be explored experimentally by examining their effects on the performance – specifically, the growth and survival – of ant colonies in competitive settings.

We conducted a field study and mesocosm experiment to understand how traits influence the assembly of local ant communities over fine spatial scales where community structure was most likely shaped by interspecific competition. We achieved this by leveraging a small (0.5 ha) mangrove in tropical Asia (Fig. 1) that contained taxonomically identical, relatively uniform, spatially discrete yet proximally located trees, which consequently harboured naturally confined local ant communities that were conceivably minimally affected by dispersal and environmental filtering. It is worth noting that despite being among the most ubiquitous insects in mangroves, the ecology of ants in these vital ecosystems is poorly documented (Nielsen, 2011). Virtually no investigations into community assembly mechanisms have been attempted since the pioneering work of Cole (1983) nearly half a century ago, which indeed showed competitive interactions to strongly determine the occurrences of five ant species across mangroves in the Florida Keys.

In the field study, we first robustly characterised co-occurrences of ant species on trees in the mangrove based on their recruitment to baits containing either carbohydrates or proteins, two fundamental resources required by ants (Davidson, 1997). Next, by capturing multiple individuals of each species, we measured a diverse suite of traits spanning morphology, diet (stable isotope trophic position), and physiology (critical thermal maximum, CT_{max}). We then used meta-analytical models to test the nature, strength, and consistency of the effects of individual traits in structuring co-occurrences across all ant species in the mangrove. We tested the hypothesis that ant species co-occurrences in the mangrove were primarily shaped by the effects of limiting similarity competition and niche partitioning on species' traits. This would be evident from high dissimilarities in the trait values of co-occurring species. In contrast, we expected environmental filtering to have a smaller influence, which would be indicated by low dissimilarities in the trait values of co-occurring species (Kraft et al., 2008; Wong et al., 2021).

We complemented the field study with a 30-day mesocosm experiment to test empirically for trait-mediated effects of interspecific competition on ant colony performance. Briefly, we reared colonies of an abundant ant species from the mangrove (*Camoponotus vitiosus*) under one of three competition treatments: (i) no neighbouring colonies, (ii) a neighbouring colony of conspecifics, and (iii) a neighbouring colony of one of seven other ant species found in the mangrove, selected to reflect a range of functional similarity to *C. vitiosus*. We reared all colonies on shared resources and assessed each colony's survival and growth over 30 days to evaluate the competitive effects of neighbouring colonies on the performance of target colonies of *C. vitiosus*. We tested the hypothesis that when species had access to limited resources, variation in interspecific competitive effects would be driven by hierarchical differences in trait values between neighbouring and target species (Herben & Goldberg, 2014).

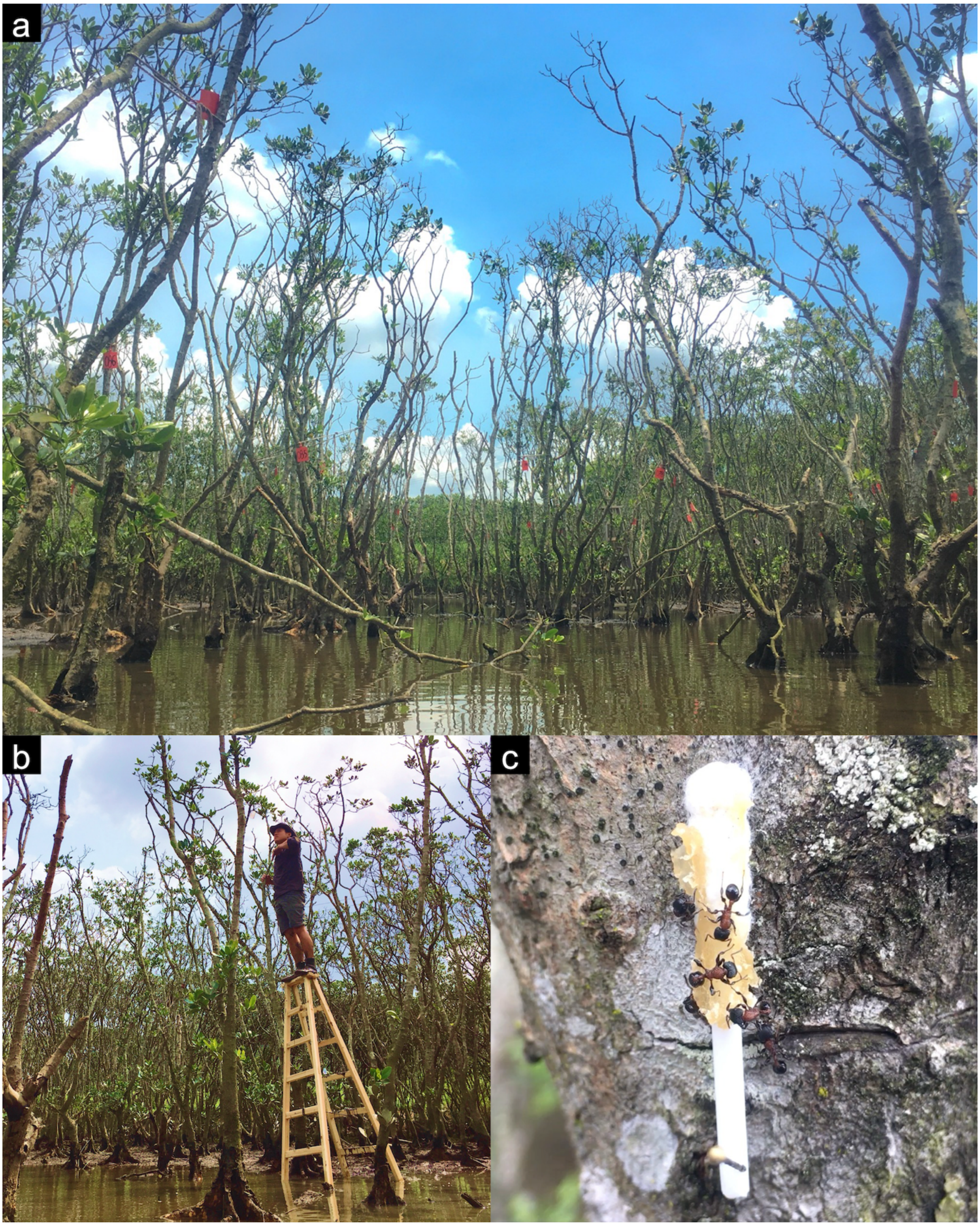

Figure 1. A field study on the arboreal ant communities of a small tropical mangrove. (a) The study site, a taxonomically homogenous stand of spatially discrete mangrove trees (species: *Kandelia obovata*) with relatively uniform structure. (b) Setting baits and observing ants on a tree in the mangrove. (c) Recruitment of workers of the species *Dilobocondyla fouqueti* to a protein-rich bait made of homogenised chicken breast.

