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

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Abstract

1. Invasive insects represent major threats to ecosystems, with known impacts on the taxonomic diversity of invaded communities. However, their effects on the functional dimension of biodiversity, measured as the diversity and distribution of traits, are poorly known. Such measures can determine the resilience of a community and of the ecosystem processes it modulates.

2. The fire ant *Solenopsis invicta* is a widespread and highly problematic invasive species. Its impacts on the taxonomic diversity of native ant communities have been widely studied, but not its impacts on their functional diversity. Comparing 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

23   within and across communities, the functional identities of communities, and

24   functionally unique species.

25   3. Using a trait-probability density framework, we estimated the functional diversity of

26   individual species, including the trait variation from intraspecific polymorphisms. We

27   then scaled up these values to calculate functional diversity at the community level.

28   4. Invasion had only limited effects on species richness and functional richness, which

29   were 13% and 8.5% lower in invaded communities respectively. In contrast, invasion

30   had pronounced effects on taxonomic and functional composition due to turnover in

31   species and trait values. Furthermore, invaded communities were functionally more

32   homogeneous, displaying 23% less turnover and 56% more redundancy than

33   uninvaded communities, as well as greater clustering and lower divergence in trait

34   values. Invaded communities had fewer functionally-unique individuals and were

35   characterized by ant species with narrower heads and bodies and shorter mandibles.

36   5. *Synthesis and applications*. Our results suggest that the full ramifications of invasions

37   are likely to be underestimated if based solely on taxonomic measures of diversity or

38   indices describing trait variety. Invasions by *S. invicta* led to significantly altered

39   functional identity and increased functional homogenization of native ant

40   communities, but only marginally lower taxonomic and functional richness.

41   Investigating the diversity and distributions of traits at species, community and

42   landscape levels can reveal the 'cryptic impacts' of invasions which, despite causing

43   little taxonomic change, may substantially modify the structure and functioning of

44   ecological communities.

45

46   **Keywords**

47   Beta diversity, functional diversity, functional trait, functional uniqueness, insect,

48   intraspecific, invasive species, turnover

49

Introduction

51   Invasions by alien species reduce native species richness, drive cascading impacts on

52   ecosystems, cause economic damage and undermine human health (Pyšek & Richardson,

53   2010). As with many ecological phenomena, invasions have long been studied by

54   summarising ecological communities using metrics based on species' taxonomic identities:

55   abundance, richness and diversity. Changes in these metrics, however, may provide only

56   limited insight into the specific mechanisms (such as novel niches and enemy escape)

57   underlying the causes of invasions (MacDougall, Gilbert & Levine, 2009). Furthermore, the

58   effects of biodiversity on ecosystem processes often depend on the functions performed by

59   the different species, rather than on species numbers and identities *per se* (Gagic et al., 2015).

60   Summarising biodiversity in terms of the traits that directly impact organisms' ecological

61   interactions (Functional Diversity) (McGill et al., 2006) may advance understanding of the

62   causes and consequences of invasions.

63

64   Traits are the specific phenotypic properties of organisms which modulate their ecological

65   interactions. The interactions of key 'functional traits' influence organism fitness and may

66   also contribute to ecosystem functions (Wong, Guénard & Lewis, 2018). Thus, studying the

67   diversity of functional traits in an ecological community can simultaneously reveal how

68   biodiversity and ecosystem processes are impacted by disturbances such as invasive species.

69   For instance, trait-based studies of plant and vertebrate communities undergoing invasion by

70   alien species revealed declines in functional richness (the variety of trait values in individual

71   communities) and a tendency for functional homogenization (i.e., an increased similarity in

3

72 trait values between communities) (Villéger, Grenouillet & Brosse, 2014; Castro-Díez et al.,

73 2016). Crucially, invasion-driven changes in functional structure were linked to altered

74 ecosystem functions (Castro-Díez et al., 2016).

75

76 One general limitation of earlier trait-based studies, including those on invasions, has been

77 the exclusive use of mean trait values for species to estimate community functional diversity.

78 This approach underestimates intraspecific trait variation, which can strongly influence

79 community dynamics and ecosystem processes (Des Roches et al., 2018). Intraspecific trait

80 variation has also been implicated in the success of some invasive species (González-Suárez,

81 Bacher, & Jeschke, 2015). Recently-developed statistical tools such as the Trait Probability

82 Density (TPD) framework can incorporate intraspecific trait variation into estimates of

83 functional diversity (Carmona et al., 2016), but few studies have explored this within the

84 context of invasions. Additionally, although trait-based studies are advancing understanding

85 of invasions by plants and vertebrates, there is a shortage of similar work on invasive insect

86 species (Wong et al., 2018), despite their ubiquity and widespread impacts on biodiversity

87 and ecosystem services (Bradshaw et al., 2016).

