The cryptic impacts of invasion: functional homogenization of tropical ant communities by invasive fire ants

Mark K. L. Wong[1], Benoit Guénard[2] and Owen T. Lewis[1]

[1]Dept of Zoology, Univ. of Oxford, South Parks Road, Oxford OX1 3PS, UK
[2]School of Biological Sciences, The Univ. of Hong Kong, Hong Kong SAR, PR China

Corresponding author: Mark K. L. Wong, Dept of Zoology, Univ. of Oxford, South Parks Road, Oxford OX1 3PS, UK. E-mail: mark.wong@zoo.ox.ac.uk

Abstract

The diversity and distribution of traits in an ecological community shapes its responses to change and the ecosystem processes it modulates. This 'functional diversity', however, is not necessarily a direct outcome of taxonomic diversity. Invasions by exotic insects occur in ecosystems worldwide, but there is limited understanding of how they impact functional diversity. We present the first comprehensive trait-based investigation of the impacts of an ant invasion, and the first incorporating intraspecific polymorphisms in species-level functional diversity. The fire ant *Solenopsis invicta* is an invasive species with a global distribution. Focusing on invaded and uninvaded plots in tropical grasslands of Hong Kong, we investigated how the presence of *S. invicta* affects the diversity and distribution of ant species and traits within and across communities, the functional identities of communities, and functionally unique species. Using trait probability density functions, we built trait spaces for 29 different species, and scaled up these components to calculate functional diversity at community and landscape levels. We found that invasion had limited effects on species and functional richness but pronounced effects on functional composition. Specifically, invaded communities had fewer functionally-unique individuals, and were characterized by species with narrower heads and bodies and shorter mandibles. Moreover, invaded communities showed substantially higher levels of functional redundancy (+56%) due to a clustering of trait values. Consequently, across the landscape, invaded communities displayed 23% less functional turnover than uninvaded communities despite showing comparable levels of taxonomic turnover – a result confirming theoretical predictions of the effects of high local functional redundancy. In sum, the presence of *S. invicta* alters the functional properties of multiple local communities selectively, resulting in functional homogenization across the landscape. The disparities between taxonomic and functional impacts of invasion highlight the need to consider how trait diversity across ecological scales shapes biodiversity and its responses to change.

Keywords: beta diversity, functional diversity, functional trait, functional rarity, insect, intraspecific, invasive species, turnover

Introduction

Invasions by exotic species are not only the second most common cause of extinctions (Bellard, Cassey and Blackburn, 2016) but also drive cascading impacts on ecosystems, cause economic damage and undermine human health (Pyšek and Richardson, 2010). As with many ecological phenomena, invasions have long been studied by summarising ecological communities using metrics based on species' taxonomic identities: abundance, richness and diversity. Changes in these metrics, however, may provide only limited insight into the specific mechanisms underlying the causes of invasions (MacDougall, Gilbert and Levine, 2009). Furthermore, subsequent effects of invasion on ecosystem processes are more likely to depend on the ecological interactions of species, than on species numbers and identities *per se* (Gagic et al., 2015). To this end, summarising biodiversity in terms of the traits that directly impact organisms' ecological interactions (Functional Diversity) (McGill et al., 2006) may advance understanding of the causes and consequences of invasions.

Traits are the phenotypic properties of organisms which modulate their ecological interactions. The ecological interactions modulated by key 'functional traits' influence organism fitness and may also contribute to ecosystem functions (Wong, Guénard and Lewis, 2019). Thus, changes in the diversity of functional traits in an ecological community can simultaneously reveal how biodiversity and ecosystem processes are impacted by disturbances such as invasive species. For instance, trait-based research on plant and vertebrate communities undergoing invasion by exotic species reveal declines in functional richness (the variety of trait values in individual communities) and a tendency for functional homogenization (i.e., an increased similarity in trait values between communities) (Villéger, Grenouillet and Brosse, 2014; Castro-Díez et al., 2016). Crucially, invasion-driven changes in functional structure are further linked to altered ecosystem functions (Castro-Díez et al., 2016).

One general limitation of most trait-based analyses is the exclusive use of mean trait values for species to estimate community functional diversity. This approach underestimates intraspecific trait variation, which can strongly influence community dynamics and ecosystem processes (Des Roches et al., 2018). Intraspecific trait variation is also implicated in the success of some invasive species (González-Suárez, Bacher, and Jeschke, 2015). Recently-developed statistical tools such as the Trait Probability Density (TPD) framework can incorporate intraspecific trait variation into estimates of functional diversity (Carmona et al., 2016, 2019), but few studies have explored this within the context of

invasions. Additionally, although trait-based research is advancing the understanding of invasions by plants and vertebrates, there is a shortage of similar work on invasive insect species (Wong et al., 2019), despite their ubiquity and widespread impacts on biodiversity and ecosystem services (Bradshaw et al., 2016).

Several ants, for instance, are contenders for the world's most harmful invasive species (Lowe et al., 2000). Documented impacts of ant invasions on native ant communities include declines in species richness, taxonomic homogenization, and phylogenetic clustering (reviewed in Lessard et al., 2009). Invasive ant species were also observed to alter the ecosystem functions performed by native ant species (Ness et al., 2004). However, the consequences of ant invasions for the functional diversity of individual communities (functional alpha diversity) and patterns across multiple communities (functional beta diversity) are relatively unexplored. This is in spite of substantial progress in the understanding of ant communities' trait-environment relationships (Bihn, Gebauer and Brandl, 2010; Arnan et al., 2014; Retana et al., 2015).

To our knowledge, no trait-based studies on ants, and few for insects in general include intraspecific trait variation in estimates of community functional diversity (Wong et al., 2019). Intraspecific trait variation is expected to be high in polymorphic species, and it may influence how such species respond to or effect ecological change. Some ant species display marked variation in the body size and morphology of their worker caste (worker polymorphism), a feature which may contribute to colony fitness and ecological success (Tschinkel, 1988; Wilson, 2003). While the adaptive benefits of worker polymorphisms remain unclear (Wills et al., 2018), polymorphic ant species are known to surpass monomorphic ones in their abilities to collect resources varying in size and to access environments varying in rugosity (Farji-Brener, Barrantes and Ruggiero, 2004). That is, polymorphic species may access a wider variety of niches than monomorphic species. Thus, a basic yet apparently untested assumption is that polymorphic species have higher functional (trait) richness than monomorphic species.