METHODS

Study site

The field site ('Nam Chung', 22°31'17"N, 114°12'27"E, Fig. 1) was a small (0.5 ha) tropical mangrove on Hong Kong's northeastern coast. The mangrove was comprised entirely of *Kandelia obovata*, a tree species which occurs in brackish coastal habitats throughout southeast Asia and is the dominant mangrove species in Hong Kong (Sheue et al., 2003). The individual trees were <4 m in height, and adjacent trees were spaced 1–4 m apart, their branches failing to meet. We observed colonies of different native ant species nesting within standing dead twigs and crevices on the trees. All trees were partially submerged at high tide (1.2 m), and the ants on each tree clearly restricted their activities to the tree, refraining from crawling across the exposed mud even when the tide was 0 m (also noted by Nielsen, 2011). In other words, each tree supported an isolated – and for our purposes easily accessible – local ant community. As with other mangroves (Simberloff & Wilson, 1969), Nam Chung presented an ideal system where community composition could be comprehensively described at fine scale to effectively discern ecological process from pattern. Most crucially, the homogeneous taxonomic composition of the mangrove trees (Tam et al., 1997) and their distribution over a small area suggested minimal influences of dispersal- and environmental filtering on local ant community structure, making this system ideal for discovering how biotic interactions such as competition drive community assembly.

Sampling arboreal ant communities

From June to August 2019, we used liquid baits to systematically sample the arboreal ant community at Nam Chung. The baits separately offered two trophic resources essential for ant survival and growth: carbohydrates (honey) and proteins (homogenised chicken breast) (Feldhaar, 2014). Each liquid bait was smeared onto a cotton swab and pinned onto the surface of the tree with a needle (Fig. 1). We designated bait stations at 1 m height intervals spanning the trunk and all main branches of each tree; depending on the number of branches (which ranged from 2–6), between 6–19 stations were used on each tree. At each station, we pinned a bait for one resource (e.g. carbohydrate) onto the side of the tree and another bait for the other resource (i.e. protein) on the opposite side, varying the orientation of these baits arbitrarily between stations, and using a ladder to reach the highest branches (Fig. 1) We conducted baiting on sunny days between 1000–1500 h. We operated all baits for 1.5 h, during which we recorded the identities and abundances of all ant species recruiting. We followed the returning individuals to ascertain the locations of their nests on the trees, and used an aspirator to collect multiple individuals for trait measurements in the lab (below). We also spent 15 minutes visually searching each tree for any species that could have been missed; only 5.3% of all species records were derived from visual searches, and all species found by visual search were also recorded at baits. In total, we used 2,179 baits to sample 115 trees. Ants were detected on 99 trees. We measured the diameters of the trunk and all main branches of each tree and summed the values to obtain a measure of tree size. We characterised the spatial and temporal variation in microclimate across 30 representative trees spanning the area of the mangrove at Nam Chung from July to August 2019. We affixed two dataloggers (Elitech RC-51 Waterproof USB Temperature and Humidity Data Logger) on separate branches of each tree, which operated continuously to record values of air temperature and humidity at 30 min intervals over 30 days.

Measuring morphological, dietary and physiological traits

In the laboratory, we measured a suite of morphological, dietary and physiological traits using multiple workers of each ant species collected from the field.

We measured 10 morphological traits (body size i.e. Weber's length, head width, head length, interocular width, eye width, mandible length, antennal scape length, pronotum width, femur length, tibia length) on at least 10 individual workers of every species (range: 10–44 individuals per species; N=245 individuals). We selected these traits for their links to ant physiology and behaviour and hypothesised impacts on ant species performance and fitness (Wong et al., 2020; Boudinot et al., 2025).

We measured the relative trophic position of each ant species using stable isotope ratios of nitrogen (δ15 N) (Tillberg et al., 2006). The live ants collected from the field were first killed in a −20°C freezer. We then rinsed the ants with distilled water, removed their abdomens to avoid contamination by undigested material in the gut (Tillberg et al., 2006), and dried the samples in an oven at 40°C until a constant mass was reached. We combined dried samples such that each comprised ≥5 workers, and transferred these into an aluminium capsule weighing 0.3–1 mg. The workers of larger species were first ground and homogenized using a mortar and pestle following Tillberg et al. (2006). We measured the δ15 N values of each sample using a Nu Perspective Isotope Ratio Mass Spectrometer coupled to a Eurovector Elemental and reported values in ‰ (Tillberg et al., 2006). We used separate samples of the bark and leaves of *K. obovata* collected from Nam Chung for baseline calibration, and samples of caterpillars, spiders and parasitoid wasps to compare the δ15 N values of ants to those of organisms from different trophic levels at Nam Chung.

We measured the critical thermal maximum (CT_{max}) of at least 10 individual ants of each species (range: 10–46 individuals per species; N=302 individuals) following established protocols for CT_{max} assays (Diamond et al., 2017). We first acclimated all ants at 25°C for at least 2 h in the laboratory. We then placed individual ants in 1.5 ml Eppendorf tubes, plugging the entrance of each tube with dry cotton wool to confine each ant to an area of even temperature distribution. We placed the tubes in a digital dry bath (Benchmark Scientific BSH1004) connected to an additional thermometer (UEi Test Instruments DT302 Dual Input IP67) to ensure temperature accuracy (Leong et al., 2022). We began the assay at 36°C and increased the temperature at a constant rate of 1°C min^{-1}. Every 1 min, we rotated each tube and visually determined whether the ant had lost muscle coordination; the temperature at which this occurred was recorded as the individual's CT_{max}.

Mesocosm competition experiment

We conducted a mesocosm experiment in which colonies of *Camponotus vitiosus*, an abundant ant species at Nam Chung, were reared for 30 days under one of three competition treatments: (i) no neighbouring colonies, (ii) a neighbouring colony of conspecifics, and (iii) a neighbouring colony of one of seven other ant species found in Nam Chung (Table 1).

We built the mesocosms using branches of *K. obovata* collected from the field and dried in the sun for a month. We used concrete to seal existing crevices and made a weighted base that allowed each branch to stand freely. Each mesocosm comprised a 0.7 m-tall Y-shaped branch standing in a basin of saltwater (Fig. 2) (concentration of 3.5%). The saltwater mimicked mangrove conditions, isolated the ants to the 'tree', and prevented infestations of pests (e.g. algae and mosquito larvae). We coated the rim of each basin with glue (Tanglefoot) to prevent access by other organisms. We made nest tubes to house arboreal ant colonies using 2 ml plastic vials. Using a glue gun, we made nest tubes with entrances of different sizes (1.6, 2.0, or 2.8 mm) to reflect the natural dimensions of nest entrances of different ant species observed in the field. We shielded out light from each nest tube using a black plastic drinking straw which could easily be detached to observe the ants within ().