88

89 Many ants, for instance, are contenders for the world's most harmful invasive species (Lowe

90 et al., 2000). Numerous studies have documented the consequences of ant invasions for

91 native ant communities, which include declines in species richness, taxonomic

92 homogenization, and phylogenetic clustering (reviewed in Lessard et al., 2009). These studies

93 focus on taxonomic and phylogenetic patterns, and rarely consider trait values directly. Few

94 such studies document the phenotypes that were lost or gained at the community level, and

95 none directly assessed the impacts of invasions on the functional diversity of individual

96 communities (functional alpha diversity) or patterns across multiple communities (functional

97   beta diversity). Furthermore, no trait-based studies on ants, and few for insects in general

98   include intraspecific trait variation in estimates of community functional diversity (Wong et

99   al., 2018). Intraspecific trait variation is expected to be high in polymorphic species and it

100   may influence how such species respond to or effect ecological change. Some ant species

101   display marked variation in the body size and morphology of their worker caste (worker

102   polymorphism), a feature which may contribute to colony fitness and ecological success

103   (Tschinkel, 1988; Wilson, 2003). It has been observed that polymorphic ant species can

104   surpass monomorphic ones in their abilities to collect resources varying in size, and to access

105   environments varying in rugosity (Farji-Brener, Barrantes & Ruggiero, 2004); that is,

106   polymorphic species may access a wider variety of niches than monomorphic species. Thus, a

107   basic yet apparently untested assumption is that polymorphic species have higher functional

108   (trait) richness than monomorphic species.

109

110   The Red Imported Fire Ant, *Solenopsis invicta* Buren, 1972, is native to South America but

111   its expanding global range already encompasses five continents (Guénard et al., 2017). The

112   species has been an extensive ecological problem throughout the United States for decades

113   due to its strong impacts on native biodiversity at multiple trophic levels (including native

114   ants) and the subsequent cascading effects on ecosystems (Porter & Savignano, 1990;

115   Vinson, 1997). *Solenopsis invicta* are dietary generalists and mature colonies consist of a

116   polymorphic worker caste (Tschinkel, 2006), a factor which, alongside their strong

117   interspecific aggression, may contribute to the success of invasive populations (Tschinkel,

118   1988; 2006). *Solenopsis invicta* was first reported in Taiwan in 2003, and in continental

119   China in 2005 (Ascunce et al., 2011). In spite of their devastating impacts elsewhere, studies

120   on the ecology of *S. invicta* invasions in Asia have been limited. Preliminary observations

121   from agrosystems in China suggest *S. invicta* invasions may be associated with declines in

122   the species richness of arthropod communities (Wang et al., 2018).

123

124   Here, we investigate the impacts of the invasion of *S. invicta* on taxonomic and functional

125   diversity within (alpha diversity) and between (beta diversity) native ant communities in

126   Hong Kong. This is the first comprehensive trait-based study of an ant invasion's impact on

127   the functional facet of biodiversity, as well as the first to incorporate polymorphisms in

128   calculations of functional diversity at the species level.

129

130   At the scale of the individual community, we examined how invasion by *S. invicta* affected

131   (i) species and functional richness, (ii) abundance-weighted indices of multidimensional

132   functional diversity, and (iii) functional identity, the dominant value of a trait in the

133   community. We predicted lower species and functional richness as well as altered functional

134   identities in communities invaded by *S. invicta* (Porter & Savignano, 1990; Castro-Díez et al.,

135   2016). At the multi-community (landscape) scale, we investigated how *S. invicta* invasion

136   affected taxonomic and functional beta diversity (the dissimilarities in species and traits

137   between communities). We predicted that invasion by *S. invicta* would lead to taxonomic

138   homogenization (Lessard et al., 2009), which would be associated with functional

139   homogenization, as observed for other alien taxa (Villéger et al., 2014). Using measures of

140   species-level functional diversity, we also identified functionally unique species and

141   compared their relative uniqueness to uninvaded and invaded communities. Lastly, we

142   measured and compared the functional richness of different species, with the prediction that

143   the functional richness of polymorphic species such as *S. invicta* would exceed that of

144   monomorphic species.

145

Materials and methods

146

Study area and sampling design

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148 Our study sites are two (<2 km apart) wetland reserves in northern Hong Kong: Lok Ma

149 Chau (22.512°N, 114.063°E) and Mai Po (22.485°N, 114.036°E). Both reserves encompass

150 abandoned fish farms that have since been conserved for >35 years as habitats for migratory

151 birds. Each contains a network of bunds (width ≤5 m) which separate individual ponds (Fig.

152 S1). The habitat is relatively homogeneous and comprises exposed grasslands with native tree

153 species interspersed throughout. Ant communities in this landscape are comprised mostly of

154 native species but pilot surveys from 2015 to 2017 revealed that colonies of *S. invicta* are

155 present at high densities at multiple locations. We marked these locations, and in 2018

156 selected a total of 61 plots, each a 4 × 4 m quadrat, to reflect two ant community types:

157 communities with *S. invicta* absent (uninvaded; 37 plots), and those with *S. invicta* present

158 (invaded; 24 plots). A minimum distance of 20 m between individual plots facilitated

159 independent observations since most ant species in the region forage no further than 5 m from

160 their nests (Eguchi, Bui & Yamane, 2004) and *S. invicta* forage within 4 m of their nests

161 (Weeks, Wilson & Vinson, 2004). Given the homogeneity of the landscape we assumed that

162 any community differences observed between uninvaded and invaded plots would primarily

163 be a consequence of invasion by *S. invicta*; environmental data collected at fine spatial

164 resolutions were used to test this assumption (see below). Sampling was conducted from

165 April to September 2018. At each plot, six pitfall traps (55 mm in diameter) were installed to

166 sample the ant community over 48 hours. All specimens were sorted into morphospecies and

167 subsequently most were identified to species using taxonomic keys.