The Red Imported Fire Ant, *Solenopsis invicta* Buren, 1972, is native to South America, but has spread globally to four other continents (Ascunce et al., 2011; Guénard et al., 2017), with vast areas throughout the tropics and subtropics susceptible to future invasion (Morrison et al., 2004). The species is a pervasive ecological problem in North America owing to its strong impacts on biodiversity at multiple trophic levels – including native ants (e.g., Gotellia and Arnett, 2002) – and the subsequent cascading effects on ecosystems (Porter and Savignano, 1990; Vinson, 1997). *Solenopsis invicta* are dietary generalists and mature colonies contain a polymorphic worker caste, factors which, alongside their strong interspecific aggression, may contribute to the success of invasive populations (Tschinkel, 1988; 2006).

In Asia, *Solenopsis invicta* was first reported from Taiwan in 2003, and from continental China in 2005 (Ascunce et al., 2011). There is limited ecological research on *S. invicta* in Asia; nonetheless declines in the species richness of arthropod communities in agrosystems in China were recently attributed to the presence of this exotic species (Wang et al., 2018).

Here we investigate the impacts of the invasion of *S. invicta* on taxonomic and functional diversity within (alpha diversity) and between (beta diversity) native ant communities in Hong Kong. This is the first comprehensive trait-based study of an ant invasion's impact on the functional facet of biodiversity, as well as the first to incorporate polymorphisms in calculations of functional diversity at the species level.

At the scale of the local community, we examine how invasion by *S. invicta* affects (i) species and functional richness, (ii) abundance-weighted indices of multidimensional functional diversity, and (iii) functional identity, the dominant value of a trait in the community. We predict lower species and functional richness as well as altered functional identities in communities invaded by *S. invicta* (Porter and Savignano, 1990; Castro-Díez et al., 2016).

At the multi-community (landscape) scale, we investigate how *S. invicta* invasion affects taxonomic and functional beta diversity (the dissimilarities in species and traits between communities). We predict that invasion by *S. invicta* will lead to taxonomic homogenization (Lessard et al., 2009), which will be associated with functional homogenization, as observed in other species introductions (Villéger et al., 2014). Using measures of species-level functional diversity, we also calculate species' functional uniqueness in terms of the extents to which they possess unique traits in the regional species pool as well as in uninvaded and invaded local communities (Violle et al., 2017). Lastly, we measure and compare the functional richness of different species, with the prediction that the functional richness of polymorphic species such as *S. invicta* will exceed that of monomorphic species.

Material and methods

Study area and sampling design

Our study sites are two (<4 km apart) wetland reserves in northern Hong Kong: Lok Ma Chau (22.512°N, 114.063°E) and Mai Po (22.485°N, 114.036°E). Both reserves encompass abandoned fish farms that have since been conserved for >35 years as habitats for migratory birds. Each contains a network of bunds (width ≤5 m) which separate individual ponds (Fig. S1). The habitat is relatively homogeneous and comprises exposed grasslands with native tree species interspersed throughout. Ant communities in this

landscape are comprised mostly of native species but pilot surveys from 2015 to 2017 revealed that colonies of *S. invicta* are present at high densities at multiple locations. We marked these locations, and in 2018 selected a total of 61 plots, each a 4 × 4 m quadrat, to reflect two ant community types: communities with *S. invicta* absent (uninvaded; 37 plots), and those with *S. invicta* present (invaded; 24 plots) (Fig. S1). A minimum distance of 20 m between individual plots facilitated independent observations since most ant species in the region forage no further than 5 m from their nests (Eguchi, Bui and Yamane, 2004) and *S. invicta* forage within 4 m of their nests (Weeks, Wilson and Vinson, 2004). Given the homogeneity of the landscape we assumed that any community differences observed between uninvaded and invaded plots would primarily be a consequence of invasion by *S. invicta*; environmental data collected at fine spatial resolutions were used to test this assumption (see below).

Sampling was conducted from April to September 2018. At each plot, six pitfall traps (55 mm in diameter) were installed to sample the ant community over 48 hours (Fig. S2) . The maximum distance between any two traps in each plot was 5.65 m; this sampling density (i.e., traps / m^2) was comparable to (if not higher than) previous studies characterizing ant communities which placed adjacent pitfall traps at distances of 5–10 m in individual plots (Sanders, Moss and Wagner, 2003; Parr, 2008), thus allowing better characterization of fine scale communities. All specimens were sorted into morphospecies and subsequently most were identified to species using taxonomic keys.

Environmental data

We used local GIS models (Morgan and Guénard, 2019) to obtain high-resolution data (30 × 30 m rasters) for three environmental variables corresponding to each plot: Normalized Difference Vegetation Index (NDVI), mean annual temperature, and mean annual precipitation.

Assembling the individual-level trait dataset

Here we aimed to obtain values of functional diversity that incorporated intraspecific trait variation, including the variation arising from worker polymorphisms. We assembled an individual-level trait dataset comprising data for seven morphological traits that influence ant physiology and behaviour and that are hypothesized to impact performance and fitness (see Table 1). Using mounted specimens from the pitfall traps and a Leica M165c stereo microscope paired with Leica Application Suite software, we recorded high-resolution images and performed trait measurements on at least 10 individual workers of every species (N=319). For dimorphic species of *Camponotus* and *Pheidole* where workers comprise two distinct sub-castes (minors and majors), we included trait data for individuals of both sub-castes based on

caste-ratios documented in natural colonies in previous studies (in both genera majors comprise ≤10% of all workers; Passera, 1984; Wilson, 2003). The invader *S. invicta* has a polymorphic worker caste, and Tschinkel (1988) showed that this polymorphism is mainly expressed in the morphological variation displayed by the 'majors' (head width >0.7 mm), which are present only in mature colonies where they comprise 35% of the worker population ('minors' of head width <0.7 mm comprise the remaining 65%); juvenile colonies consist only of minors. We observed that majors were present in all invaded plots, indicating the presence of mature colonies; thus, our trait data for *S. invicta* (n=20) included both minors (65% of individuals) and majors (35% of individuals).

