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Research

Trait-similarity and trait-hierarchy jointly determine fine-scale spatial associations of resident and invasive ant species

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Interspecific competition, a dominant process structuring ecological communities, is influenced by species' phenotypic differences. Limiting similarity theory holds that species with similar traits should compete intensely ('trait-similarity'). In contrast, competing theories including modern coexistence theory emphasize that species with traits conferring competitive advantages should outcompete others ('trait-hierarchy'). Either or both of these mechanisms may drive competitive exclusion, but their relative importance and interacting effects are rarely studied. Here, we explore empirically whether trait-similarity and trait-hierarchy can explain fine-scale spatial associations observed between invasive and native ant species in a tropical assemblage. We find that pairwise co-occurrences between the invasive red imported fire ant *Solenopsis invicta* and 28 other species across relatively homogenous grasslands can be explained largely by an interaction of trait-similarity and trait-hierarchy in a single morphological trait, relative pronotum width. Specifically, higher trait-hierarchy values are associated with negative co-occurrences; however, these effects are counteracted when species are increasingly dissimilar in their trait ranges. These findings are consistent with the notion that limiting similarity and competitive hierarchies are interactive rather than discrete mechanisms driving competitive exclusion.

Keywords: assembly, coexistence, competition, exclusion, functional trait, invasion, limiting similarity, niche

Introduction

Interspecific competition, a primary driver of community assembly and biodiversity patterns, is a process that is both well-known and yet stubbornly enigmatic. Patterns consistent with competitive interactions have been widely documented in a variety of ecological communities (Schoener 1974, Calatayud et al. 2020), but precisely how phenotypic differences between species determine the nature of competitive exclusion has remained highly contested (D'Andrea and Ostling 2016). Limiting similarity theory (MacArthur and Levins 1967) holds that species of similar niches compete more intensely, with competitive exclusion eventually leading to co-occurring species displaying dissimilar niches. Studies investigating limiting similarity have measured



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resource overlap (Schoener 1974) and phylogenetic distances (Mayfield and Levine 2010) between species as proxies for their niche dissimilarity; recent work also emphasized differences in species' functional traits (D'Andrea and Ostling 2016). A focus on traits is particularly useful for understanding and predicting ecological mechanisms because traits can have both mechanistic (i.e. tied to physical, chemical and biological processes) and general (i.e. quantifiable and comparable across taxa) properties (McGill et al. 2006). One trait-based proxy for the niche dissimilarity between two species is a non-directional or 'absolute' measure of their dissimilarity in trait space (Fig. 1a) (Carmona et al. 2019a). Accordingly, the trait-similarity hypothesis predicts that the likelihood of co-occurrence will decrease with increasing overlap in trait space, such that co-occurring species display 'overdispersion': high absolute dissimilarity in trait space (Fig. 1a).

In contrast to limiting similarity, more recent theories on interspecific competition such as modern coexistence theory (Chesson 2000) as well as colonization–competition (Tilman 1994) and tolerance–fecundity (Muller-Landau 2010) trade-off models emphasize that species' niche dissimilarities are not the only factors determining competitive outcomes. Common to these theories is the notion that species can be organized along competitive hierarchies (D'Andrea and Ostling 2016), where differences in competitive ability drive the exclusion of weaker competitors (Kunstler et al. 2012). Directional measures of trait differences, such as the 'hierarchical difference' in species' mean trait values, provide a proxy for differences in competitive ability (Fig. 1b) (Kunstler et al. 2012). Contrary to the trait-similarity hypothesis, the trait-hierarchy hypothesis predicts that the likelihood of co-occurrence will decrease with increasing hierarchical difference (and dissimilarity), while decreasing hierarchical difference promotes 'clustering': the co-occurrence of similar species (Fig. 1b).

Despite a lasting focus on limiting similarity theory, empirical support for the trait-similarity hypothesis has been mixed (Mayfield and Levine 2010). Some studies documented patterns of trait overdispersion consistent with limiting similarity (Wilson 2007), but others found patterns of trait clustering consistent with competitive hierarchies (Kunstler et al. 2012, Herben and Goldberg 2014). Furthermore, studies applying modern coexistence theory showed recently that outcomes of competition between plant species can be predicted by hierarchical differences in traits governing resource acquisition (e.g. leaf area for light interception, Kraft et al. 2015, Kunstler et al. 2016, Pérez-Ramos et al. 2019). The majority of such studies have focused on plants, and have used experimentally-assembled communities (Grainger et al. 2019), which may not adequately represent the dynamics of natural communities (Carpenter 1996). Most observational studies investigating the role of competition in structuring communities, however, measure only trait dissimilarities and test for overdispersion (D'Andrea and Ostling 2016, Münkemüller et al. 2020). The potential for species' trait differences to reflect competitive ability differences may

therefore be underestimated (Kunstler et al. 2012, Kraft et al. 2015).

Inferences of assembly processes from patterns in community structure are ubiquitous in the literature (Münkemüller et al. 2020). However, this approach assumes that all species within a community are subject to the same 'dominant' assembly process (Siepielski and McPeck 2010). Rather than assuming that competition acts uniformly across all species at the community level, it can be informative to investigate whether and how competitive exclusion occurs for individual pairs of species. At this finer scale, competitive outcomes may be driven by an interaction between trait-similarity and trait-hierarchy (Chesson 2000). That is, competitive exclusion only occurs for pairs of species which are insufficiently dissimilar in niches relative to their differences in competitive abilities (Fig. 1c; Mayfield and Levine 2010). This interplay of trait-similarity and trait-hierarchy in determining competitive outcomes between species pairs is relatively unexplored. Nonetheless, it was anticipated by Abrams (1983): 'What is needed instead is a broader definition of limiting similarity. The concept should be represented as a relationship between the difference in competitive ability and the maximum similarity that will permit coexistence. Such a relationship has the potential to be different for every different pair of species.'

Biological invasions, which often lead to intense competitive interactions, are choice settings for investigating competition (Shea and Chesson 2002). Moreover, many classical invasion hypotheses (empty niche, enemy escape, novel weapons, etc.) essentially attribute invasion outcomes to niche dissimilarities and competitive ability differences between invasive and native species (MacDougall et al. 2009). This framework of modern coexistence theory has been used to identify the trait values conferring competitive advantages and promoting the success of invasive plant species (Gross et al. 2015) – but its potential to explain invasions in other taxa is untapped. Ecological literature on the ants (Hymenoptera: Formicidae) is replete with studies identifying competition as a strong driver of community structure (Fayle et al. 2015) as well as reports of competitive exclusion by exotic species (Holway et al. 2002). In the presence of invasive ant species, many ant communities show patterns of phylogenetic clustering (Lessard et al. 2009), which could arise as a result of either environmental filtering or competitive hierarchies. Distinguishing these two processes solely on the basis of phylogenetic relationships is difficult (Cadotte and Tucker 2017), but a focus on species' traits, which govern their abiotic and biotic interactions in real time, may help resolve their importance.