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Environmental data

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170   We used local GIS models (Morgan & Guénard, 2019) to obtain high-resolution data (30 ×

171   30 m rasters) for three environmental variables corresponding to each plot: Normalized

172   Difference Vegetation Index (NDVI), mean annual temperature, and mean annual

173   precipitation.

174

Assembling the individual-level trait dataset

176   Here we aimed to obtain values of functional diversity that incorporated intraspecific trait

177   variation, including the variation arising from worker polymorphisms. We assembled an

178   individual-level trait dataset comprising data for seven morphological traits that regulate ant

179   physiology and behaviour and that are hypothesized to impact performance and fitness (Table

180   1). Using mounted specimens from the pitfall traps and a Leica M165c stereo microscope

181   paired with Leica Application Suite software, we recorded high-resolution images and

182   performed trait measurements on at least 10 individual workers of every species (N=319).

183   For dimorphic species of *Camponotus* and *Pheidole* where workers comprise two distinct

184   sub-castes (minors and majors), we included trait data for individuals of both sub-castes

185   based on the relative proportions (i.e., ratio of minors to majors) observed in natural colonies

186   (Passera, 1984; Wilson, 2003). The invader *S. invicta* has a polymorphic worker caste, and

187   Tschinkel (1988) showed that this polymorphism is mainly expressed in the morphological

188   variation displayed by the 'majors' (head width >0.7 mm), which are present only in mature

189   colonies where they comprise 35% of the worker population; 'minors' of head width <0.7

190   mm comprise the remaining 65% in mature colonies and juvenile colonies only consist of

191   minors. We observed that all invaded plots contained majors (head width >0.7 mm),

192   suggesting they were mature colonies; thus, our trait data for *S. invicta* (n=20) included both

193   minors (65% of individuals) and majors (35% of individuals).

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195   Table 1. The seven traits measured on each individual, and each trait's hypothesized links to

196   the performance and fitness of ants.

Trait	Measurement	Hypothesized link to performance and fitness
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 & Brandão, 2010).
head width	Width of head including eyes	Determines the size of gaps through which an individual can pass (Schofield, Bishop & 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 & Brandão, 2010).
mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva & Brandão, 2010).
scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva & 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).

197

Compressing trait variation

199   We divided the measurements of six traits (*head width*, *eye width, mandible length, scape*

200   *length*, *pronotum width* and *leg length*) by *size* to reduce correlation with body size. We then

201   log-transformed the values of all seven traits to reduce the influence of extreme values, and

202   standardized trait values to have mean of zero and unit variance. Next, we used Principal

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203   Components Analysis (PCA) to synthesize the major axes of variation in multidimensional

204   trait space and to reduce the number of dimensions used to calculate functional diversity

205   indices. We performed the PCA using the mean trait values of each species and subsequently

206   predicted the values of the PCA components for all individuals in the dataset. We used

207   species means instead of individual trait values in the PCA because using the latter could bias

208   the analysis if some species had disproportionately large numbers of individuals in the

209   dataset. We retained the first two components of the PCA, which had eigenvalues greater

210   than unity, and which captured 76.9% of the total variance in traits. We then predicted the

211   values of these two components for every individual in the trait dataset and used these new

212   'traits' to calculate functional diversity indices.

213

214   **Functional diversity from species to communities**

215   All functional diversity indices were calculated using the Trait Probability Density

216   framework which incorporates intraspecific variation, the multidimensional nature of traits,

217   species abundances, and probabilistic trait distributions (see Carmona et al., 2016). First, we

218   used multidimensional probability density functions to calculate trait probability distributions

219   (which reflect the probabilities of observing different trait values) at the level of individual

220   species (TPDsp). Next, we scaled up TPDsp to local community levels (TPDcom) by

221   summing the TPDsp of all species in each local ant community, weighted by their relative

222   abundances – which we estimated as frequencies of occurrence. Finally, five different indices

223   for functional diversity were calculated using each community's TPDcom. The indices were

224   Functional Richness (FRic), the volume of functional space occupied by the community;

225   Functional Evenness (FEve), the regularity of the distribution of abundance in functional

226   space; Functional Divergence (FDiv), a measure of how abundances tend to be on the outer

227   margins of the functional space while controlling for functional richness; Rao, the

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228   abundance-weighted dispersion of individuals (or species) in functional space; and

229   Functional Redundancy (FRed), the degree to which trait values are represented by multiple

230   species in the community (Carmona et al., 2016). We used this multi-index approach to

231   measure functional diversity because no one index can encapsulate the independent

232   components of functional diversity (Mouchet et al., 2010). In addition to calculating the

233   observed values of the functional diversity indices, we calculated Standardized Effect Size

234   (SES) values for all indices so as to estimate community-level functional diversity that had

235   been corrected for potential effects of species richness (Swenson, 2014). SES values were

236   calculated by comparing the observed values to values generated from 999 constrained null

237   models randomizing the community data matrix using the "Independent Swap" algorithm.