Compressing trait variation

Prior to all statistical analyses, we applied size-correction to six traits (*head width*, *eye width, mandible length*, *scape length*, *pronotum width* and *leg length*) by dividing their values by *body size* (measured as Webers' Length; see Table 1). With the new trait dataset containing values of *body size* and the six size-corrected traits, we then applied log-transformations to reduce the influence of extreme values, and standardized trait values to have mean of zero and unit variance. Next, we used Principal Components Analysis (PCA) to synthesize the major axes of variation in multidimensional trait space and to reduce the number of dimensions used to calculate functional diversity indices. We performed the PCA using the mean trait values of each species and subsequently predicted the values of the PCA components for all individuals in the dataset. We used species means instead of individual trait values in the PCA because using the latter could bias the analysis if some species had disproportionately large numbers of individuals in the dataset. We retained the first two principal components, which had eigenvalues greater than unity and which also satisfied the broken-stick criterion (Peres-Neto et al., 2003). The first principal component explained 55.1% of the variation and was negatively correlated with *head width* and *pronotum width* and positively correlated with *leg length.* The second principal component explained 21.6% of the variation and was strongly negatively correlated with *eye width* and positively correlated with *body size.* We predicted the values of these two components for every individual in the trait dataset and used these new 'traits' to calculate functional diversity indices.

Functional diversity from species to communities

All functional diversity indices were calculated using the Trait Probability Density framework which incorporates intraspecific variation, the multidimensional nature of traits, species abundances, and probabilistic trait distributions (see Carmona et al., 2016, 2019). First, we used multidimensional

probability density functions to calculate trait probability distributions (which reflect the probabilities of observing different trait values) at the level of individual species (TPDsp) (Fig. S3). Next, we scaled up TPDsp to local community levels (TPDcom) by summing the TPDsp of all species in each local ant community (i.e., plot), weighted by their frequencies of occurrence (i.e., the proportion of the six pitfall traps capturing each species). Here, we estimated species' relative abundances in each local community using their frequencies of occurrence instead of the numbers of individual workers in the pitfall traps because the latter could overestimate the relative abundances of species with large colonies (Gotelli et al., 2011).

Five different indices for functional diversity were calculated using each community's TPDcom. The indices were Functional Richness (FRic), the volume of functional space occupied by the community; Functional Evenness (FEve), the regularity of the distribution of abundance in functional space; Functional Divergence (FDiv), a measure of how abundances tend to be on the outer margins of the functional space while controlling for functional richness; Rao, the abundance-weighted dispersion of individuals (or species) in functional space; and Functional Redundancy (FRed), the degree to which trait values are represented by multiple species in the community (Carmona et al., 2019). We used this multi-index approach to measure functional diversity because no one index can encapsulate the independent components of functional diversity (Mouchet et al., 2010).

In addition to calculating the observed values of the functional diversity indices, we calculated Standardized Effect Size (SES) values for all indices so as to estimate community-level functional diversity that had been corrected for potential effects of species richness (Swenson, 2014). SES values were calculated by comparing the observed values to values generated from 999 constrained null models randomizing the community data matrix using the "Independent Swap" algorithm. The formula for calculating SES is:

$$SES = (Mean_{observed} - Mean_{null})/s.d._{null}$$

Functional identity

To estimate functional identity, we calculated the community-weighted mean (CWM) for each trait in every local ant community. A CWM reflects the dominant value of a given trait in a given community (Swenson, 2014). We calculated CWMs using mean trait values of species weighted according to their frequencies in the different communities. Size-correction was applied to all traits except *body size* (see above).

Taxonomic and functional beta diversity

We calculated six pairwise measures of taxonomic and functional beta diversity for all possible pairs of local ant communities. We followed the framework of Baselga (2010) to calculate pairwise Taxonomic Dissimilarity (Sørensen dissimilarity), and to further partition this into components of Taxonomic Turnover and Taxonomic Nestedness, which reflect species replacement and the loss of species between sites, respectively. We calculated the Functional Dissimilarity between paired communities using their TPDcom, and further decomposed this into Functional Turnover (dissimilarities in the trait values between communities), and Functional Nestedness (dissimilarities in the relative abundances of trait values shared between communities); for details, see Carmona et al. (2019).

In addition to observed values, we calculated SES values (from comparisons with 999 constrained null models using the "Independent Swap" algorithm) for all components of functional beta diversity. Although the "Independent Swap" algorithm may not be optimal for generating null models of beta diversity patterns shaped by dispersal limitation (Swenson, 2014), this is unlikely to be a problem for the present study because all species disperse by flying alates that can travel distances exceeding the scale of the study landscape (the maximum distance between any two plots was 4 km).

Species' functional richness and functional uniqueness

We calculated functional richness and functional uniqueness values for all species. Functional richness was calculated based on each species' trait probability distribution (TPDsp) (Carmona et al., 2019). Species' functional uniqueness values were calculated relative to individual local communities, based on the degree to which a species' functional space (TPDsp) did not overlap with a local community's functional space (TPDcom) (Carmona et al., 2019). We calculated each species' 'relative uniqueness' with respect to the different uninvaded and invaded communities, as well as its 'objective uniqueness' in the species pool (using a hypothetical community containing all species at equal abundance).

Statistical analysis

Taxonomic and functional alpha diversity, CWMs, and environmental variation
We used separate linear mixed-effects models with maximum likelihood estimation to assess whether the values of alpha taxonomic diversity, functional diversity indices (including observed and SES values) and CWMs differed significantly between uninvaded and invaded local ant communities, while including a random effect of environmental variation that was captured in the first component of a PCA for the three environmental variables, which explained 91% of the variation and had eigenvalues greater than unity.

Using generalized linear models, we tested for environmental heterogeneity between invaded and uninvaded communities after using a Levene's test to test for homogeneity of variance within each group. We also tested for the effects of variation in the three environmental variables on alpha taxonomic diversity, functional diversity (including observed and SES values) and CWMs.

Taxonomic and functional beta diversity

We used non-metric multidimensional scaling (NMDS) to scrutinize the relationships between and among invaded and uninvaded local ant communities in multidimensional space (Fig. S4). We used PERMANOVA (9,999 permutations) to quantify dissimilarity, turnover and nestedness between the observed taxonomic and functional compositions of uninvaded and invaded communities. We used permutation tests for multivariate dispersions to assess whether the levels of taxonomic and functional beta diversity (in three components) observed among uninvaded communities differed from those observed among invaded communities. We also used nonparametric Mann-Whitney U tests to compare SES values of the three functional beta diversity components between uninvaded and invaded communities.