Both theory and experimental evidence suggest that ecological interactions may affect patterns of species co-occurrence. However, observed patterns of species co-occurrences can be poor proxies for ecological interactions (reviewed in Blanchet et al. 2020). Rather than treating species co-occurrences as standalone proxies of interactions, co-occurrence analysis can be one component in an integrative approach for

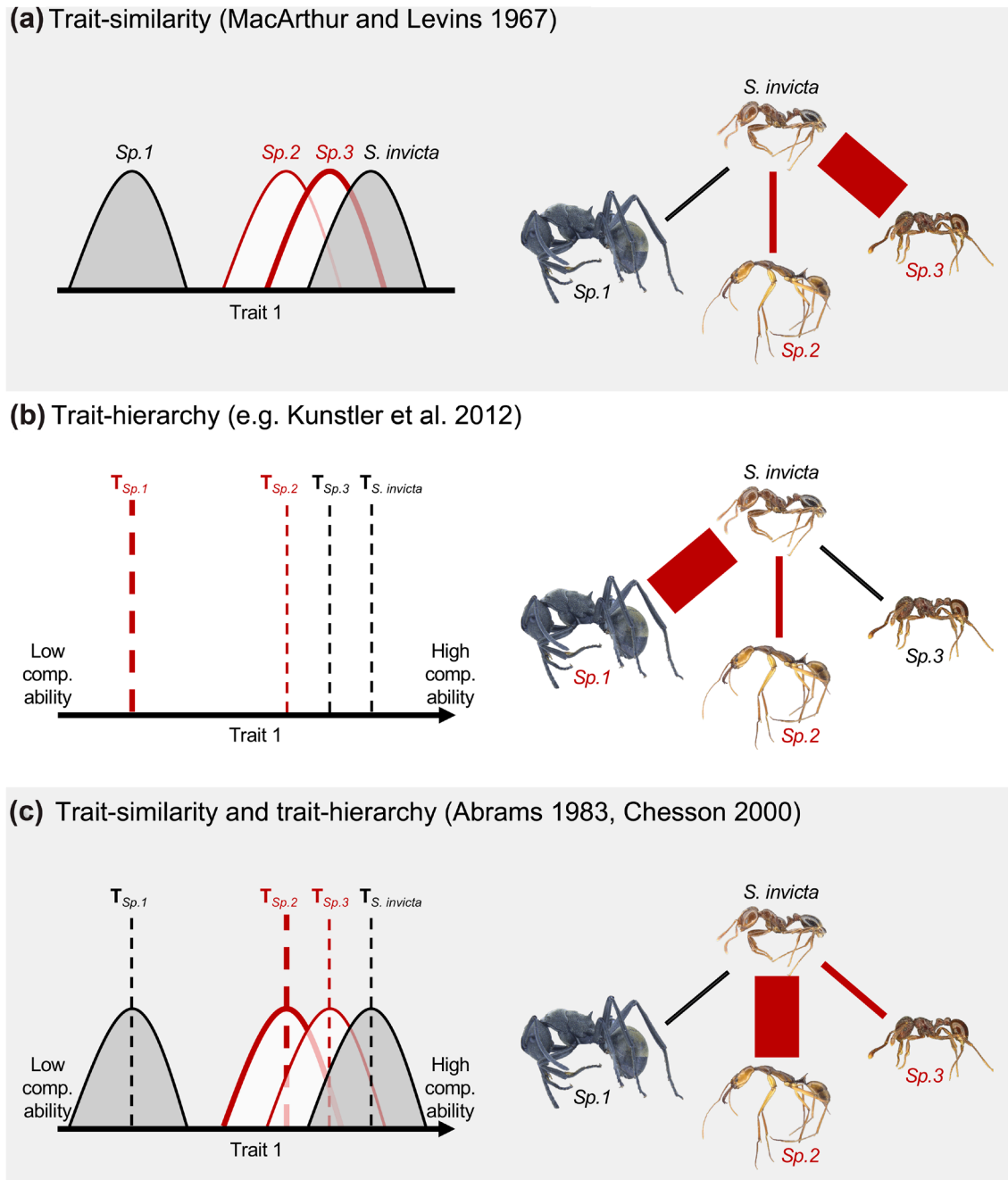


Figure 1. The trait-similarity and trait-hierarchy hypotheses of competition predict different outcomes for species co-occurrences separately and in combination. Panels show hypothetical relationships between three ant species and the invader *S. invicta* for one trait (left) and the corresponding pairwise co-occurrences (right) as predicted under specific hypotheses. In each panel, species in red experience competitive exclusion and negative co-occurrence with *S. invicta* (i.e. they are not found in the same plots), with thicker lines indicating stronger relationships; species in black can co-occur with *S. invicta* in the same plots. (a) If competitive exclusion is driven entirely by trait-similarity for all pairs of species (MacArthur and Levins 1967), decreasing absolute dissimilarity (i.e. increasing overlap) between a species' range of trait values and that of *S. invicta* increases the strength of negative co-occurrence, while increasing absolute dissimilarity (decreasing overlap) promotes co-occurrence. (b) If competitive exclusion is driven only by trait-hierarchy (Kunstler et al. 2012) and species' mean trait values (T) correspond to their competitive abilities along a directional axis, then a larger hierarchical difference, $T_{Sp,x} - T_{Sp,y}$, between a species and *S. invicta* increases the strength of the negative co-occurrence, while a smaller hierarchical difference promotes co-occurrence. (c) Trait-similarity and trait-hierarchy may jointly determine co-occurrences because niche dissimilarities and competitive hierarchies interact to determine competitive outcomes across different species pairs (Abrams 1983, Chesson 2000). The likelihood of competitive exclusion (and strength of the negative co-occurrence) between a species and *S. invicta* increases with increasing hierarchical difference in competitive ability; however, this competitive effect can also be counteracted and overcome by a large absolute dissimilarity in trait space, promoting co-occurrence.

detecting the effects of ecological mechanisms. Approaches emphasizing traits over taxonomic identities are well-suited to detecting mechanisms (McGill et al. 2006). Thus, integrating information on species' traits with observed co-occurrences may improve inferences of underlying mechanisms (Veech 2014, Morales-Castilla et al. 2015). Recent studies have integrated pairwise co-occurrence and trait-similarity analyses to investigate the relative importance of limiting similarity and environmental filtering in community assembly (Kohli et al. 2018, He and Biswas 2019). However, the potential influence of competitive ability differences, which can be reflected by hierarchical differences in trait values (Kunstler et al. 2012), has not been explored.