238   The formula for calculating SES is:

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

240

241   **Functional identity**

242   To estimate functional identity, we calculated the community-weighted mean (CWM) for

243   each trait in every local ant community. A CWM reflects the dominant value of a given trait

244   in a given community (Swenson, 2014). We calculated CWMs using mean trait values of

245   species weighted according to their relative abundances in the different communities. Size-

246   correction was applied to all traits except *size* (see above).

247

248   **Taxonomic and functional beta diversity**

249   We calculated six pairwise measures of taxonomic and functional beta diversity for all

250   possible pairs of local ant communities. We used matrices of species' abundances to calculate

251   the Taxonomic Dissimilarity between each pair, and further decomposed this into Taxonomic

252   Turnover (dissimilarities arising from the replacement of species between communities), and

253   Taxonomic Nestedness (dissimilarities in the relative abundances of species that occurred in

254   both communities). We calculated the Functional Dissimilarity between paired communities

255   using their TPDcom, and further decomposed this into Functional Turnover (dissimilarities in

256   the trait values between communities), and Functional Nestedness (dissimilarities in the

257   relative abundances of trait values shared between communities). In addition to observed

258   values, we calculated SES values (from comparisons with 999 constrained null models using

259   the "Independent Swap" algorithm) for all components of functional beta diversity. Although

260   the "Independent Swap" algorithm may not be optimal for generating null models of beta

261   diversity patterns shaped by dispersal limitation (Swenson, 2014), this is unlikely to be a

262   problem for the present study because all species disperse by flying alates that can travel

263   distances exceeding the scale of the study landscape (the maximum distance between any two

264   plots was 4 km).

265

266   **Species' functional richness and functional uniqueness**

267   We calculated functional richness and functional uniqueness values for all species.

268   Functional richness was calculated based on each species' trait probability distribution

269   (TPDsp) (Carmona et al., 2016). Species' functional uniqueness values were calculated

270   relative to individual local communities, based on the degree to which a species' functional

271   space (TPDsp) did not overlap with a local community's functional space (TPDcom)

272   (Carmona et al., 2016). We calculated each species' 'relative uniqueness' with respect to the

273   different uninvaded and invaded communities, as well as its 'objective uniqueness' in the

274   species pool (using a hypothetical community containing all species at equal abundance).

275

276   **Statistical analysis**

277   *Taxonomic alpha diversity, functional diversity and CWMs*

278   We used separate linear mixed-effects models to assess whether the values of alpha

279   taxonomic diversity, functional diversity indices (including observed and SES values) and

280   CWMs differed significantly between uninvaded and invaded local ant communities, while

281   including a random effect of environmental variation that was captured in the first component

282   of a PCA for the three environmental variables, which had eigenvalues greater than unity.

283   *Taxonomic and functional beta diversity*

284   We used non-metric multidimensional scaling (NMDS) to scrutinize the relationships

285   between and among invaded and uninvaded local ant communities in multidimensional space

286   (Fig. S2). We used PERMANOVA (9,999 permutations) to quantify dissimilarity, turnover

287   and nestedness between the observed taxonomic and functional compositions of uninvaded

288   and invaded communities. We used permutation tests for multivariate dispersions to assess

289   whether the levels of taxonomic and functional beta diversity (in three components) observed

290   among uninvaded communities differed from those observed among invaded communities.

291   We also used nonparametric Mann-Whitney U tests to compare SES values of the three

292   functional beta diversity components between uninvaded and invaded communities.

293   *Functional uniqueness of individual species*

294   We calculated each species' average relative uniqueness to uninvaded and invaded

295   communities and regressed these against its objective uniqueness in a linear model.

296   *Software*

297   We used the following packages in R software version 3.3.3 (R Core Team, 2017): *TPD*

298   (Carmona, 2018) for calculating trait probability distributions, functional diversity indices,

299   functional dissimilarity and functional uniqueness measures, *FD* (Laliberté, Legendre &

300   Shipley, 2014) for calculating CWMs, *betapart* (Baselga et al., 2018) for beta diversity

301   analyses, *lme4* (Bates et al., 2015) for linear mixed-effects models, *MASS* (Venables &

302   Ripley, 2002) for NMDS, and *ggplot2* (Wickham, 2009) for the production of graphics.

303

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).

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Functional diversity and CWMs

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. CWMs for the traits *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).

323

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

328   dissimilarities among both uninvaded and invaded communities were comparable (Table 4),

329   but SES values revealed that total functional dissimilarity was lower among invaded

330   communities when corrected for species richness (Mann-Whitney U test: $P < 0.001$) (Fig. 3).

331   Invaded communities had significantly lower levels of functional turnover (by 23%) and

332   higher functional nestedness (by 20%) in observed values; these relationships were

333   maintained in SES values (Mann-Whitney U tests: $P < 0.001$) (Table 4). Likewise, invaded

334   communities were significantly more taxonomically nested than uninvaded communities (by

335   42%, Table 4; Fig. 3). That is, in comparison to uninvaded communities, relatively greater

336   proportions of the total taxonomic and functional dissimilarities among invaded communities

337   were driven by losses of species than by replacements of species, and by changes in the

338   abundances of trait values than by changes in the trait values themselves, respectively.