We collected 190 nests of different ant species found in Nam Chung by snapping branches of *K. obovata* from similar mangroves in the vicinity (so as not to interfere with the field study). In the lab, we carefully dismantled each nest and transferred all adult ants and brood (larvae and pupae) into a plastic container. While we had initially intended to run the experiment with colonies with queens, this was unfeasible as queens were absent from many nests. Nevertheless, it was the availability of brood that was integral to the experiment, as it is the brood – and not the queens – that critically regulate all foraging and defensive activities of the workers in ant colonies (Ulrich et al., 2016). We marked *C. vitiosus* workers from separate colonies with different coloured enamel paints (Tamiya Inc.) to differentiate them.

To set up the experimental colonies, we transferred 16 adult workers and 10 larvae of each ant species into a nest tube that had an entrance corresponding to the size of the species. For two species which had polymorphic worker castes, we included individuals of both the minor and major worker castes according to their approximate natural proportions observed during the nest excavations (Table 1). As far as possible, we used relatively large larvae of similar sizes (i.e. larvae of similarly late instar stages) in all colonies of the same species. Once the larvae were placed in the tube, the adults moved in within 12 h. We then introduced the ants to the mesocosms by fastening their nest tubes to the terminal ends of the trees with wire. We set up a total of 47 mesocosms with 100 ant colonies (53 *C. vitiosus* and 34 colonies of other ant species). These included seven replicate mesocosms which contained only a target *C. vitiosus* colony (the 'no competition' control), six containing a target *C. vitiosus* colony and a neighbouring colony of conspecifics (the 'intraspecific competition' treatment), and 34 containing a target *C. vitiosus* colony and a neighbouring colony of one of seven other ant species (with at least four replicate mesocosms set up for each unique pairing) (the 'interspecific competition' treatment) (Table 1). We plugged the entrances of all nest tubes with cotton wool during the first 24 h of the experiment to allow the colonies to settle, after which the plugs of the nest tubes in each mesocosm were removed simultaneously.

The mesocosms were placed on an open-air floor of a building shielded from any direct sun. A canopy made from green netting was laid over the arena to prevent interference from birds and wind. The positions of the individual mesocosms were arranged such that no two mesocosms of the same treatment or neighbour species were adjacent. Twelve dataloggers (same specifications as above) showed negligible spatial variability in climate across the arena. We supplied the ants in each mesocosm with water in a test tube plugged with cotton, fixed at a point equidistant to all nest tubes present. We varied the supply of food resources to the ants in each mesocosm to simulate the relative abundance of carbohydrate-rich resources and scarcity of protein-rich resources in the mangrove (as observed in the field – see Supporting information; also confirmed in Results). As an abundant carbohydrate-rich resource, we pinned one cube (0.1 g) of carbohydrate-rich agar jelly made from an agar–sucrose solution (after Dussutour & Simpson, 2008) proximally to each nest tube (Fig. 2), and replaced it whenever it was depleted. As a scarce protein-rich resource, once every 48 hours, we pinned one cube (0.1 g) of insect-protein-rich agar jelly (made from combining agar solution with blended *Tenebrio molitor* larvae) at a point equidistant to all nest tubes and removed the cube after 24 h.

The experiment ran for 30 days (29 Sep to 29 Oct 2019), a duration approximating the maximum developmental time from the first larval instar to adult in *Camponotus* (the genus of the target species) (Ito et al., 1988). We inspected all colonies once per day, gently sliding the black covers of the nest tubes to determine each colony's composition – including the numbers of live workers, larvae, pupae, and freshly pupated workers (callows). We checked that these corresponded with the numbers and identities of any dead individuals observed in the nest tubes or collected from the water basin. We also noted all interactions observed between individuals of different colonies and their foraging behaviours during both the day and night. At the end of the experiment, we collected all individuals in ethanol and dismantled all nest tubes to examine their contents.

Table 1. Summary of the mesocosm ant competition experiment. Shown are numbers of replicate mesocosms (n) for each of three competition treatments, the identities and colony compositions of different neighbour species used in the mesocosms, as well as their head widths and the designated sizes of their nest entrances in the experiment. Each mesocosm contained a target colony of *Camponotus vitiosus.* Colonies comprised ant larvae (L) as well as adult workers (W); colonies of species with polymorphic worker castes included both major (M) and minor (m) workers.

Treatment	**n**	**Neighbour species**	**Colony composition**	**Head width (mm)**	**Nest entrance (mm)**
No competition	7	-	-	-	-
Intraspecific	6	*Camponotus vitiosus*	16 W (4 M, 12 m), 10 L	1.52	2.8
Interspecific	4	*Cardiocondyla* sp.1	16 W, 10 L	0.38	1.6
	6	*Colobopsis nipponica*	16 W (4 M, 12 m), 10 L	1.0	2.0
	6	*Crematogaster dohrni*	16 W, 10 L	1.23	2.8
	4	*Dilobocondyla fouqueti*	16 W, 10 L	1.35	2.8
	6	*Dolichoderus taprobanae*	16 W, 10 L	0.78	2.0
	4	*Monomorium floricola*	16 W, 10 L	0.35	1.6
	4	*Technomyrmex albipes*	16 W, 10 L	0.55	2.0

Data analysis

All data analysis was performed in R version 4.3.0 (R Core Team, 2023).

Building the co-occurrence network

Using data on ant species' recruitment to baits, we built a co-occurrence network describing all pairwise co-occurrence relationships between all ant species across all 99 occupied trees. Our approach, which has been described in detail (see Wong et al., 2021), explicitly incorporated signals of asymmetry in species co-occurrences using odds ratios (Lane et al., 2014). It also assessed observed patterns against null expectations of random co-occurrences using null models (Blanchet et al., 2020), thereby yielding values of standardized effect size (SES). A co-occurrence relationship was more positive or negative than expected by chance if its SES value was greater or less than zero, respectively, and statistically significant when it exceeded a magnitude of 1.96 (Wong et al., 2021). We calculated the co-occurrence values for each pair of species in the network (SES_{pair}), as well as the overall co-occurrence value for each ant species (SES_{all}), which indicates whether it is predominantly characterised by positive or negative co-occurrences with other species (Wong et al., 2021).

Identifying key traits and standardising trait measurements

We corrected all morphological traits (excluding body size) by dividing their values by the value of body size. We then used correlation and principal components analysis (PCA) to identify a set of traits that best captured interspecific variation in multidimensional trait space while reducing redundancy caused by trait collinearity. Among traits with strong correlations ($|r| > 0.7$), we chose those with stronger loadings on the first and second principal components (Supporting information). Our final selection of traits included six morphological traits, one dietary trait, and one physiological trait: body size, head width, eye width, pronotum width, mandible length, antennal scape length, δ15 N, and CT_{max}.