Here, we test trait-based hypotheses from limiting similarity theory and modern coexistence theory. We focus on the invasion of the non-native red imported fire ant *Solenopsis invicta* in grassland ant communities in Hong Kong (reported in Wong et al. 2020a). In these relatively homogenous landscapes, communities are more likely to be structured by competition than by other mechanisms such as environmental filtering (Keddy 1992). Furthermore, Wong et al. (2020a) reported a weak environmental gradient in this system and the occurrences of several 'tramp' taxa (e.g. species of *Tetramorium*, *Monomorium* and *Brachyponera*) known for their ecological plasticity (McGlynn 1999). There is some disagreement as to whether *S. invicta* competes strongly with resident ant species during invasion. While some studies report competitive exclusion by *S. invicta* (Porter and Savignano 1990, Gotelli and Arnett 2000), others contend that altered abiotic conditions under anthropogenic disturbances – which happen to favour *S. invicta* – are directly responsible for the decline of resident species (King and Tschinkel 2008). To this end, trait-based tests for theoretical mechanisms of competition in a system with relatively low levels of environmental variation may clarify the interactions between *S. invicta* and other species.

We integrate trait-based and co-occurrence analyses to investigate whether trait-similarity and/or trait-hierarchy determine how *S. invicta* affect other ant species. There are two advantages to this approach. First, it allows for detecting potentially varying relationships at the fine ecological scales (species pairs) where competition unfolds (Abrams 1983, Araújo and Rozenfeld 2014). Second, it allows for testing more specific predictions about assembly processes than would be possible with standalone co-occurrence analyses (Veech 2014, Morales-Castilla et al. 2015). We first use a network of species' co-occurrences to reveal the spatial associations between *S. invicta* and other ants across multiple plots. To address some of the limitations of co-occurrence approaches (Blanchet et al. 2020), we sample ant species at fine spatial scales most relevant to biotic interactions, incorporate asymmetric co-occurrence signals into the network with odds ratios, assess observed patterns against null expectations of random co-occurrences, and test for the influence of environmental heterogeneity. Next, for distinct morphological traits that regulate ant physiology and behaviour, we use non-directional and directional measures of species' trait

differences as proxies for species' niche dissimilarities (absolute dissimilarity) and competitive ability differences (hierarchical difference) respectively (after Kunstler et al. 2012, Carmona et al. 2019a). We then integrate species' trait differences and co-occurrences to evaluate three hypotheses on the likelihood and nature of pairwise competitive exclusion between *S. invicta* and all resident ant species (Fig. 1).

If competitive exclusion is driven mainly by trait-similarity, absolute dissimilarity will strongly determine species co-occurrences, with decreasing absolute dissimilarity leading to more negative co-occurrence (Fig. 1a). Alternatively, if competitive exclusion is driven mainly by trait-hierarchy, hierarchical difference will strongly determine species co-occurrences, with larger hierarchical difference leading to more negative co-occurrence (Fig. 1b). Finally, if both mechanisms operate, we expect an interaction of absolute dissimilarity and hierarchical difference to determine species co-occurrences. Specifically, we expect absolute dissimilarity to modulate the effect of hierarchical difference, such that hierarchical difference determines species co-occurrences only if absolute dissimilarity is sufficiently low (Fig. 1c).

Material and methods

Sampling ants at fine spatial scales relevant to biotic interactions

To maximise the likelihood of detecting community patterns reflecting biotic assembly processes such as interspecific competition (de Bello et al. 2012, Blanchet et al. 2020), we characterized ant communities at fine spatial scales in a relatively homogenous landscape (Wong et al. 2020a). We selected two adjacent reserves in Hong Kong – Lok Ma Chau (22.512°N, 114.063°E) and Mai Po (22.485°N, 114.036°E) – which have been protected for > 35 yr, and which contain networks of exposed grass bunds (width ≤ 5 m) separating individual ponds (Wong et al. 2020a). These habitats are relatively homogeneous in terms of vegetative composition and structure and microclimate, comprising exposed grasslands with native tree species interspersed throughout. The ant communities are comprised mainly of native species in terms of species richness, although exotic species have a high numerical dominance in this system; pilot surveys from 2015 to 2017 revealed that colonies of *S. invicta* are present at high densities at multiple locations (Wong et al. 2020a). We marked these locations, and in 2018 designated 61 plots, each a 4 × 4 m quadrat, targeting both plots where *S. invicta* were absent ($n=37$; 20 in Lok Ma Chau, 17 in Mai Po) and plots where they were present ($n=24$; 18 in Lok Ma Chau, 6 in Mai Po). We sampled the local ant community in each plot using six pitfall traps which were exposed for 48 h. The maximum distance between any two traps in each plot was 5.65 m (Supporting information), a higher sampling density (i.e. traps m^{-2}) than in previous studies characterising ant communities (Parr 2008). We intentionally sampled at these fine spatial scales to enhance the detection of species' co-occurrences driven by biotic interactions (Araújo and Rozenfeld 2014,

Blanchet et al. 2020), as most ant species in the region forage within 5 m of their nests (Eguchi et al. 2004) and *S. invicta* forage within 4 m of their nests (Weeks et al. 2004). For the same reasons, a minimum distance of at least 20 m between individual plots facilitated independent observations. All specimens were sorted into morphospecies and subsequently identified to species (Wong et al. 2020a). We compiled a matrix of ant species' occurrences (i.e. presence/absence data) across all 61 plots. In addition, we used digital photographs taken in field to estimate the percentage of ground cover at each plot using colour thresholding techniques in ImageJ (Abràmoff 2004), and obtained data on the NDVI and mean annual temperature from local climate models at 30-m resolution (Morgan and Guénard 2019) at each plot. We later used these data to investigate whether environmental heterogeneity influenced species co-occurrences (Blanchet et al. 2020).