339

340   **Species' functional richness and functional uniqueness**

341   Functional richness varied over four-fold among species (Min. = 0.86, Max. = 3.61) (Fig. 4).

342   The four most functionally-rich species were two dimorphic species of *Camponotus*, another

343   dimorphic species, *Pheidole nodus*, followed by the polymorphic invader *S. invicta*. In

344   separate linear regressions, species' relative uniqueness to both uninvaded and invaded

345   communities increased with their objective uniqueness (Fig. 5). However, there was

346   relatively more overlap between the functional spaces of less unique species and the

347   functional spaces of invaded communities (Intercept$_{Invaded}$ = -0.15; Intercept$_{Uninvaded}$ = 0.45).

348   Furthermore, the relative uniqueness of species to invaded communities increased more

349   steeply with an increase in objective uniqueness (Slope$_{Invaded}$ = 1.17; Slope$_{Uninvaded}$ = 0.52), such that

350   very unique species were more unique to invaded communities than to uninvaded

351   communities (Fig. 5).

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354 Table 2. Summary statistics for response variables in separate linear mixed-effects models

355 with community type (uninvaded vs. invaded) as fixed effects and environmental variation as

356 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*	0.76 ± 0.005	0.72 ± 0.007	23.7	1	<0.001***
CWM*pron*	0.52 ± 0.003	0.48 ± 0.004	85.8	1	<0.001***
CWM*mand*	0.42 ± 0.003	0.40 ± 0.005	10.1	1	<0.01**

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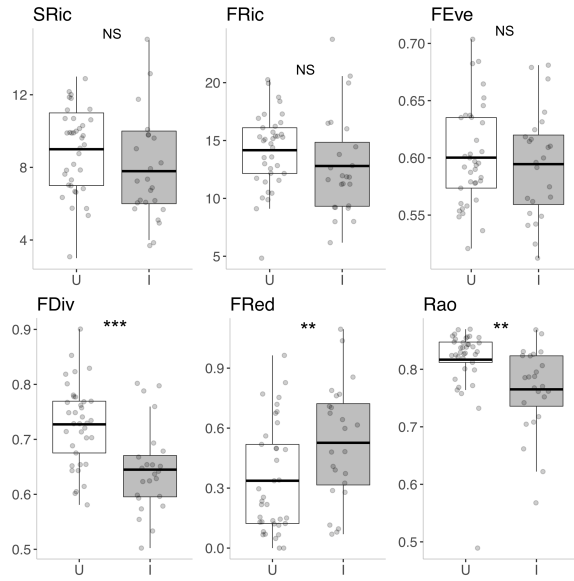
Figure 1. Boxplots showing species richness and observed values of five functional diversity indices in 37 uninvaded and 24 invaded local communities. Dots show values of individual co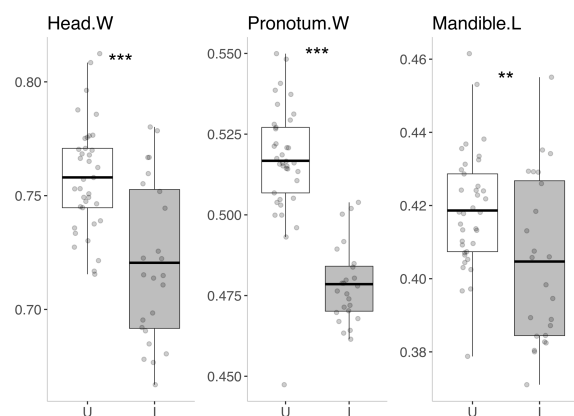mmunities, thick bars show means, boxes show inter-quartile range and vertical lines extend to maximum and minimum values (excluding outliers). Asterisks indicate statistical significance (*** *P*<0.001, ** *P*<0.01, * *P*<0.05, NS, not significant).

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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

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371   show standard deviations, and vertical lines extend towards minimum and maximum values.

372   Asterisks indicate statistical significance (*** $P<0.001$, ** $P<0.01$).

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374

375   Table 3. Results of PERMANOVA tests for dissimilarities between uninvaded and invaded

376   communities in their observed taxonomic and functional compositions.

Beta diversity	Component	F	R²	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

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378

379   Table 4. Permutation tests for multivariate dispersions, with calculations based on the

380   average distances to centroids of uninvaded and invaded communities for different