Modelling the effects of trait differences on species co-occurrences in field

We used a meta-analytical approach to investigate the nature, strength, and consistency of the effects of individual traits in structuring co-occurrences across all ant species in the mangrove. Focusing on one ant species at a time, we first calculated two metrics of trait difference between the focal species and every other species in the mangrove: Absolute Dissimilarity (AD), where $AD = |T_{other} - T_{focal}|$, and Hierarchical Difference (HD), where $HD = T_{other} - T_{focal}$ (Wong et al., 2021). Focusing on one trait at a time, we then built one linear regression model for each metric (e.g. 'BodySize.AD' or 'BodySize.HD') for the focal species; that is, using the focal species' pairwise co-occurrence values with all other species in the network (SES_{pair}) as the response variable, and the value of each pair's metric (e.g. 'Body Size.AD') as the predictor. After building the models for all ant species, we fitted a meta-analytical model for each metric of each trait. We examined the direction and magnitude of the pooled regression coefficient ($\hat{\beta}$) to understand the nature and strength of the effect that a given difference in a given trait had on ant species' co-occurrences. The level of heterogeneity (I^2) (Higgins & Thompson, 2002) associated with the effect revealed whether it was consistent or varying across different ant species. For trait difference metrics which had a significant amount of heterogeneity in effects across different ant species (as determined by Cochran's Q test), we further investigated whether the effects were moderated by the ant species' body size or the overall nature of their co-occurrences in the network (SES_{all}), by adding these terms as moderators (i.e. fixed effects) to the models. All meta-analytical models were built using the ‘rma’ function in the *metafor* package, and results were visualised using the *orchaRd* package.

Measuring competitive effects on colony survival and growth in mesocosms

We first determined the survival and growth rates of each target *C. vitiosus* colony in the mesocosm experiment. Survival was measured as the proportion of adults that survived, while growth was calculated as the proportion of larvae that developed into adults by the end of the 30-day period. Next, we calculated the mean survival and growth rates of *C. vitiosus* in the ‘no competition’ treatment. For each of these rates, we then calculated the competitive effect of each neighbour colony as the difference between the performance of the target *C. vitiosus* colony (with the neighbour present) and the mean performance of *C. vitiosus* in the ‘no competition’ treatment.

Modelling the effects of trait differences on competitive effects in mesocosms

We used linear models to examine whether trait differences explained variation in the competitive effects of different neighbour species on the survival and growth of the target species *C. vitiosus*. The analyses were performed separately for survival and growth rates. First, we built a null model with only the mean competitive effect of each neighbour species as the response variable. Then, we added a trait difference metric (e.g., ‘BodySize.AD’ or ‘BodySize.HD’) as the sole predictor, comparing the AIC of this model to the null model to assess the metric’s importance. Next, we excluded data from mesocosms that promoted intraspecific competition and repeated the analyses to assess whether the effects remained consistent when only interspecific competition was considered. Note that trait data were obtained from specimens not used in the mesocosm experiment (detailed in ‘*Measuring morphological, dietary and physiological traits*’ above), as it was not possible to measure the traits of the experimental individuals due to destruction from fighting and decomposition.

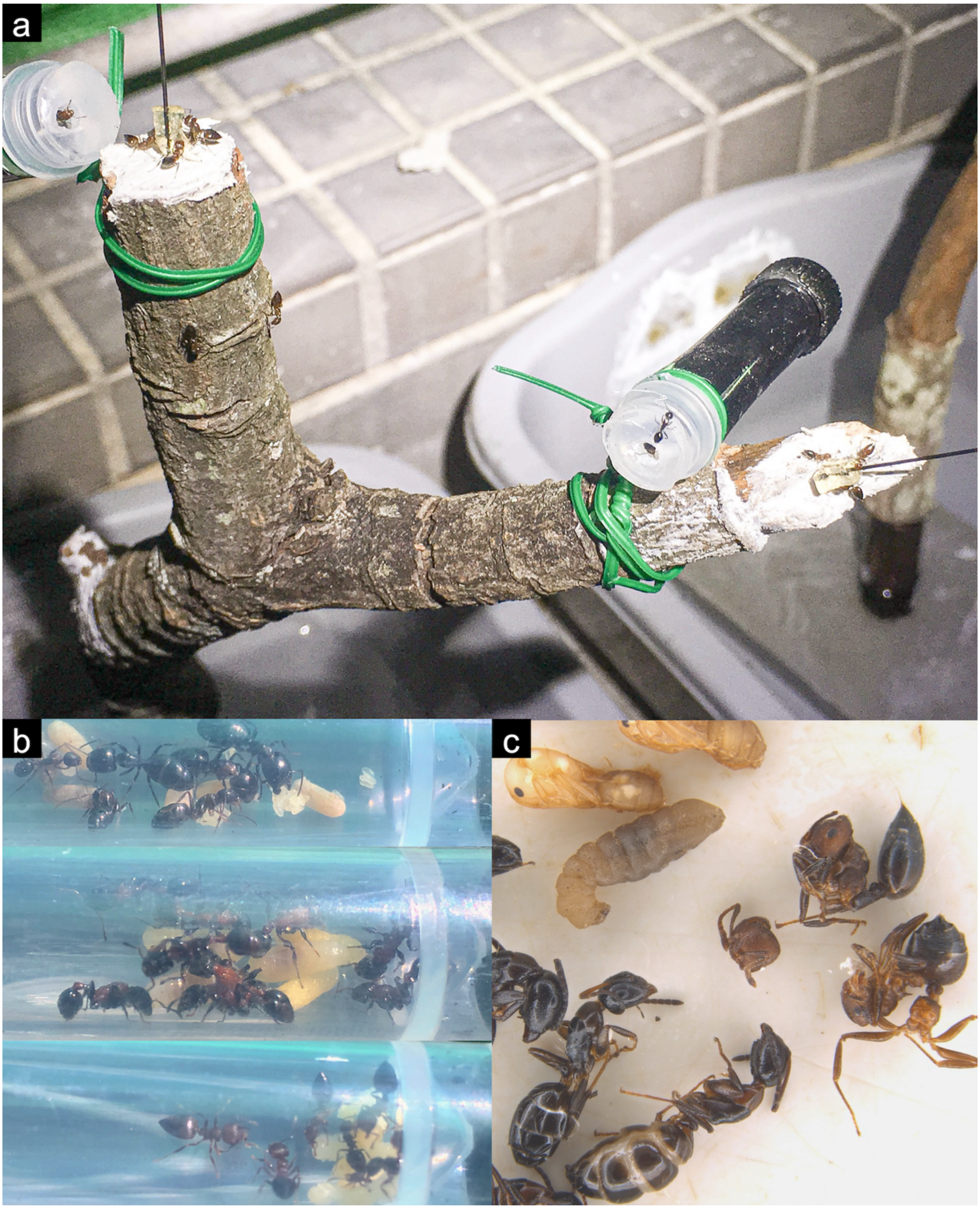

Figure 2. The mesocosm competition experiment. (a) Setup of a mesocosm, comprising a Y-shaped branch of *Kandelia obovata* standing in a basin of saltwater, onto which nest tubes housing competing ant colonies were affixed by wire to each terminal end. A black cover over each tube recreated the dark environment of a nest; the cover could be gently slid away to allow brief visual inspections of colony status. Photograph shows a worker of the target species *Camponotus vitiosus* which stood guard at the entrance to its nest tube on the right, as multiple workers of a neighbour species, *Crematogaster dohrni* (which occupied the nest tube on the left) foraged at both pieces of carbohydrate-enriched agar jelly that were pinned proximally to each nest tube. (b) Composite image showing experimental colonies (including adult workers, and larvae in yellow) of three different ant species in