Functional uniqueness of individual species

We calculated each species' average relative uniqueness to uninvaded and invaded local communities, and regressed these against its objective uniqueness in the species pool in a linear model.

Software

We used the following packages in R software version 3.3.3 (R Core Team, 2017): *TPD* (Carmona, 2018) for calculating trait probability distributions, functional diversity indices, functional dissimilarity and functional uniqueness measures; *FD* (Laliberté, Legendre and Shipley, 2014) for calculating CWMs, *betapart* (Baselga et al., 2018) for beta diversity analyses; *lme4* (Bates et al., 2015) for linear mixed-effects models; *MASS* (Venables and Ripley, 2002) for NMDS; and *ggplot2* (Wickham, 2009) for graphics.

Results

Community composition and species richness

A total of 29 ant species (including *S. invicta*) were collected from 366 pitfall traps in 37 uninvaded plots and 24 invaded plots (Table S1). The species composition across invaded and uninvaded communities was similar overall, with 27 of the 28 native species occurring in both community types, and only one

species not found in invaded communities. On average, the species richness of invaded communities was marginally and non-significantly lower (by 13%) than that of uninvaded communities (Table 2; Fig. 1).

Functional diversity, functional identity, and environmental variation

Uninvaded and invaded communities had similar levels of FRic and FEve for both observed and SES values. However, in linear mixed-effects models, the observed FDiv and Rao of invaded communities were significantly lower than those of uninvaded communities by 11% and 7% respectively, and the FRed of invaded communities was significantly higher than that of uninvaded communities by 56% (Table 2; Fig. 1); similar relationships were observed for SES values. Community-weighted means for the traits *body size*, *scape length*, *eye width* and *leg length* did not differ significantly between uninvaded and invaded communities. By contrast, the CWMs for *head width*, *pronotum width* and *mandible length* were significantly smaller (by 4–7%) in the invaded communities (Table 2; Fig. 2). In generalized linear models, no significant differences were found between the environmental variables of invaded and uninvaded communities, and no environmental variables significantly predicted the taxonomic and functional diversity or CWMs of local communities.

Taxonomic and functional beta diversity

Uninvaded and invaded communities were significantly dissimilar in both taxonomic and functional composition, and these dissimilarities were driven by turnover in species as well as trait values (Table 3; Fig. 3). The observed levels of total taxonomic and functional dissimilarities among both uninvaded and invaded communities were comparable (Table 4), but SES values revealed that total functional dissimilarity was lower among invaded communities when corrected for species richness (Mann-Whitney U test: $P < 0.001$) (Fig. 3). Invaded communities had significantly lower levels of functional turnover (by 23%) and higher functional nestedness (by 20%) in observed values; these relationships were maintained in SES values (Mann-Whitney U tests: $P < 0.001$) (Table 4). Likewise, invaded communities were significantly more taxonomically nested than uninvaded communities (by 42%, Table 4; Fig. 3). That is, in comparison to uninvaded communities, relatively greater proportions of the total taxonomic and functional dissimilarities among invaded communities were driven by losses of species than by replacements of species, and by changes in the abundances of trait values than by changes in the trait values themselves, respectively.

Species' functional richness and functional uniqueness

Functional richness varied over four-fold among species (Min. = 0.86, Max. = 3.61) (Fig. 4). The four most functionally-rich species were two dimorphic species of *Camponotus*, another dimorphic species, *Pheidole nodus*, followed by the polymorphic invader *S. invicta*. In separate linear regressions, species' relative uniqueness to both uninvaded and invaded communities increased with their objective uniqueness in the species pool (Fig. 5). However, there was relatively more overlap between the functional spaces of objectively less unique species and the functional spaces of invaded communities (Intercept$_{Invaded}$ = -0.15; Intercept$_{Uninvaded}$ = 0.45). Furthermore, the relative uniqueness of species to invaded communities increased more steeply with an increase in objective uniqueness (Slope$_{Invaded}$ = 1.17; Slope$_{Uninvaded}$ = 0.52), such that very unique species in the species pool were more unique to invaded communities than to uninvaded communities (Fig. 5).

Discussion

Multiple lines of evidence suggest that the *S. invicta* invasion has had significant impacts on the ant community in Hong Kong, and that these impacts are still unfolding. At local scales, the most striking differences between uninvaded and invaded ant communities are the abundance distributions of their trait values. These are mainly evidenced by (i) the community-weighted means – i.e., the abundance-weighted functional identities of the communities – which differ significantly (Fig. 2), and (ii) multiple abundance-weighted functional diversity indices (Fig. 1: FDiv, Rao and FRed), which show a general pattern of species' abundances converging towards particular trait values in invaded communities, or 'functional clustering'. While the precise mechanisms driving these directional changes in the abundance distributions of trait values are unknown (possible explanations are discussed further below), the patterns indicate that invasions by *S. invicta* exert a non-random selection (*sensu* Vellend, 2016) on local ant communities, determined largely by the trait values of individuals.

At the same time, marginal differences in the taxonomic and functional richness of uninvaded and invaded communities (Fig. 1) also suggest that the impacts of the *S. invicta* invasion on the diversity of local communities are still unravelling. That is, the invasion has led to reduced abundances of a select group of species with particular 'vulnerable' trait values, but these effects have not (yet) culminated in local extinctions that would substantially change total species richness or functional richness (Mouillot et al., 2013). Our hypothesis is further supported by the fact that two thirds of all native ant species have lower relative abundances in *S. invicta*-invaded communities (Fig. S5), despite similar levels of taxonomic richness.

If decreases in the abundances of native species are indeed driven deterministically by the invasion of *S. invicta* and acting through some trait-based mechanism, then future resampling of the same sites should eventually reveal (i) significantly lower species richness in invaded communities, and (ii) the complete loss of the trait values which are uncommon in the invaded communities at present, independent of the identities of resident species that eventually become locally extinct, or of species that newly enter the communities. Notably, the former condition is often documented in longitudinal studies of ant invasions (Sanders et al., 2001; Hoffmann and Parr, 2008). The latter condition remains unexplored.