Building a co-occurrence network incorporating asymmetric relationships

We built a network documenting all pairwise co-occurrence relationships between all species across all 61 plots. To incorporate signals of asymmetry in species co-occurrences (Araújo et al. 2011, Blanchet et al. 2020) into the network, we summarized the presence and absence of paired species in 2×2 contingency tables and calculated the strength of co-occurrences as their asymmetrical odds ratios (Lane et al. 2014). For example, given paired species A and B, the odds ratio for indication of B by A (OR_{AB}) measures how the probability of B's presence at a plot changes under the presence of A in the same plot, and vice versa for OR_{BA} :

$$OR_{AB} = \frac{N(B=1 \text{ and } A=1) + 0.5}{N(B=0 \text{ and } A=1) + 0.5} \cdot \frac{N(A=0 \text{ and } B=1) + 0.5}{N(A=1 \text{ and } B=1) + 0.5} \quad OR_{BA} = \frac{N(A=1 \text{ and } B=1) + 0.5}{N(A=0 \text{ and } B=1) + 0.5} \cdot \frac{N(B=1) + 0.5}{N(A=0) + 0.5}$$

where N represents the number of plots. We applied Haldane's correction and added 0.5 to all components to avoid odds ratios becoming infinity or undefined (Agresti 2018). We further log-transformed the odds ratios in subsequent analyses such that they could be compared arithmetically (Agresti 2018). The co-occurrence network was derived from odds ratios of all possible pairs of species.

Assessing observed species co-occurrences against null models

Since observed patterns could be driven by random co-occurrences (Gotelli 2000, Blanchet et al. 2020), we used null models to calculate standardized effect sizes (SES), which compared any observed co-occurrence relationships between paired species to random expectation (Supporting information). A co-occurrence relationship was more positive or negative than expected by chance if its SES was greater or less than zero, respectively, and statistically significant when it exceeded 1.96 (Gotelli and Arnett 2000). We calculated 1) whether each species was on the whole characterized by positive or negative co-occurrences relative to all other species in the network (SES_{all}), and 2) whether each resident species was characterized by positive or negative co-occurrences with *S. invicta* (SES_{inv}). The degree to which the presence of *S. invicta* affected the likelihood that a resident species occurred in the same plots determined that resident species' SES_{inv} .

Measuring traits and trait ranges of species

We measured seven morphological traits (body size, and six size-corrected traits: head width, eye width, mandible length, scape length, pronotum width, leg length) of ≥ 10 individual workers of every species ($n = 319$ individual ants), including different subcastes (minor and major workers) of polymorphic species such as *S. invicta* (Supporting information and Wong et al. 2020a). The selected traits regulate ant physiology and behaviour and are hypothesized to impact performance and fitness (Table 1). For each trait, we built species-level

Table 1. The seven traits measured on each individual, and each trait's hypothesized links to the performance and fitness of ants. All measurements are consistent with those used in the GlobalAnts trait database (Parr et al. 2017). All traits except body size were size-corrected prior to analyses.

Trait	Measurement	Hypothesized link to performance and fitness
Body size	Weber's length: diagonal length of mesosoma	Modulates vital and physiological rates, determines physical constraints and exposure to predators, influences resource type and acquisition efficiency (Silva and Brandão 2010).
Head width	Width of head including eyes	Determines the size of gaps through which an individual can pass (Schofield et al. 2016) and the volume of muscles powering the mandibles during foraging (Richter et al. 2019).
Eye width	Width of left eye	Determines ability in navigation, foraging, predator and prey detection, and indicative of activity times (Silva and Brandão 2010).
Mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva and Brandão 2010).
Scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva and Brandão 2010).
Pronotum width	Width of pronotum	Determines volume of muscles for head-control/support, and load-bearing (Keller et al. 2014). Differentiates species in foraging strategy (Gibb and Parr 2013).
Leg length	Combined length of femur and tibia of left hind leg	Determines mobility; leg length influences running speed, which affects success in foraging or escape from predators (Silva and Brandão 2010).

probability density functions (Carmona et al. 2019b) to calculate trait probability distributions (the curves in Fig. 1a). These distributions – or trait ranges – reflect the probabilities of observing different trait values within individual species; they were subsequently used to quantify absolute dissimilarities between species in trait (niche) space (below).

Species' dissimilarities in traits, phylogeny and environmental preferences

For each of the seven traits, we quantified differences between *S. invicta* and each resident ant species with a non-directional measure of niche dissimilarity (absolute dissimilarity, AD), and a directional measure of competitive ability difference (hierarchical difference, HD). We focused on differences in individual traits, as combining all traits into a composite index requires the assumption that all traits affect interspecific competition uniformly. We measured AD as the proportion of a resident species' trait probability density function which did not overlap with *S. invicta*'s trait probability density function (i.e. the proportion of trait space exclusive to the resident species' trait range) (Carmona et al. 2019b). AD values range from 0 (when a resident species' trait range is identical to that of *S. invicta*) to 1 (no overlap with trait range of *S. invicta*; e.g. Sp. 1 in Fig. 1a). Our overlap-derived measure of AD was based on the concept of niche overlap under limiting similarity (Abrams 1983). We measured HD as $T_{\text{Species}} - T_{S. \text{invicta}}$ where T is the mean trait value for the given species (after Kunstler et al. 2012).

To control for the effects of phylogenetic relationships or environmental heterogeneity (Blanchet et al. 2020) in shaping co-occurrences between *S. invicta* and each resident species, we quantified their phylogenetic dissimilarity (as pairwise distances between species in phylogenetic trees) as well as their dissimilarities in environmental preferences in terms of ground cover, NDVI and temperature. We quantified phylogenetic dissimilarity based on the branch length distance between tips within a phylogenetic tree. We used 100 posterior samples of the phylogenetic tree from Economo et al. (2018) to quantify phylogenetic dissimilarities between species. As the ant phylogeny was available only at the genus level, we included phylogenetic uncertainties in creating species-level trees (after Arnan et al. 2018). We randomly generated 100 species-level trees by assigning species into their genus following a Yule (pure-birth) process and removing genera not detected in our study. Phylogenetic trees were generated using the R package 'phytools' (Revell 2012). To incorporate phylogenetic uncertainty, we calculated phylogenetic dissimilarities for 100 randomly-generated trees, using the R package 'ape' (Paradis et al. 2019). We quantified dissimilarities in environmental preferences between *S. invicta* and every resident species to investigate whether environmental heterogeneity in 1) ground cover, 2) NDVI and 3) mean annual temperature influenced their co-occurrences (Blanchet et al. 2020). We first calculated the 'preference value' of each species for each variable by averaging the values for that variable from all plots where the species was present.