nest tubes. Species shown from top to bottom: *C. vitiosus*, *Dilobocondyla fouqueti*, and *C. dohrni*. (c) Contents of a nest tube of the target species *C. vitiosus* at the end of the experiment, which contained adult workers (bottom left), brood including larva and pupae (top left), as well as the severed remains of adult workers of the neighbour species *C. dohrni* (top right).

RESULTS

Species recruitment and co-occurrence structure

We documented 14 ant species occurring in 99 trees in the mangrove (Fig. 3a). Individual trees supported between one to four species, and tree size correlated weakly with ant species richness (*r*=0.34; Supporting information). All except two species (*Technomyrmex albipes* and *Ochetellus glaber*) showed substantially higher recruitment (135–1017%) to protein than carbohydrate baits (Fig. 3a). In the co-occurrence network of the ant community (Fig. 3b), multiple significantly negative ($SES_{pair}<-1.96$) and positive ($SES_{pair}>1.96$) associations of species pairs were detected (Fig. 3b). At the network level, eight and six species were predominantly characterised by negative ($SES_{all}<0$) and positive ($SES_{all}>0$) associations with other species, respectively (Fig. 3b). Species with more negative associations generally occupied more trees, as species' SES_{all} were weakly negatively correlated (*r*=-0.33) with the number of trees they occupied. The target of the mesocosm experiments, *C. vitiosus*, was the most frequent species in the mangrove, occurring on 30 trees (30.3% of trees with ants, Fig. 3a), and was predominantly characterised by negative associations with other species in the network ($SES_{all}=-2.0$) (Fig. 3b).

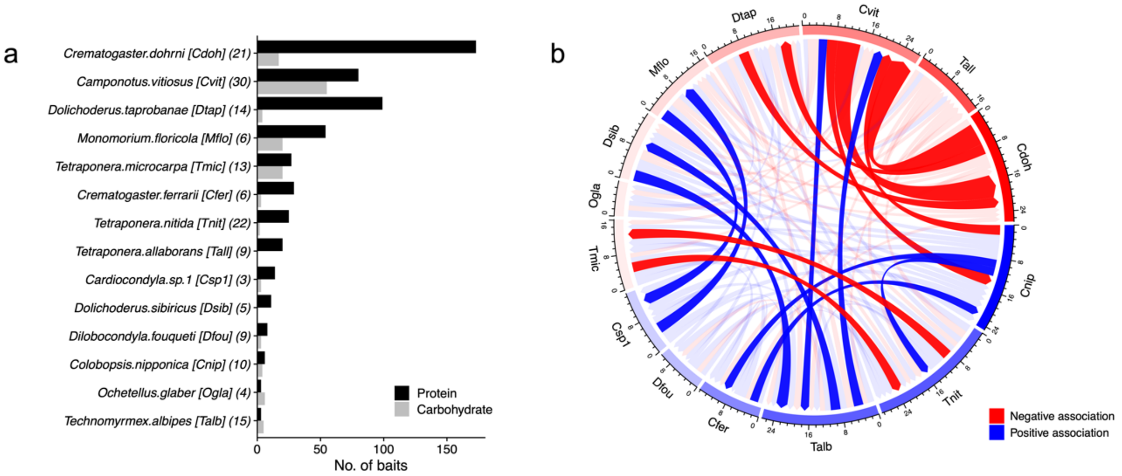

Figure 3. Patterns of ant species recruitment and co-occurrence in a tropical mangrove. (a) Bar chart summarising the recruitment patterns of 14 ant species to protein and carbohydrate baits on 99 mangrove trees. Abbreviated species names are in square brackets. The number of trees on which each species occurred is indicated in parentheses. (b) Chord diagram illustrating the structure of the co-occurrence network for the 14 ant species in the mangrove (species names have been abbreviated). Each arrow describes the asymmetric co-occurrence relationship between a unique pair of species ('SES_{pair}' in main text); that is, the likelihood that the species at the head of the arrow will occur on a tree, given that the species at the tail of the arrow occurs on that tree. The width of the arrow indicates the strength of the co-occurrence relationship (magnitude of SES_{pair}), while the colour indicates its direction, with negative and positive relationships coded in red and blue, respectively. Arrows showing statistically significant relationships ($|\text{SES}_{\text{pair}}|>1.96$) are highlighted while all others are muted. The overall nature of each ant species' associations in the network ('SES_{all}' in main text) is indicated by the colour on its section of the rim. Species predominantly characterised by negative and positive associations are coded in red and blue, respectively.

Traits influencing species co-occurrences in field

An analysis of the effect sizes extracted from species-specific linear regressions identified four traits which consistently shaped ant species' pairwise co-occurrences (SES_{pair}) on trees: pronotum width, eye width, antennal scape length, and thermal tolerance (measured by CT_{max}) (Fig. 4). For pronotum width (pooled regression coefficient $\hat{\beta}$= 0.35, 95% CI: 0.07–0.63, P=0.01, AIC=22.8) (Fig. 4a), eye width (pooled regression coefficient $\hat{\beta}$= 0.30, 95% CI: 0.07–0.53, P=0.01, AIC=10.6) (Fig. 4b), and antennal scape length (pooled regression coefficient $\hat{\beta}$= 0.26, 95% CI: 0.04–0.49, P=0.02, AIC=19.2) (Fig. 4c), increasing absolute dissimilarities between species pairs had a positive effect on co-occurrence. That is, species occurring on the same trees tended to have dissimilar values in these three traits. In contrast, increasing absolute dissimilarities in CT_{max} had a negative effect on co-occurrence ($\hat{\beta}$= -0.26, 95% CI:-0.50–-0.01, P=0.04, AIC=24.5), indicating that species with similar thermal tolerances tended to occur on the same trees (Fig. 4d).