Invasion alters functional identity and drives functional clustering

The presence of *S. invicta* in individual communities selected for individuals with narrower heads and pronotums and shorter mandibles (Fig. 2: 4-7% decrease in community-weighted means for size-corrected *head width*, *pronotum width* and *mandible length*), significantly altering the functional identities of those communities. One hypothesis is that the observed patterns relate to mobility. The width of an ant's head and pronotum determine the size of gaps through which it can pass (Schofield et al., 2016). Narrower heads and pronotums of ants in invaded communities may thus reflect demands for moving through tighter spaces to avoid the behaviourally-dominant *S. invicta* during foraging (Tschinkel, 2006) or to exploit resources in less accessible locations. In invasions by Argentine ants, *Linepithema humile*, native species specialised to forage in soil increase in relative abundance and are relatively unaffected as compared to surface-dwelling species (Ward, 1987; Menke, Ward and Holway, 2018). Likewise, smaller-bodied native ant species appear to be less impacted than larger-bodied ones during ant invasions (Holway and Suarez, 2006), possibly because narrower nest entrances are more resistant to raiding by invasive species (LeBrun, Abbott and Gilbert, 2013).

An alternative hypothesis relates to diet. In ants, long mandibles of many predatory species are specialized adaptations for prey capture (Silva and Brandão, 2010). Selection for relatively shorter mandibles in *S. invicta*-invaded communities may be associated with a decline in the abundance of ant species that are specialized predators (e.g., Fig. S5: species of *Anochetus* and *Strumigenys* have lower abundances in invaded communities). This would occur if particular arthropod prey were at lower abundance at invaded sites due to an overall depletion of the arthropod community by *S. invicta* (Tschinkel, 2006). By contrast, generalist ant species would be favoured for their abilities to exploit a variety of resources opportunistically. Separately, although we did not observe any clear environmental gradients or environmental effects on diversity, microclimates or biotic factors varying at finer scales could still influence the assembly of the communities.

That ant communities invaded by *S. invicta* tend towards functional clustering (Fig. 2: FDiv: -11%, Rao: -7%, FRed: +56%) is particularly interesting, and consistent with patterns of phylogenetic clustering observed in other ant invasions (Lessard et al., 2009). The latter has been attributed to the effect of invasive species acting as "strong environmental filters" which "prune the phylogenetic tree of native species in a non-random manner" (Lessard et al., 2009, p.2664). Still, this fails to address why, in the first instance, invasive species should impact a subset of species distributed non-randomly across the phylogeny or in trait space.

Theory holds that patterns of functional or phylogenetic clustering emerge in communities when their assembly is driven primarily by environmental filtering, or alternatively by competitive hierarchies (Mayfield and Levine, 2010; Herben and Goldberg, 2014). We found no evidence for strong environmental gradients spanning from uninvaded to invaded sites. We suspect that communities invaded by *S. invicta* may be structured by competitive hierarchies (Savolainen and Vepsäläinen, 1988), where species with trait values linked to high competitive abilities dominate, decreasing the abundances of other species through competitive exclusion associated with specific trait values (Gross et al., 2015).

Notably, King and Tschinkel (2006) showed that experimental suppression of *S. invicta* abundance over two years did not significantly change the diversity of co-occurring ant species, suggesting an absence of a competitive hierarchy. However their study examined ant communities 50 years post-invasion, so weaker competitor species may have been excluded long before the start of the experiment. Further, even if the *S. invicta* suppression facilitated the re-establishment of these other species, their colonies may not have reached sizes or densities sufficient for detection within two years. By contrast, both distribution records (Ascunce et al., 2011) and our findings of unfolding impacts indicate that the *S. invicta* invasion in Hong Kong is far younger. Future work could thus pair suppression or addition experiments with trait-based approaches to investigate the potential competitive advantages associated with the head, pronotum and mandible morphology of ants in this system.

Uniform selection promotes functional homogenization

As discussed above, the direct impacts of the *S. invicta* invasion mainly unfold at local scales. However, their synergistic effects also significantly alter ant diversity at the landscape scale. Because a selection based on specific trait values has repeated uniformly over separate communities invaded by *S. invicta*, functional beta diversity patterns across multiple ant communities show a trend towards functional homogenization. This is evident from the significantly lower functional dissimilarity among communities where *S. invicta* is present (Fig. 3).

Contrary to our hypothesis, functional turnover did not track taxonomic turnover. In other words, changes in the species found in different *S. invicta*-invaded communities were not matched proportionately by changes in those communities' trait values. The invaded communities actually retained similar levels of taxonomic turnover to uninvaded communities (Fig. 3). However, the former displayed significantly less functional turnover in observed structure (by 23%; Table 4), as well as in SES values of functional beta diversity corrected for the effects of species richness (Fig. 3).

Simulation analyses show that patterns of low functional turnover amid higher taxonomic turnover emerge most frequently when there are high levels of functional redundancy in individual communities (Baiser and Lockwood, 2011). Given that communities invaded by *S. invicta* show 56% more functional redundancy than uninvaded communities (Fig. 1), our observations in an invasion context provide empirical support for previous theoretical predictions (Baiser and Lockwood, 2011).

Ordinary winners and unique losers of invasion

Examining the responses of functionally unique species may help predict the impacts of invasions (Flynn et al., 2009). Previous studies have used trait patterns of aggregated communities or regional species pools to define functionally unique groups or species (e.g., Coetzee and Chown, 2016); these can be deemed 'objective' measures of uniqueness. A species' functional uniqueness, however, is also a relative property – it depends on the values and abundances of other traits present within the same community (Violle et al., 2017).

Using both objective and relative measures of functional uniqueness, we found that objectively unique species were on the whole more unique than others across different uninvaded and invaded communities (Fig. 5: positive linear relationships for both lines). Next, we found that the functional spaces of objectively non-unique (i.e. ordinary) species constituted more of the functional spaces of invaded communities than uninvaded communities (Fig. 5: lower intercept of the 'invaded' line). Furthermore, the functional spaces of objectively very-unique species constituted less of the functional spaces of invaded communities than uninvaded communities (Fig. 5: steeper slope of the 'invaded' line).

Collectively, the findings suggest that the *S. invicta* invasion leads to multiple communities becoming more comprised of a subset of species (winners) sharing trait values which are common in the species pool, and less comprised of other species (losers) with trait values that are rare in the species pool. These patterns mirror the trend for functionally unique species to decline before functionally redundant species that has been observed in other disturbances (Flynn et al., 2009).

Implications for ecosystem function

The effects of *S. invicta* invasion on various ant-modulated ecosystem functions such as predation, nutrient cycling and bioturbation is a pertinent question to tackle in future research. If such ecosystem functions mainly respond to the functional identities of the ant communities (i.e., selection effects), we can expect that they will be impacted most by the shift in the dominant trait values in the communities. For instance, a shift in the most common foraging mode or dietary specialization in the community – as indicated by a change in the dominant head, pronotum and mandible morphology – could alter rates of predation.