Since the locality Lok Ma Chau was sampled more intensively than the locality Mai Po, we averaged the values from each locality prior to further averaging (such that estimates were not biased to Lok Ma Chau). For each of the three variables, environmental-preference dissimilarity between *S. invicta* and every other species was quantified as $|\text{Preference value}_{\text{Species}} - \text{Preference value}_{S. \text{invicta}}|$.

Statistical analyses

To investigate whether environmental heterogeneity (Blanchet et al. 2020) and phylogenetic dissimilarity influenced co-occurrences between *S. invicta* and resident species, we built separate regression models for SES_{sinv} with dissimilarities in species' environmental preferences or phylogenetic dissimilarity as predictors. We built one model with phylogenetic dissimilarity as the sole predictor, and three additional models which each included environmental-preference dissimilarity in the form of either NDVI, temperature or ground cover as the sole predictor. Environmental variables and phylogenetic dissimilarity were included in subsequent trait models (below) as covariates if they were found to be significant. This would allow the models to examine the effects of traits while controlling for environmental heterogeneity and phylogenetic non-independence. We did not conduct p-value corrections for the environmental and phylogenetic models so as to minimize the risk of falsely concluding that there were 'insignificant' effects of environmental heterogeneity and phylogenetic independence in our data and mistakenly omitting these factors from subsequent trait models. After all, a failure to account for environmental heterogeneity could result in the failure to detect trait signals driven by abiotic processes (instead of competition-related processes), while not controlling for phylogenetic non-independence could lead to enhanced type-I error.

To determine whether pairwise co-occurrences between *S. invicta* and resident species were determined by trait-similarity, trait-hierarchy or both mechanisms, we used multiple linear regression with standardized coefficients to test whether the SES_{sinv} for each species was best predicted by AD, HD or an interaction of AD and HD. Our objective here was to use species' trait differences to proxy their niche and competitive ability differences, rather than to understand the effect of different traits per se. Therefore, rather than using a full model, we built one model for each trait, with AD, HD and a two-way interaction term (AD \times HD) as predictors. We used all observed SES_{sinv} values as responses in the models (i.e. not just values meeting the arbitrary $p < 0.05$ criterion) because our hypotheses predicted that co-occurrences between ant species and *S. invicta* would be influenced by their trait differences, and this applied to all species within the community. In other words, there was no a priori reason to justify the exclusion of particular species from the analysis even if they displayed 'insignificant' co-occurrences with *S. invicta*. Furthermore, a lack of statistical significance might indicate a weak relationship, but not the absence of a relationship altogether.

We excluded the trait mandible length where strong correlation between AD and HD (Pearson's $r > 0.7$) suggested their effects could not be separated; AD and HD were not strongly correlated in other traits. As we built separate models for each trait (i.e. six models in total), we conducted Bonferroni-correction on the p-values to minimize type-I error due to multiple comparisons (Supporting information). We also ran the same set of analyses using robust linear regression to ensure our results were not driven by the presence of outliers; these regressions essentially detect outliers within the data and reweight them to minimize their drastic influences (Andersen 2008).

For any trait models (based on the multiple regressions) detecting significant effects from the interaction of AD and HD, we also built models without the interaction term, and used chi-square tests, AICc and changes in adjusted- R^2 to assess whether including the interaction term significantly improved model performance. We also used the Johnson–Neyman procedure (Johnson and Neyman 1936) to calculate the ‘zone of significance’, that is, the range of values of AD at which HD influenced SES_{sinv} significantly (or vice versa). We controlled for false discovery rates using the procedure described in Esarey and Sumner (2017). For traits that were significant in both multiple regressions and robust regressions, we further checked whether these results were invariable to the use of different density-thresholds of *S. invicta* to characterize the occurrences of this species across the plots (Supporting information). Multiple regressions were conducted using generic functions in R (<www.r-project.org>)

and robust regressions were conducted using package ‘robustbase’ (Maechler et al. 2020).

Results

We recorded 29 ant species including *S. invicta* (Fig. 2), which occurred in 39% of the sampled plots. Among these 29 species within the co-occurrence network, *S. invicta* was the species most strongly characterized by negative co-occurrences with other species ($SES_{\text{all}} = -3.62$, Fig. 2a). Four other species were characterized by statistically significant negative ($SES_{\text{all}} < -1.96$) co-occurrences, and two by significant positive ($SES_{\text{all}} > 1.96$) co-occurrences (Fig. 2a). Of the 28 resident species, pairwise co-occurrences with *S. invicta* were positive ($SES_{\text{sinv}} > 0$) for nine species and negative ($SES_{\text{sinv}} < 0$) for 19 species (Fig. 2b). Of these, one positive and seven negative co-occurrences were statistically significant (Fig. 2b).

We found little evidence to suggest that either trait-similarity or trait-hierarchy solely determined species’ co-occurrences. On their own, both AD and HD were poor predictors of co-occurrences between *S. invicta* and the 28 resident species (i.e. SES_{sinv}) in separate models for six traits (Supporting information). Rather, an interaction between niche dissimilarities and competitive ability differences best predicted co-occurrences between *S. invicta* and the 28 resident species. Among different models for the six traits (Supporting information), the most parsimonious model was that for relative pronotum width incorporating AD, HD and an interaction