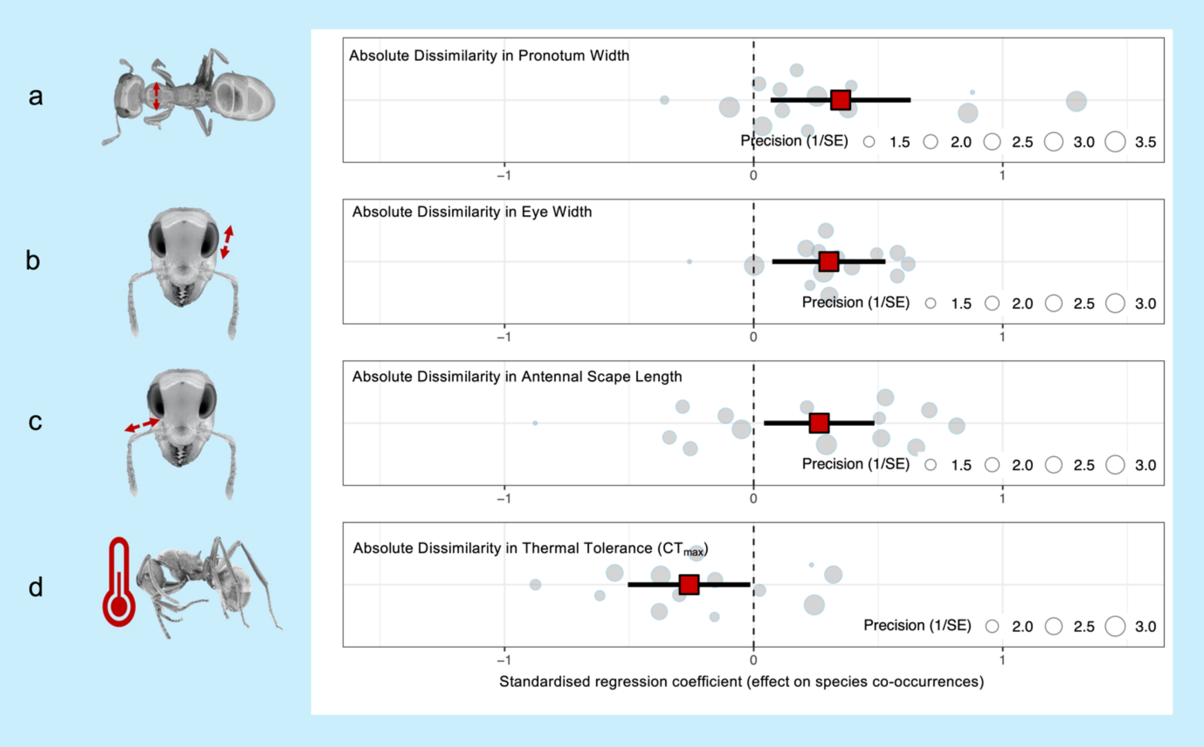

Figure 4. Co-occurrences of ant species in the mangrove are primarily shaped by interspecific differences in four traits: pronotum width (a), eye width (b), antennal scape length (c) and thermal tolerance, as measured by the critical thermal maximum (CT_{max}) (d). The overall effects were identified from a meta-analysis of species-specific linear regressions for trait effects on co-occurrences (see main text). Each plot shows the mean effect (red square), 95% confidence intervals (bold lines), and the individual effect sizes (grey circles) scaled by their level of precision (inverse standard error, 1/SE). Increasing absolute dissimilarities (i.e. non-directional differences) between species in pronotum width (a), eye width (b) and antennal scape length (c) had positive effects on their co-occurrences. However, increasing absolute dissimilarities in thermal tolerance had a negative effect on species co-occurrences (d).

Traits influencing competition in experimental mesocosms

None of the colonies of the target species *Camponotus vitiosus* suffered complete mortality by the end of the 30-day mesocosm experiment. Survival rates were generally high, ranging 31.3%–100% of the original adult worker population (Fig. 5a). Both intraspecific and interspecific competition negatively impacted survival (Fig. 5a). Compared with colonies reared without neighbours, the survival of adult workers was reduced by 40% ($P<0.05$) in the presence of conspecific neighbours, and by 5.6% ($P=0.46$) in the presence of heterospecific neighbours. In contrast, the growth rates of the target colonies – as measured by the development of larvae – did not differ significantly among treatments (Fig. 5b). Notably, the competitive effects of neighbour colonies on the survival rates of target colonies increased with increasing hierarchical differences in eye width (Fig. 5c) [$F(1,5)=8.03$, ΔAIC=-4.70, $P=0.04$, Adj. $R^2=0.54$]. In comparison, the competitive effects of neighbour colonies on the growth rates of target colonies increased with increasing hierarchical differences in pronotum width (Fig. 5d) [$F(1,5)=7.48$, ΔAIC=-4.40, $P=0.04$, Adj. $R^2=0.52$].

In addition to the quantitative trends, we observed anecdotal evidence of intense antagonistic interactions (i.e., fighting) between workers from different colonies of the target species *C. vitiosus* in all mesocosms allowing intraspecific competition. Fighting also occurred between *C. vitiosus workers* and those of three other species: *Crematogaster dohrni* (in four mesocosms) *Technomyrmex albipes* (in one mesocosm), and *Cardiocondyla sp.1* (in one mesocosm). These interactions typically took place when individuals from neighbouring colonies approached the entrances to *C. vitiosus* nests. While intraspecific fights could result in the mortality of *C. vitous* workers, interspecific fights did not. However, interspecific fights did lead to the mortality of individuals of other species. Severed remains of such individuals were found in the *C. vitiosus* nests (Fig. 2) and the water basin.