On the other hand, functional homogenization and the decline of functionally unique species in invaded communities could impact ecosystem functions driven by functional complementarity and optimized by trait value diversity. For instance, decomposition may jointly depend on individuals which break down carcasses as well as others which move small pieces into the soil. Such a process would slow down if either group became increasingly rare in the community, as indicated by the loss of specific morphological trait values.

On the subject of functional complementarity, future work would also benefit from investigating the extent to which the high trait variation within polymorphic species (Fig. 4) translates into a wider array of ecological interactions undertaken by these species. For instance, dimorphic species of *Camponotus* and *Pheidole* whose colonies contain large and powerful majors as well as lightweight and fast-moving minors (Fig. S6), do appear to excel at the two complementary tasks involved in decomposition as discussed above. Investigating whether functional richness predicts niche variety or specialisation across polymorphic and monomorphic species could thus further our understanding of how species and ecosystem processes respond to ecological change.

Mitigating the cryptic impacts of global species exchange

We have shown that a single invasive species alters the functional diversity of native communities in a selective, non-random manner. Crucially, our findings further indicate that such impacts may unfold in the absence of similar changes in both taxonomic and functional richness. Thus, investigations exclusively using taxonomic measures of diversity, or indices that only describe trait variety, may fail to detect various consequences of invasions for the structure and function of ecological communities. Cryptic impacts of invasion, such as functional clustering and homogenization, can be uncovered by investigating patterns in the diversity and distribution of traits at the species, community, and landscape scales. While our study targeted a well-known invasive species, similar approaches may be used to

identify potentially overlooked exotic species that likewise impact native biodiversity beyond the taxonomic dimension.

Data Availability Statement

Relevant data files will be archived in the Dryad Digital Repository.

Authors' Contributions

M.K.L.W., B.G. and O.T.L. designed the study. M.K.L.W. conducted fieldwork, analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to manuscript revisions.