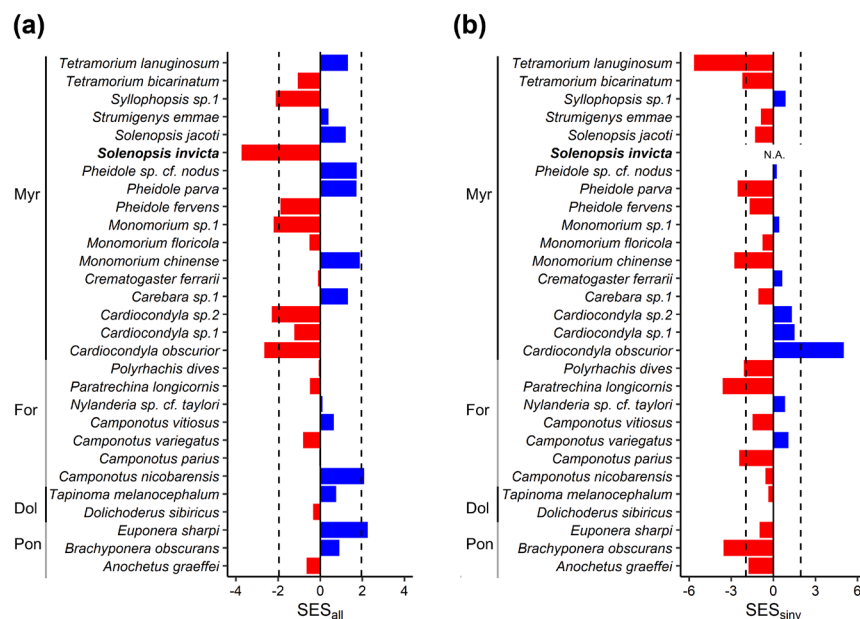


Figure 2. Of the 29 ant species sampled across 61 plots, the invasive ant *S. invicta* is most negatively associated with all other species. Plots show: (a) the degree to which each of the 29 species – including the invader *S. invicta* (in bold) – is characterised by positive (blue) or negative (red) associations within a co-occurrence network containing all species (SES_{all}); and (b) the degree to which each of the 28 resident species displays positive or negative associations with the invader *S. invicta* (SES_{sinv}). Dashed lines indicate critical values for statistical significance of co-occurrence relationships (i.e. $SES < -1.96$ or $SES > 1.96$). Ant species are grouped under four subfamilies: Myrmicinae (Myr), Formicinae (For), Dolichoderinae (Dol) and Ponerinae (Pon).

term (AD × HD), which explained 37% of the variation in SES_{inv} (Table 2). Here, the interaction term (AD × HD) significantly explained co-occurrences between *S. invicta* and the resident species (Table 2); removing the interaction term and only retaining the main effects of AD and HD significantly reduced model performance, as indicated by a Chi-square test ($\Delta AIC_c = 8.04$, $\Delta \text{Adjusted-R}^2 = 0.3$, $p < 0.001$, Supporting information). A significant interaction between AD and HD was also consistently observed in all other models for relative pronotum width using co-occurrence networks derived from different density-dependent classifications of *S. invicta*'s occurrences across the plots (Supporting information). In all relative pronotum width models (Table 2, Fig. 3, Supporting information) the significant negative effect of the interaction between AD and HD meant that the positive effect of HD on SES_{inv} was reinforced when AD was low, and this effect was counteracted (or changed to a negative effect) when AD was high.

Based on the model, we further estimated the magnitudes of niche dissimilarities (AD) between resident ant species and *S. invicta* at which competitive ability differences (HD) significantly influenced their co-occurrences. Applying the Johnson–Neyman procedure revealed that co-occurrences between resident species and *S. invicta* were significantly affected by HD when $AD < 0.37$ or $AD > 0.95$. There were 10 species for which $AD < 0.37$ and three species for which $AD > 0.95$ in relative pronotum width with respect to *S. invicta* (Fig. 3).

In models based on other traits, the main effects of AD and HD as well as their interacting effects were not consistently significant predictors among the different regression analyses (Supporting information). Phylogenetic and environmental-preference dissimilarities were also not significant predictors in any models (Supporting information).

Discussion

Here, we found that an interaction between trait-similarity and trait-hierarchy could largely explain fine-scale spatial associations between the invasive species *S. invicta* and 28 other ant species. These empirical results are consistent with

Table 2. Multiple linear regression model for relative pronotum width. For this trait, a non-directional measure of niche dissimilarity (absolute dissimilarity, AD), a directional measure of competitive ability difference (hierarchical difference, HD) and their two-way interaction (AD × HD) determine pairwise co-occurrences between the invader *S. invicta* and 28 ant species (Fig. 2b: SES_{inv}). Bold value indicates statistical significance ($p < 0.05$). 'JN intervals' indicate the range of AD values at which the effects of HD are significant, as identified from the Johnson–Neyman procedure.

Independent variable	β	p	JN intervals
AD	−0.47	1	< 0.37; > 0.95
HD	1.08	0.36	–
AD × HD	−1.47	0.012*	–
$R^2 = 0.37$			

the notion that limiting similarity and competitive hierarchies are interactive rather than discrete mechanisms driving competitive exclusion (Abrams 1983). We also found that a model of species co-occurrences, incorporating the interaction of trait-similarity and trait-hierarchy, aligned with predictions of different rules from community assembly theory (discussed further below). These findings underscore the importance of interspecific differences in niches and competitive abilities in determining patterns of species co-occurrences in communities.

The overall pattern of pronounced negative co-occurrences between the abundant *S. invicta* and many other species (Fig. 2) identifies *S. invicta* as an influential component of the community. Abundant species with many negative spatial associations have been inferred to be strong competitors (Calatayud et al. 2020), and previous studies (Gotelli and Arnett 2000) considered *S. invicta* to competitively exclude other ant species on this basis. However, negative spatial associations can also arise due to other factors, such as environmental heterogeneity (Brazeau and Schamp 2019). In the absence of significant effects of environmental factors on the co-occurrence patterns, we have little reason to suspect that, at least for the environmental parameters measured, environmental filtering had a strong effect in determining species' spatial associations with *S. invicta*. Furthermore, multiple 'tramp' species showed significant negative co-occurrences with *S. invicta* (Fig. 2). For this reason, and also considering the general limitations of using co-occurrence approaches in isolation (Blanchet et al. 2020), we explicitly scrutinized spatial associations in light of species' ecological (trait) differences within the context of dominant theories on competition (Fig. 1).

Trait-similarity and trait-hierarchy jointly influence spatial associations between invader and residents

No single mechanism of competition, trait-similarity or trait-hierarchy, sufficed to explain co-occurrences between *S. invicta* and the 28 resident ant species. However, incorporating the interactive effects of both mechanisms markedly improved explanatory power for a model based on the morphological trait, relative pronotum width (Table 2). The results suggest that competitive outcomes among the ant species may not depend on niche dissimilarities alone, but on the relative magnitudes of these in relation to differences in their competitive abilities (Chesson 2000). Competitive hierarchies in individual traits are especially known to structure plant communities (Pérez-Ramos et al. 2019) but are unexplored for most taxa. Our finding that ant species' trait differences significantly predict their spatial associations through both trait-similarity and trait-hierarchy (Table 2) highlights the value of assessing directional trait differences that may respond to competitive hierarchies among animal species.