381   components of taxonomic and functional beta diversity. These tests compare the levels of
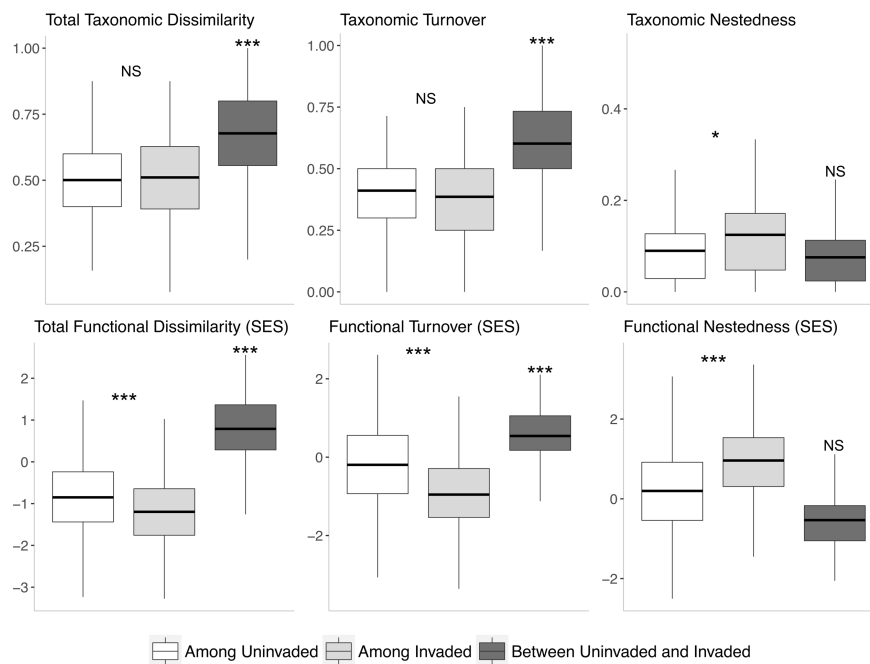
382   beta diversity observed among uninvaded communities to those observed among invaded

383   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**

384

385

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

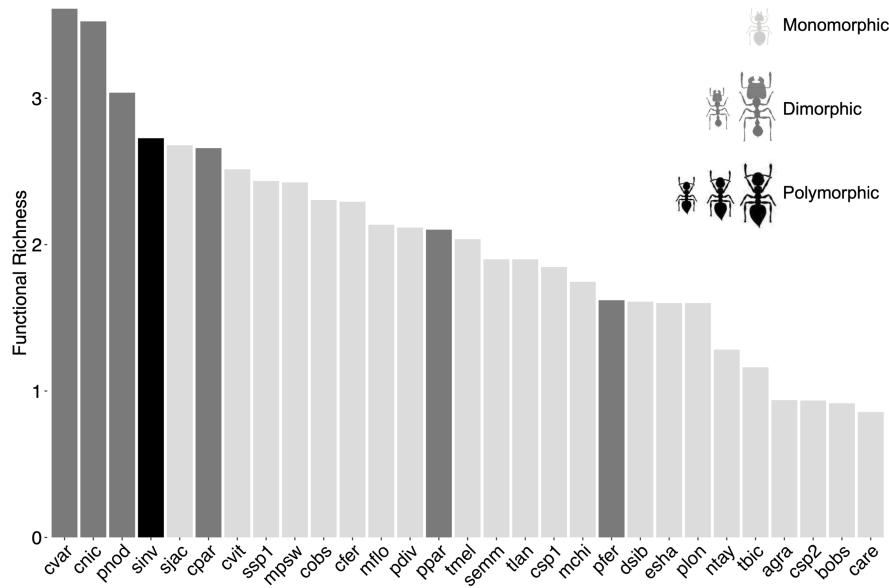Nestedness). Boxplots show values among uninvaded communities, among invaded

communities, and between uninvaded and invaded communities. Asterisks indicate statistical

significance (*** $P<0.001$, * $P<0.05$, NS, not significant).

392

393

394

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). Full species names are listed in Table S1, and

images of monomorphic, dimorphic and polymorphic species are shown in Fig. S4.
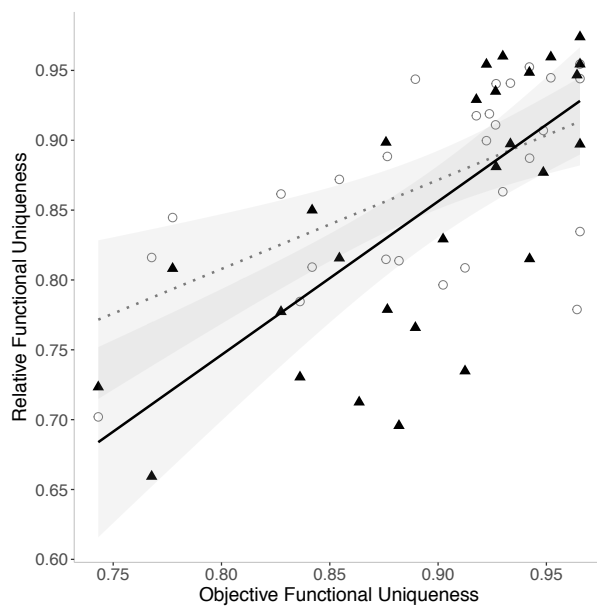
Figure 5. Species' relative functional uniqueness to local communities that were uninvaded

(grey dotted line; circles) and invaded (black solid line; triangles) plotted against their

objective functional uniqueness in the species pool.