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Figure Legends

Figure 1. Boxplots showing species richness (SRic) and observed values of five functional diversity indices – Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Redundancy (FRed) and Rao – in 37 uninvaded and 24 invaded local communities. Dots show values of individual communities, thick bars show means, boxes show inter-quartile range and vertical lines extend to maximum and minimum values (excluding outliers). Asterisks indicate statistical significance (*** $P<0.001$, ** $P<0.01$, * $P<0.05$, NS, not significant).
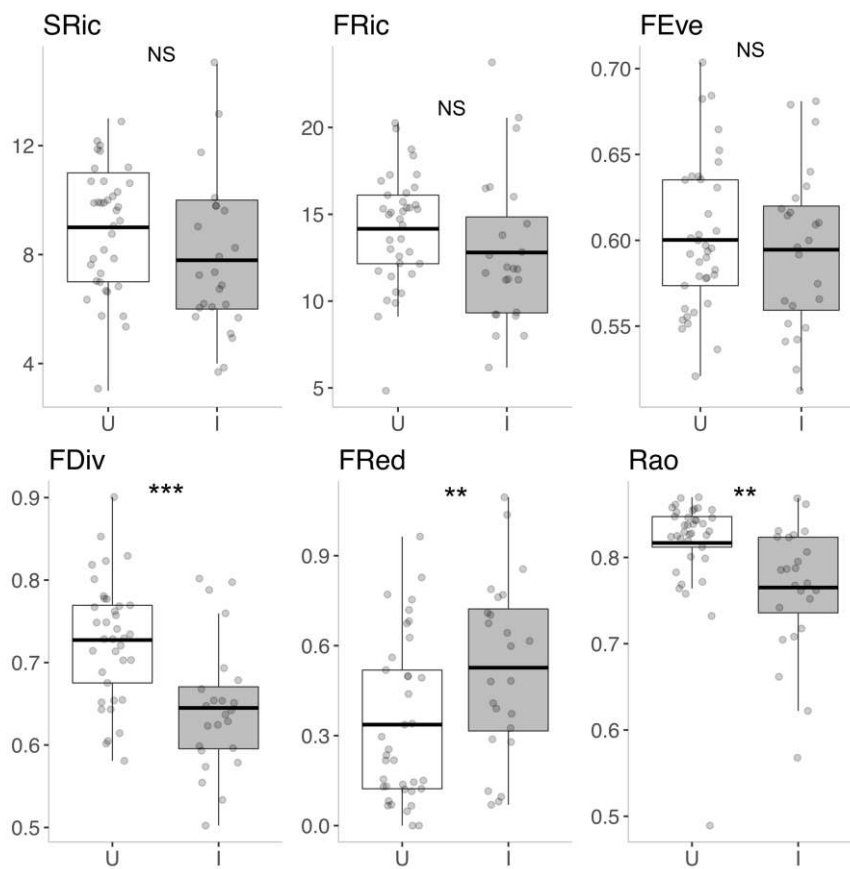
Figure 2. Boxplots displaying community-weighted mean values for size-corrected *head width*, *pronotum width* and *mandible length* in 37 uninvaded and 24 invaded communities. Dots show values of individual local communities, thick bars show mean values, box edges show standard deviations, and vertical lines extend towards minimum and maximum values. Asterisks indicate statistical significance (*** *P*<0.001, ** *P*<0.01).
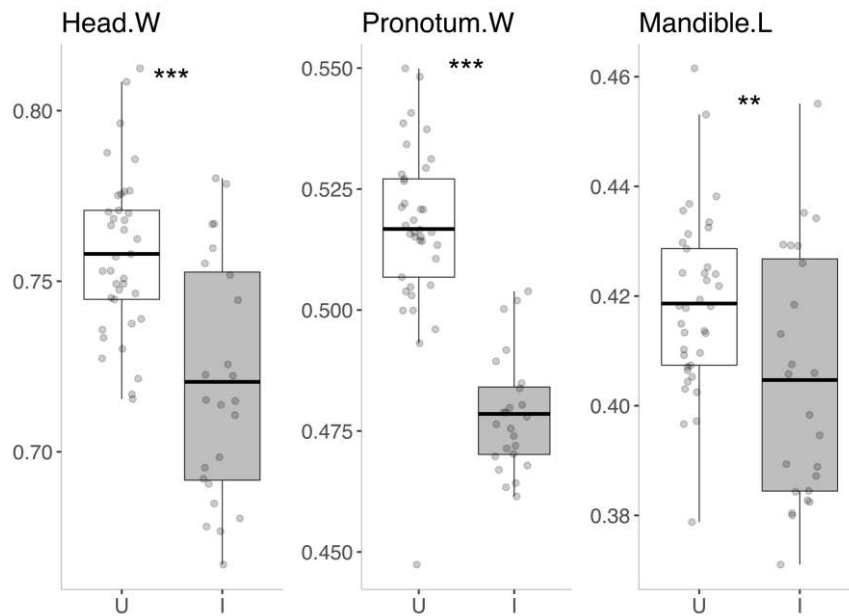
Figure 3. Observed levels of taxonomic beta diversity and functional beta diversity corrected for species-richness (SES values) in three measures of dissimilarity (Total, Turnover, and Nestedness). Boxplots show values among uninvaded communities, among invaded communities, and between uninvaded and invaded communities. Asterisks indicate statistical significance (*** $P<0.001$, * $P<0.05$, NS, not significant).
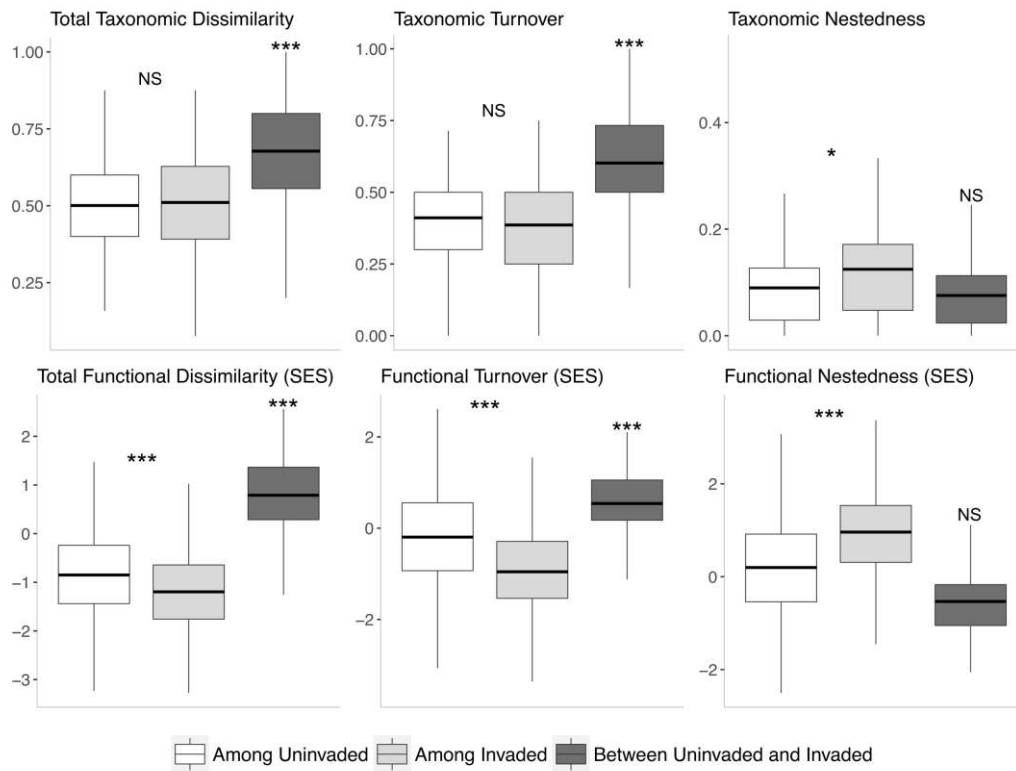
Figure 4. Functional richness of ant species with three different degrees of polymorphism. Bars show values for 22 monomorphic species (light grey), six dimorphic species (dark grey), and the polymorphic species *S. invicta* (black). Images of monomorphic, dimorphic and polymorphic species are shown in Fig. S6.
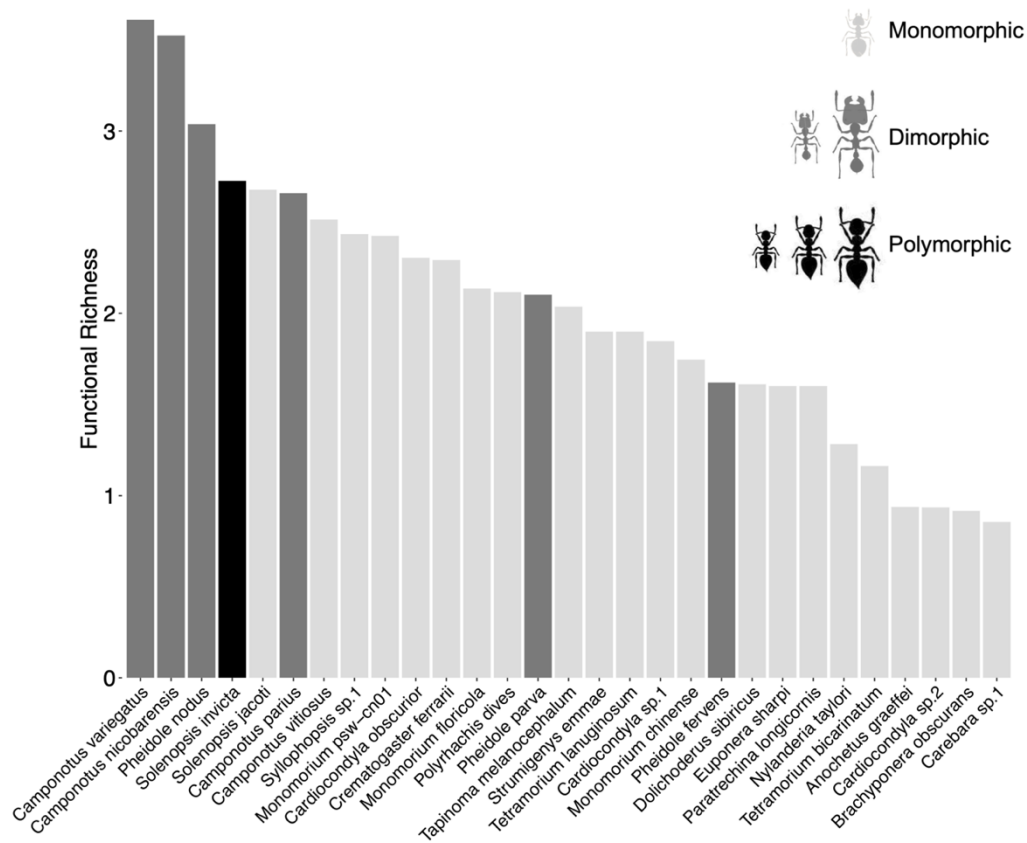
Figure 5. Species' relative functional uniqueness to local communities that were uninvaded (grey dotted line; circles) and invaded (black solid line; triangles) plotted against their objective functional uniqueness in the regional species pool.
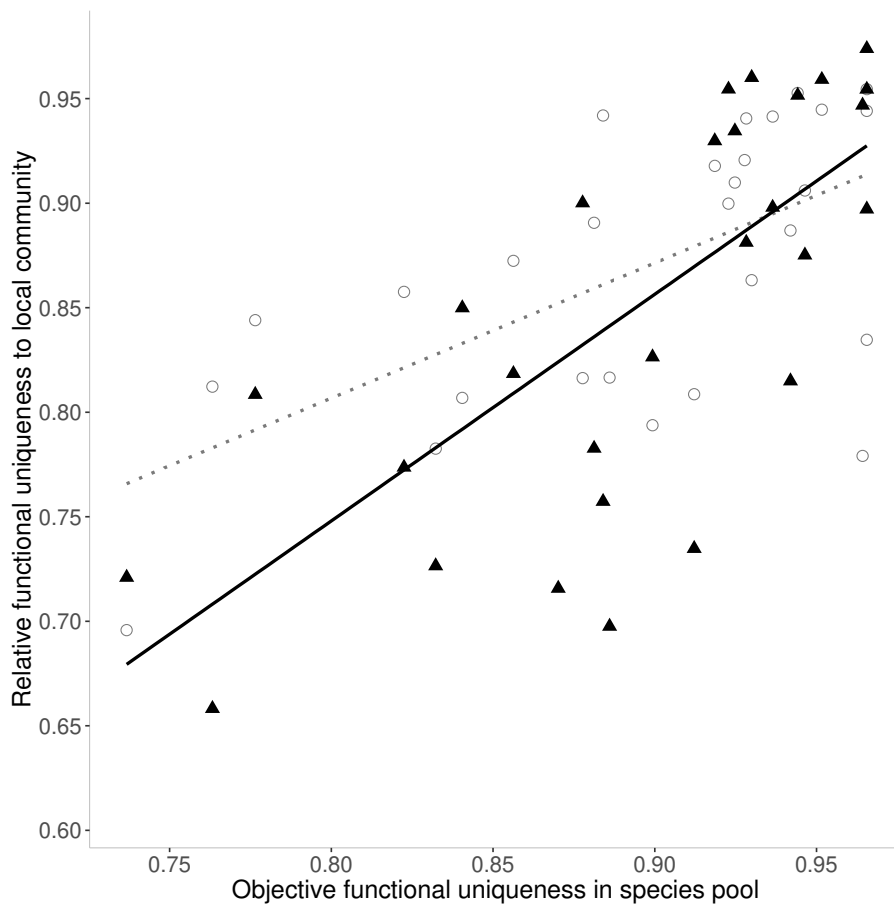
Table Legends