In a study of arboreal ant assemblages associated with epiphytic plants, absolute dissimilarities in a single morphological trait, body size, strongly predicted species' spatial associations as well as the outcomes of antagonistic interactions

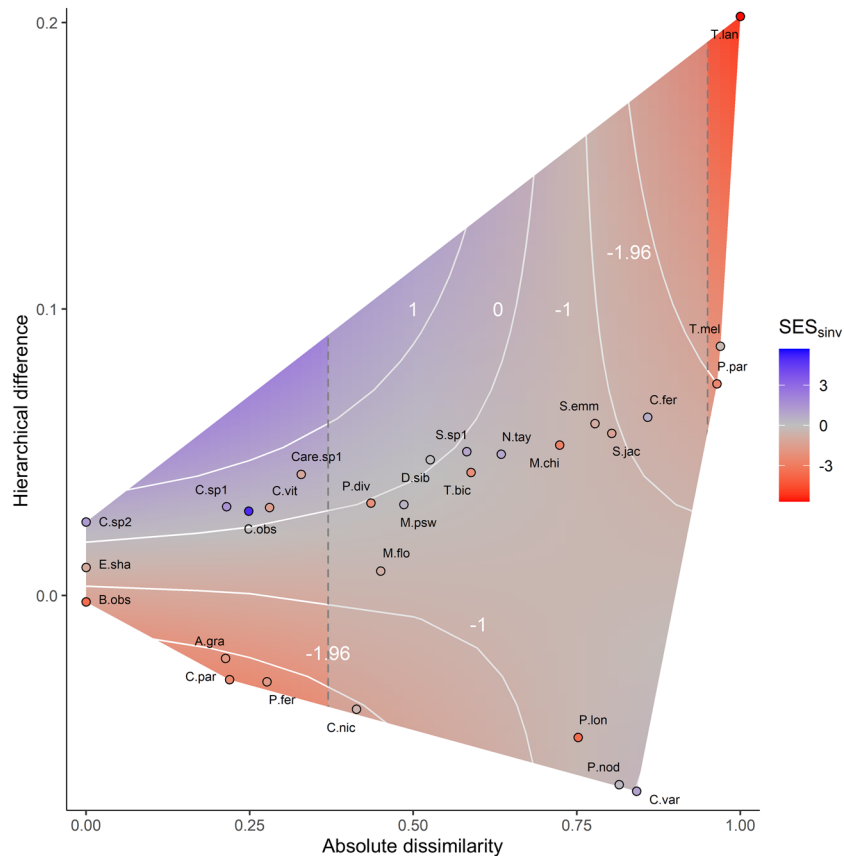


Figure 3. A response-surface showing how niche dissimilarity (Absolute dissimilarity) modulates the effect of competitive ability difference (Hierarchical difference) in determining 28 resident ant species' spatial associations with the invader *S. invicta*. The response-surface shows the predicted pairwise co-occurrence between a given ant species and *S. invicta* (SES_{sinv}) for the trait relative pronotum width, based on the multiple linear regression model in Table 2. Pairwise co-occurrences vary from negative (red) to positive (blue), with $SES_{sinv} < -1.96$ and $SES_{sinv} > 1.96$ indicating significant negative or positive associations respectively; contour lines illustrate how predicted SES_{sinv} changes across the response-surface. Coloured points on the response-surface show the observed SES_{sinv} for individual resident ant species ($n = 28$) (full names of species shown in Fig. 2). On the x-axis, increasing values indicate the decreasing overlap between a given species' range of relative pronotum width values and that of *S. invicta*. On the y-axis, a positive or negative value indicates that a given species has a relatively wider or narrower pronotum than *S. invicta*, respectively. The masked area in the centre of the response-surface corresponds to the range of absolute dissimilarity (0.37–0.95) where the positive effect of Hierarchical difference on SES_{sinv} is counteracted, as calculated from the Johnson–Neyman procedure.

(Fayle et al. 2015). Hierarchical differences proxying competitive advantages along trait axes, however, were not explored. Our findings highlight the potential importance of pronotum width – another frequently measured functional trait (Parr et al. 2017) – to competitive interactions among ant species. Keller et al. (2014) showed that the pronotum of ant workers contain the musculature controlling head movements and powering load-bearing abilities, which are distinct functional innovations underlying the ecological success of ants. Furthermore, Gibb and Parr (2013) showed empirically that species varying in relative pronotum width used different foraging strategies; species with relatively wider pronotums were often first to discover baits while those with relatively narrower pronotums had reduced discovery abilities but higher interference abilities. Thus, one testable hypothesis is that the relatively wider pronotum of *S. invicta* may afford a competitive advantage over some ant species (those with

low AD and HD and negative co-occurrences with *S. invicta* in Fig. 3) through its more efficient removal and transport of food resources. At the same time, as studies have shown that *S. invicta* have strong interference abilities but not strong resource discovery abilities (Tschinkel 2006, Calcaterra et al. 2008, Pearce-Duvet and Feener 2010), we also suspect that other ant species with relatively wider pronotums than *S. invicta* (those with low AD but high HD and non-negative co-occurrences with *S. invicta* in Fig. 3) may reduce their competitive ability differences relative to *S. invicta* through achieving more efficient resource removal and avoiding interference with *S. invicta*. This hypothesis would be consistent with observations that superior discovery ability is important for offsetting inferior fighting abilities and facilitating coexistence in ant communities (reviewed by Cerda et al. 2013). Notably, exploitative interspecific resource competition among ants is especially intense in more homogenous

habitats (Gibb 2005) such as the one studied here. If the patterns observed do relate to exploitative resource competition between *S. invicta* and the other ant species, this would be consistent with studies on plants, where traits influencing resource acquisition (in contrast to other functions, e.g. structural support) are often closely linked to competitive hierarchies (Herben and Goldberg 2014, Kraft et al. 2015). The pronotum may also be important to interference competition among ant species, where load-bearing ability likely determines the capacity of workers to lift, manipulate and displace heterospecific individuals.

Nonetheless, links between morphological traits and fitness are not yet well-established for ants, and future studies should assess the load-size selection of ants with different relative pronotum widths (Roces and Núñez 1993). Moreover, we suspect that additional factors influenced interactions between *S. invicta* and the 28 resident species, as the best individual trait model explained 37% of the variance in co-occurrences (Table 2, Supporting information). Aside from the traits measured in this study, other traits such as colony size, intra- and interspecific aggression levels, and venom chemistry are likely important for interference competition (Holway et al. 2002). While this study examined differences in morphological traits – which are accessible, basic components of trait-based research in animals (Parr et al. 2017, Pigot et al. 2020) – additional work investigating absolute dissimilarities and hierarchical differences in physiological and behavioural traits linked closely to performance will probably be most telling. Competitive exclusion may also depend on a net difference in competitive ability across multiple trait axes (Kraft et al. 2015).