20

405

Discussion

407   Most concerns surrounding biological invasions cite declines in the species richness of

408   invaded communities. However, invasions can also impact the structure and function of

409   ecological communities in ways that are less detectable with taxonomic measures of

410   diversity. Here we investigated the impacts of an invasion on the diversity and distribution of

411   species and traits in individual communities (alpha diversity) and across multiple

412   communities (beta diversity). We found that invasion by *S. invicta*, one of "the world's worst

413   invasive species" (Lowe et al., 2000), led to the functional homogenization and altered

414   functional identity of ant communities in Hong Kong despite effecting marginal changes in

415   species and functional richness. Additionally, we observed higher functional richness in

416   polymorphic species than monomorphic species. We discuss the possible ecological drivers

417   and ecosystem implications of our findings below.

418

419   **Polymorphic species are more functionally rich**

420   Polymorphisms are among the most conspicuous and pervasive sources of intraspecific trait

421   variation (Ford, 1957). It is conceivable that polymorphic species, with greater variation in

422   morphology, would display higher functional richness. We generally found this to be the case

423   among the 29 ant species studied. Dimorphic species of the genera *Camponotus* and *Pheidole*

424   and the polymorphic *S. invicta* displayed 2–322% more functional richness than

425   monomorphic species (Fig. 4). However, the functional richness of three dimorphic species

426   was higher than that of the polymorphic *S. invicta*. This likely resulted from the pronounced

427   allometry of the discrete major subcastes of dimorphic species, which generated extreme trait

428   values; polymorphic *S. invicta* workers, by contrast, display a continuous variation with size

429   (Figs. 4 and S4). While it is unlikely that the morphological traits measured were

21

430 representative of all species' multidimensional niches, our findings demonstrate that, at least

431 across multiple aspects of morphology linked to foraging, mobility and physiology (Table 1),

432 polymorphic species occupy more functional space and may have access to a greater variety

433 of niches than monomorphic species, as previously suggested (Farji-Brener et al., 2004).

434 Future work investigating whether functional richness predicts niche variety or specialisation

435 across polymorphic and monomorphic species could further our understanding of how

436 species and ecosystem processes respond to ecological change.

437

438 **Lower species and functional richness in invaded communities**

439 Disturbances drive local extinctions by decreasing the abundances of particular species with

440 vulnerable trait combinations; this process can initially occur without significantly modifying

441 community composition or affecting total species and functional richness (Mouillot et al.,

442 2013). Invasions by *S. invicta* in Hong Kong generally follow these patterns. Two thirds of

443 the native species had lower abundances in the invaded communities (Fig. S3), but the same

444 communities displayed only marginally lower species richness (by 13%) and functional

445 richness (by 8.5%) (Table 2 and Fig. 1). These results differ from previously reported

446 extensive declines (by 69%) in the species richness of ant communities invaded by *S. invicta*

447 in North America (Porter & Savignano, 1990). The current absence of an extensive decline in

448 species richness may be associated with the relatively younger *S. invicta* invasion in Hong

449 Kong (Ascunce et al., 2011), and potentially the ecological differences (and thus responses)

450 between the tropical grassland ant communities studied here, which comprised many

451 disturbance specialists, and the ant communities of temperate forests in previous studies

452 (Porter & Savignano, 1990). Aside from the marginal differences in species and functional

453 richness, multiple indices sensitive to changes in the abundance and distribution of trait

454 values differed significantly between uninvaded and invaded communities (Table 2: CWMs,

455   FDiv, Rao, and FRed). Although each index measures a unique aspect of functional identity

456   and diversity (Mouchet et al., 2010), the results collectively indicate that invasions by *S.*

457   *invicta* exert a non-random selection on native communities through the trait values of

458   individuals; we discuss these patterns in the two sections that follow.

459

460   Altered functional identity of invaded communities

461   The CWMs for size-corrected *head width*, *pronotum width* and *mandible length* of ants in

462   invaded communities decreased significantly by 4–7% (Fig. 1), in line with our hypothesis

463   that invasion would alter communities' functional identities. The results suggest that invasion

464   selects for individuals with narrower heads and pronotums and shorter mandibles. One

465   hypothesis is that the observed patterns relate to mobility. It has been shown that the width of

466   an ant's head and pronotum determine the size of gaps through which it can pass (Schofield

467   et al., 2016). Narrower heads and pronotums of ants in invaded communities could thus

468   reflect demands for moving through tighter spaces to avoid the behaviourally dominant *S.*

469   *invicta* during foraging (Tschinkel, 2006) or to reach resources in less accessible locations.

470   For instance, studies on other ant invasions reported that native hypogaeic species,

471   specialised to forage and move through soil, increased in relative abundance by 50% (Human

472   & Gordon, 1997). A second hypothesis relates to diet. In ants, long mandibles of many

473   predatory species are specialized adaptations for prey capture (Silva & Brandão, 2010), and

474   larger heads and pronotums afford more space for the musculature powering snapping,

475   gripping and load-bearing abilities (Keller et al., 2014; Richter et al., 2019). Hence, the

476   shorter mandibles and narrower heads and pronotums of ants in invaded communities may

477   reflect a less specialized or more herbivorous diet. Such ants may use more liquid foods (e.g.,

478   honeydew from hemipterans) that can be ingested relatively quickly, and which require less

479   manipulation (capture, ripping, transport) than solid foods. The presence of the behaviourally

480   dominant *S. invicta* may select for ants that 'grab and go' over those which remain at food

481   sources for longer periods.