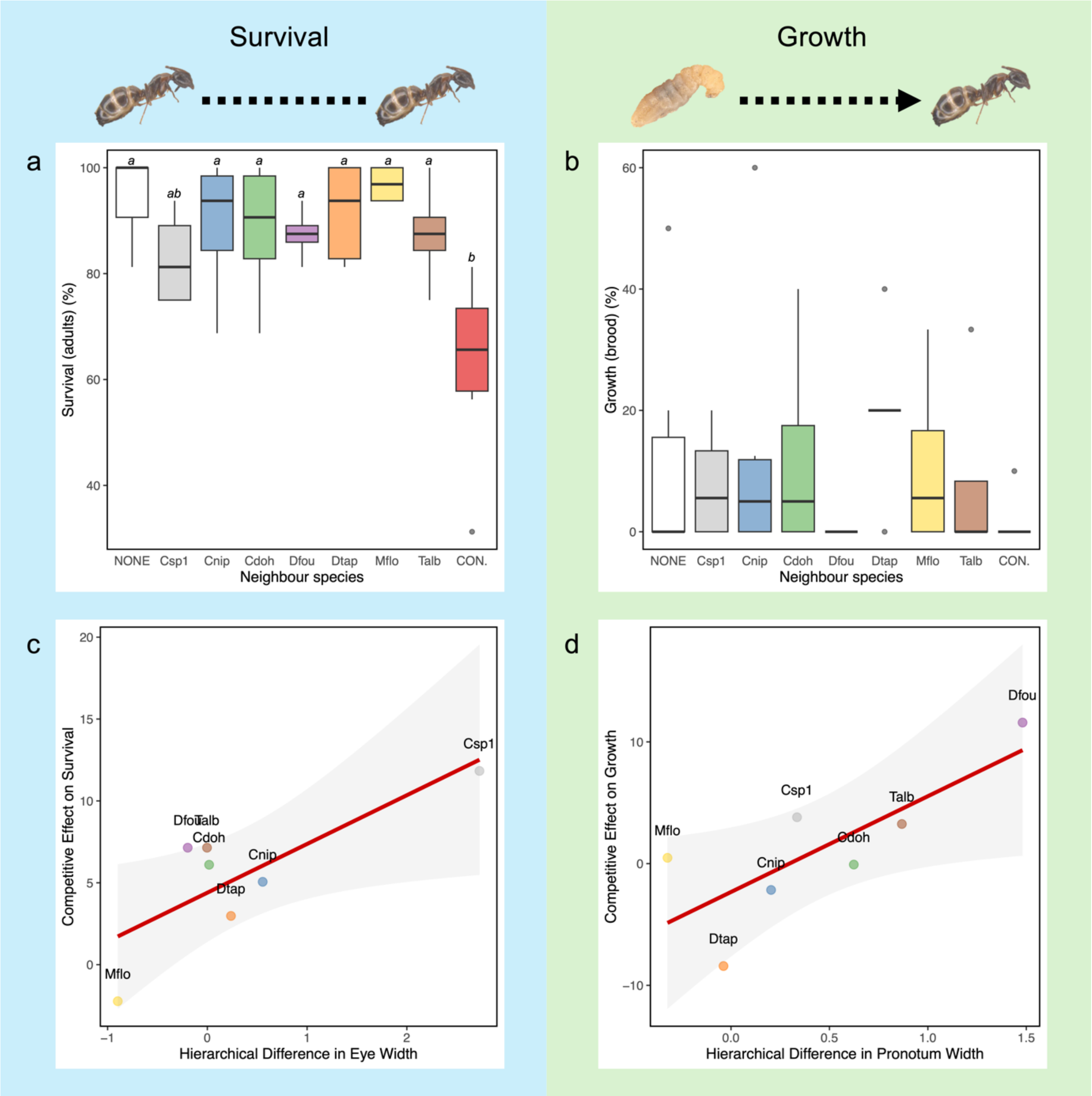

Figure 5. Results from the ant competition mesocosm experiment. (a) Boxplot showing the survival rates of adults in colonies of a target ant species when reared in isolation (‘NONE’), the presence of a heterospecific colony of one of seven other ant species, and the presence of a conspecific colony (‘CON.’). Bars show mean values and vertical lines show 95% confidence intervals. Different letters indicate statistically different means ($P<0.05$). (b) Boxplot showing the growth rates of the target colonies in the treatments defined in (a). The growth rate of each colony was measured as the percentage of its larvae that had developed into adults by the end of the experiment. (c) Plot from linear regression showing that the mean competitive effects of neighbour species on the survival rate of the target species increased with increasing hierarchical differences (i.e. directional differences) in eye width between neighbour and target species. (d) Plot from linear regression showing that the mean competitive effects of neighbour species on the growth rate of the target species increased with increasing hierarchical differences in pronotum width between neighbour and target species.

DISCUSSION

In studying arboreal ant communities on tropical mangrove islands, we aimed to explore the role of species' trait differences in shaping competitive interactions within local communities and to directly assess their impact on species performance in experimental settings. Consistent with our assumption of low environmental heterogeneity in the small mangrove, we observed a relatively weak influence of environmental filtering on community structure. Instead, we found that competition played a dominant role in driving niche partitioning among ant species. This was realised mechanistically via the effects of limiting similarity in three morphological traits associated with resource acquisition. Importantly, interspecific differences in two of these traits also explained interspecific competitive effects on the performance of ant colonies in the mesocosm experiment, empirically evidencing their functionality. However, the precise mechanisms by which trait differences affected competitive outcomes varied; whereas increasing trait dissimilarities promoted co-occurrences in the mangrove, increasing hierarchical differences strengthened competitive effects in the mesocosms. This discrepancy between the field observations and experimental results – a phenomenon not unique to ants (e.g. greenhouse experiments for plants; Kennedy, 1995) – underscored the limitations of controlled experiments in capturing the nuances of mechanisms in natural systems. Nonetheless, it also shed light on a potentially important and poorly understood aspect of trait-based competition among animal species: the influence of trait hierarchies when resources are scarce. We discuss these findings and the functional significance of trait differences to ant competition below.

Trait dissimilarities facilitate niche partitioning in mangrove ant communities

The co-occurrence patterns observed in the mangrove demonstrate that species traits play a significant role in structuring local ant communities, particularly through competitive mechanisms. Species dissimilarities in pronotum width, eye size, and antennal scape length were the strongest predictors of co-occurrence (Fig. 4), reflecting the importance of limiting similarity and niche partitioning. Dissimilarities in these traits likely allowed co-occurring species to avoid overlap in foraging strategies, activity patterns, or resource types. Differences in pronotum widths may have reflected differences in locomotion and load-bearing capacity (Boudinot et al., 2025), which influenced resource capture and interspecific interactions. For instance, one study observed that ant species with wider pronotums were often first to discover resources, while those with narrower pronotums were effective at displacing species from occupied resources (Gibb & Parr, 2013). Interestingly, interspecific differences in pronotum widths outperformed body size and other morphological traits in explaining the competitive structuring of ground-foraging ant communities in an invasion context (Wong et al., 2021). The length of the antennal scape, an apparatus used in foraging, communication and the manipulation of food (Boudinot et al., 2025) and possibly indicative of a specific diet (see Drager et al., 2023) may have further differentiated species based on their ability to discover and exploit different resources in the mangrove. Meanwhile, eye size likely played a role in the partitioning of activity times and foraging strategies, with enlarged eyes possibly representing adaptations to specific temporal niches, microhabitats, or hunting strategies (Jelley & Barden, 2021; Boudinot et al., 2025). Clearly exemplifying this trend of limiting trait similarity and competitive exclusion, the three species of *Tetraponera*, which were all characterised by distinctly larger eyes than all other ant species, were never observed to co-occur with one another.