As the present study involved ‘snapshot’ observations of ant communities in two adjacent grasslands, the relatively small spatial and temporal scales likely explain why, in line with the goals of this study, competition was detected as an important (but not overriding) driver of the patterns observed (McGill 2010). Nonetheless, it should be noted that processes unrelated to biotic interactions such as environmental filtering, dispersal and stochastic factors might exert stronger effects on community structure with increasing temporal and spatial scales (McGill 2010). Therefore, while the findings provide empirical evidence for the importance of trait-hierarchy and trait-similarity in jointly shaping communities at small scales, the generality of this phenomenon at other scales deserves further examination.

How trait differences affect spatial associations: four rules from assembly theory

The trait model incorporating the interaction term reconciled the varying co-occurrences between *S. invicta* and individual ant species to the varying nature of each pair’s trait differences in terms of trait-similarity and trait-hierarchy (Fig. 3). We note that the distinct ways by which species’ trait differences with *S. invicta* determine their co-occurrences, as reflected in the model, are consistent with predictions under different rules from community assembly theory. With reference

to Fig. 3, our ecological interpretation of the model identifies four rules that predict the spatial associations between a given ant species and *S. invicta* across the landscape. Each rule is distinguished by the specific magnitudes of niche dissimilarities (AD) and competitive ability differences (HD) between paired species. The rules are: 1) competitive exclusion at $HD < 0$ and $AD < 0.37$, leading to negative co-occurrence; 2) approximate competitive equivalence and coexistence at $HD > 0$ and $AD < 0.37$, leading to non-negative co-occurrence; 3) sufficiently large niche dissimilarity and coexistence at $AD = 0.37–0.95$, leading to non-negative co-occurrence; and 4) environmental filtering at $AD > 0.95$, leading to negative co-occurrence.

Rules 1 and 2 apply to species which are largely similar to *S. invicta* in niches and trait values ($AD < 0.37$). Here the model predicts increasingly negative co-occurrence with increasingly negative HD. It suggests that for ant species with similar trait values to *S. invicta*, interspecific competition with *S. invicta* is likely to be intense, such that large differences in species’ competitive abilities drive exclusion, causing negative co-occurrence (Kunstler et al. 2012) (rule 1). However, for some species, small differences in competitive abilities with *S. invicta* may facilitate coexistence in the fashion of neutral-like dynamics (Scheffer and van Nes 2006) (rule 2). This is evident from the model, which predicts that co-occurrences between *S. invicta* and most similar species ($AD < 0.37$) do not differ significantly from the null expectation (i.e. coexistence is plausible) when HD becomes less negative (Fig. 3: left unmasked area: $-1.96 < SES_{\text{sinv}} < 1.96$).

In contrast to rules 1 and 2 which apply to species sharing high niche similarity with *S. invicta* and potentially competing intensely, rule 3 applies to species largely dissimilar ($AD = 0.37–0.95$) from *S. invicta* in niches and trait values – to the extent that niche dissimilarity may mitigate negative effects of competitive imbalances (e.g. individual traits in Pérez-Ramos et al. 2019). For these species, differences in competitive abilities do not appear to influence co-occurrences with *S. invicta* significantly (Fig. 3: masked area: SES_{sinv} does not significantly respond to HD). Furthermore, if niche dissimilarities are sufficiently large, coexistence is plausible and the likelihood of these species occurring with *S. invicta* generally does not differ from null expectations (Fig. 3: masked area: $-1.96 < SES_{\text{sinv}} < 1.96$).

Rules 1–3 above concern interspecific competition, which was predicted to be an important driver of the ant species’ spatial associations given the relatively homogeneous landscape. Less anticipated was an additional rule (4), which likely relates to environmental factors, and applies to species most dissimilar ($AD > 0.95$) from *S. invicta* in niches and trait values (Fig. 3: right unmasked area). The model inherently predicts significant negative co-occurrence ($SES_{\text{sinv}} < -1.96$) between such species and *S. invicta*. The extensive dissimilarities between these species and *S. invicta*, and their low likelihood of co-occurrence, may reflect environmental filtering by unmeasured factors varying across the plots (e.g. ants’ relative pronotum widths responded to soil fertility gradients in Fichaux et al. 2019). If such trait-based

environmental filtering occurs, directional differences in trait values could further reinforce their deterministic effects, leading to increasingly negative co-occurrence with increasing HD (Fig. 3: right unmasked area).

Not discounting the limitations of a single-trait model (discussed further above), it appears that separate but coherent trait-based rules from community assembly theory can collectively account for spatial associations between the invader *S. invicta* and the 28 resident ant species across the landscape. If different rules do indeed act on different pairs or sets of species, this may explain the context-dependent nature of the impacts of *S. invicta* invasions on native ants observed previously (e.g. competitive exclusion in Porter and Savignano 1990, Gotelli and Arnett 2000; environmental filtering in King and Tschinkel 2008).

Abundant species, ranging from ants and beetles to trees and corals, often display negative and positive spatial associations with many other species (Calatayud et al. 2020). While experimental manipulations and mesocosm studies are invaluable for understanding the precise mechanisms underlying such community structure, their applicability decreases with increasing ecological, spatial and temporal scales (Levin 1992). Integrating co-occurrences with species' trait differences within a theoretical framework can provide stronger inferences for the mechanistic bases of observed community patterns than the use of co-occurrence approaches in isolation (Veech 2014, Blanchet et al. 2020). Here, a model encompassing species' trait differences (in terms of trait-similarity, trait-hierarchy and their interacting effects) (Table 2, Fig. 3) suggests that an abundant, invasive species competes intensely with a subset of similar species, may coexist with species that are sufficiently different, and is further unlikely to co-occur with other species of different environmental requirements. While these findings strictly describe relationships between a single invader and multiple resident species (and not all relationships among all species in the community), they are consistent with the notion that community assembly is a dynamic and multifaceted process acting variably on different pairs or sets of species (Abrams 1983), and not discrete 'filters' acting on the whole community (Cadotte and Tucker 2017). If so, detailed assessments of interspecific trait differences at fine spatial and organizational scales (e.g. species pairs and guilds) may clarify the contributions of distinct assembly mechanisms to overall community structure. Additional work investigating trait-relationships and associations among the resident ant species will help reveal other processes, such as competition, indirect interactions and facilitation. These, in combination with the competitive effects of *S. invicta* on many species, will ultimately determine community structure.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.9ghx3ffg5>> (Wong et al. 2020b).

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