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).

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, Bishop and Parr, 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-support and load-bearing (Keller et al., 2014).
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 (Grevé et al., 2019).

Table 2. Summary statistics for response variables in separate linear mixed-effects models with community type (uninvaded vs. invaded) as fixed effects and environmental variation as a random effect.

Index	Uninvaded (mean ± SE)	Invaded (mean ± SE)	χ^2	df	*P*
Species Richness	8.97 ± 0.42	7.80 ± 0.67	3.06	1	0.08
FRic	14.1 ± 0.61	12.9 ± 0.97	1.59	1	0.21
FRic.SES	-0.008 ± 0.15	0.22 ± 0.24	0.86	1	0.35
FEve	0.60 ± 0.007	0.59 ± 0.01	0.24	1	0.62
FEve.SES	0.14 ± 0.16	-0.09 ± 0.26	0.83	1	0.36
FDiv	0.73 ± 0.01	0.65 ± 0.02	17.8	1	<0.001***
FDiv.SES	0.61 ± 0.15	-0.46 ± 0.24	20.7	1	<0.001***
Rao	0.82 ± 0.01	0.76 ± 0.02	7.97	1	<0.01**
Rao.SES	0.44 ± 0.13	-0.42 ± 0.2	18.0	1	<0.001***
FRed	0.34 ± 0.05	0.53 ± 0.07	13.8	1	<0.01**
FRed.SES	-0.48 ± 0.13	0.55 ± 0.21	23.9	1	<0.001***
CWM*head.width*	0.76 ± 0.005	0.72 ± 0.007	23.7	1	<0.001***
CWM*pronotum.width*	0.52 ± 0.003	0.48 ± 0.004	85.8	1	<0.001***
CWM*mandible.length*	0.42 ± 0.003	0.40 ± 0.005	10.1	1	<0.01**

Table 3. Results of PERMANOVA tests for dissimilarities between uninvaded and invaded communities in their observed taxonomic and functional compositions.

Beta diversity	Component	F	R^2	*P*
Taxonomic	Total Dissimilarity	22.4	0.28	<0.001***
	Turnover	31.9	0.35	<0.001***
	Nestedness	13.6	0.31	1.0
Functional	Total Dissimilarity	33.1	0.36	<0.001***
	Turnover	32.7	0.36	<0.001***
	Nestedness	14.7	0.33	1.0

Table 4. Permutation tests for multivariate dispersions, with calculations based on the average distances to centroids of uninvaded and invaded communities for different components of taxonomic and functional beta diversity. These tests compare the levels of beta diversity observed among uninvaded communities to those observed among invaded communities.

Beta diversity	Component	Uninvaded	Invaded	F	*P*
Taxonomic	Total Dissimilarity	0.35	0.36	0.10	0.77
	Turnover	0.29	0.28	0.20	0.66
	Nestedness	0.07	0.10	5.89	0.02*
Functional	Total Dissimilarity	0.32	0.31	0.01	0.91
	Turnover	0.30	0.23	5.01	0.03*
	Nestedness	0.41	0.49	7.37	<0.01**