Interestingly, dissimilarities in the trophic positions of ant species, as indicated by their stable isotopic composition, did not significantly predict co-occurrences. This may have been due to the small ant community comprising 14 species occupying relatively similar trophic positions (Supporting information), which aligned with the fact that almost all species exhibited an asymmetric preference for proteins over carbohydrates at baits (Fig. 3). This absence of clear niche partitioning in the ant species' diets was likely a result of the limited variety of trophic resources in the small mangrove which comprised just a single plant species. In contrast, ant communities in forest habitats have been found to partition dietary niches across a wide range of resources, such as various carbohydrates from extrafloral nectars, fruits and seeds of different plant species, as well as the abundant proteins in diverse forest invertebrate communities (Grevé et al., 2019). The lack of obvious partitioning in trophic position among ant species in the mangrove further highlighted the possibility that the limited trophic resources available were partitioned among species via their dissimilar foraging strategies, activity patterns, or the use of different microhabitats for foraging, rather than through pronounced dietary differences.

While community structure was largely explained by competition and niche partitioning along trait axes linked to resource acquisition, abiotic filtering had a weaker influence, as indicated by the lower effect size and higher AIC value associated with critical thermal maximum in our models. The relatively homogenous environmental conditions of the mangrove habitat, with trees closely spaced and of the same species, likely limited the role of abiotic filtering in shaping community structure. This would be consistent with other studies that have shown how abiotic factors tend to exert stronger influences in more heterogeneous environments, where thermal or moisture gradients are more pronounced (e.g. Boyle et al., 2021). In contrast, our results demonstrate that biotic interactions, particularly competition driven by trait differences, were more significant in structuring the ant community at this small spatial scale.

Trait hierarchies influence competitive interactions in resource-limited mesocosms

The mesocosm experiment provided further insights into how trait differences determined competitive outcomes under conditions of low resource heterogeneity. It is worth noting that two traits found to influence competition in the mangrove, namely eye size and pronotum width (Fig. 4), also influenced competition in the experimental mesocosms (Fig. 5). However, it was hierarchical differences in trait values, rather than absolute dissimilarities, that best explained the competitive effects that neighbour species produced on the performances of the target ant colonies. This finding contrasted the field study, where – in line with the effects of niche partitioning – absolute dissimilarities in species traits consistently explained co-occurrences (Fig. 4). In the mesocosms, all species were supplied with limited dietary resources; the only protein resource was a single *T. molitor* agar jelly provided every 48 hours. This homogeneous and scarce resource likely restricted the potential for resource-based niche partitioning. Similarly, the shared climate to which all mesocosms were exposed may have also explained the absence of observed effects of abiotic filtering on the thermal tolerances of ant species in the field. Rather, the findings from the mesocosm experiment indicated that hierarchical differences in ant species' trait values were key determinants of competitive success under conditions of low environmental and resource heterogeneity. Notably, the emergence of trait hierarchies in competition for limited resources have been well-documented in plant communities, with height hierarchies in light competition serving as a classic example (e.g. Kunstler et al., 2016). However, the relationship between trait hierarchies and resource diversity remains largely unexplored for animal communities.

Interestingly, we found that colonies of the target ant species (*C. vitiosus*) exhibited poorer growth outcomes in the presence of other ant species possessing wider pronotums; that is, fewer larvae from the target colonies successfully developed into adult workers (Fig. 5). The differences in growth parameters among the target colonies appeared to be largely due to larval mortality rather than incomplete larval development. In several cases, it appeared that the larvae were consumed by the adult workers, a possible response to nutritional stress under resource scarcity. Given the essential role of protein for larval development in ants (Davidson, 1997), we suspect that hierarchical differences in pronotum widths influenced the ant species' relative abilities to exploit resources or engage in competitive interactions in the arboreal environment. This hypothesis is supported by the functional significance of ant pronotums discussed above (Gibb & Parr 2013; Boudinot et al., 2025), as well as the observation that *Dilobocondyla fulva*, the species with the widest pronotum and the strongest competitive effect on the target species, maintained a firm grip on the branches. This may have provided an advantage in accessing and successfully exploiting protein resources, thereby limiting their availability to the target colonies and impacting larval development.

Competition and dominant species structure the mangrove ant community

Our findings also shed light on how dominant ant species contribute to structuring communities and maintaining diversity within the mangrove ecosystem. We found that most numerically dominant ant species displayed many negative associations with other species, while rarer species showed positive associations. These patterns were archetypal of competition as a major force structuring the ant communities (Calatayud et al., 2020). Moreover, we found that *Camponotus vitiosus* was not only the numerically dominant species in the mangrove (where it occupied 30.3% of trees), but potentially also a behaviourally dominant species, given anecdotal observations in the mesocosms of *C. vitiosus* winning fights against three other species, including *Crematogaster dohrni*, another abundant species that occupied 21.2% of the trees in the mangrove. Importantly, the mesocosm experiment also revealed very strong intraspecific competition among *C. vitiosus* colonies, which impacted colony survival to a far greater degree than interspecific competition (Fig. 5). This intense intraspecific competition may have counterbalanced the numerical and behavioural dominance of *C. vitiosus* in the mangrove, preventing it from completely outcompeting other species and promoting coexistence.

Limitations and future directions

Despite the valuable insights gained, our study had several limitations, foremost among them the inadvertent exclusion of other traits or niche axes that could influence competition and coexistence among ant species. For example, colony size plays a significant role in competition (Palmer, 2004). However, it was logistically unfeasible to incorporate rigorous measures of colony sizes for all ant species into our study; moreover, colony size varies widely within and between ant species (Burchill & Moreau, 2016). While we paired colonies of similar size in the mesocosm experiment, such uniformity would seldom occur under natural conditions. Likewise, our experimental setup did not account for density effects, which are known to influence competition dynamics (Goldberg et al., 2001). Another key area for future research would be to examine how competitive interactions between ant colonies at different developmental stages affect coexistence. For example, in the mangrove, we observed *Crematogaster dohrni* workers killing an alate female *C. vitiosus* that had landed on their host tree, preventing her from founding a colony. The impact of such antagonistic interactions – between heterospecific individuals, different castes, or colonies at varying developmental stages – on ant community dynamics and structure certainly warrants further investigation. Finally, although we found statistically significant relationships between ant species' traits and co-occurrences in the mangrove that were consistent with theoretical expectations of competition, we cannot rule out the possibility that dispersal dynamics – for instance the colonization-competition trade-off – also influenced community assembly, as has been observed in other arboreal ant systems (Stanton et al., 2002).

ACKNOWLEDGEMENTS

MKLW was supported by a Clarendon Scholarship and Varley-Gradwell Travelling Fellowship from the University of Oxford and a Forrest Fellowship from the Forrest Research Foundation. We are grateful to Sum Leung Kit for assistance with stable isotope measurements as well as members of the Insect Biodiversity and Biogeography Lab at The University of Hong Kong for assistance with fieldwork.

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