482

Functional clustering and redundancy of invaded communities

484   In invaded communities, values of FDiv and Rao decreased significantly by 11% and 7 %

485   respectively, while FRed increased significantly by 56% (Fig. 2). These patterns arose due to

486   the presence of more individuals with similar trait values in invaded communities.

487   Specifically, FDiv reflects the degree to which the distribution of species' abundances in

488   functional space maximizes total community variation in trait values (and niches) (Mouchet

489   et al., 2010). Hence, the results suggest that the most abundant species in uninvaded

490   communities are more differentiated in their niches (higher FDiv), while those in invaded

491   communities have more similar niches (lower FDiv). As observed for FDiv, the lower Rao in

492   invaded communities is indicative of niche clustering (species' abundances are relatively

493   more clustered in functional space) (Mouchet et al., 2010). FRed reflects the degree to which

494   specific trait values are represented by multiple species in the community (Carmona et al.,

495   2016). In uninvaded communities (lower FRed) fewer species share the same trait values,

496   suggesting less niche overlap. By contrast, more species share the same trait values in

497   invaded communities (higher FRed), suggesting more niche overlap. Therefore, as observed

498   for the CWMs, the results for FDiv, Rao and FRed show a general pattern of species'

499   abundances converging towards particular trait values in invaded communities, which is one

500   signature of selection (Vellend, 2016).

501

Functional homogenization across invaded communities

503   Our analysis of functional alpha diversity suggests that *S. invicta* invasions are associated

504   with a selection for specific trait values in individual communities. Because such selection

505 has repeated over separate communities invaded by *S. invicta*, functional beta diversity

506 patterns across multiple communities show a trend towards functional homogenization. This

507 is evident from the significantly lower functional dissimilarity among communities where *S.*

508 *invicta* is present (Fig. 3). Contrary to our hypothesis, however, functional turnover did not

509 track taxonomic turnover; changes in the species found in different invaded communities

510 were not matched proportionately by changes in those communities' trait values. The invaded

511 communities actually retained similar levels of taxonomic turnover to uninvaded

512 communities (Fig. 3). However, the former displayed significantly less functional turnover in

513 observed structure (by 23%; Table 4), as well as in SES values of functional beta diversity

514 corrected for the effects of species richness (Fig. 3). In previous analyses using computer

515 simulations, such patterns of low functional turnover amid higher taxonomic turnover were

516 predicted to emerge most frequently when there are high levels of functional redundancy in

517 individual communities (Baiser & Lockwood, 2011). Given that communities invaded by *S.*

518 *invicta* displayed 56% more functional redundancy than uninvaded communities (Fig. 2), our

519 observations in an invasion context provide empirical support for the theoretical predictions

520 (Baiser & Lockwood, 2011).

521

522 **Functionally ordinary winners and functionally unique losers across invaded**

523 **communities**

524 Invasions and other disturbances can result in losses of functionally unique species before

525 functionally redundant species (Flynn et al., 2009). Thus, examining the abundance and

526 distribution of functionally unique species may promote the advanced detection of invasion

527 impacts. Previous studies used trait patterns of aggregated communities to define functionally

528 unique groups or species, then analysed their abundances within each community (e.g.,

529 Coetzee & Chown, 2016). A species' functional uniqueness, however, is a relative property,

530   dependent on the value and abundance of other traits present in the particular community.

531   Thus, also measuring species' functional uniqueness as *relative to specific communities* may

532   improve the understanding of changes in functional space and how shifting species

533   abundances contribute to these changes. Here we first assigned each species an objective

534   value of functional uniqueness in the species pool using a community containing all species

535   at equal abundance. We then validated this measure by showing that objectively unique

536   species were on the whole more unique than others across different uninvaded and invaded

537   communities (Fig. 5: positive linear relationships for both lines). Next, we found that

538   objectively non-unique (functionally ordinary) species constituted more of the functional

539   spaces of invaded communities than uninvaded communities (Fig. 5: lower intercept of the

540   'invaded' line). We further found that objectively very-unique species constituted less of the

541   functional spaces of invaded communities than uninvaded communities (Fig. 5: steeper slope

542   of 'invaded' line). Together, these findings suggest that the *S. invicta* invasion has led to

543   invaded communities becoming more comprised of a subset of species (winners) sharing trait

544   values which are common in the species pool, and less comprised of other species (losers)

545   with trait values that are rare in the species pool. These patterns mirror the decline of

546   functionally unique species before functionally redundant species observed in other

547   disturbances (Flynn et al., 2009).

548

549   **Implications for ecosystem function**

550   The consequences of an invasion will extend to the ecosystem if the affected taxa are also

551   key modulators of ecosystem functions. Ants are such organisms, and the effects of *S. invicta*

552   invasion on various ant-modulated ecosystem functions such as predation, nutrient cycling

553   and bioturbation is a pertinent question to tackle in future research. These effects will hinge

554   on the particular relationships between ant diversity and ant-modulated ecosystem functions

26

555 in the tropical grassland communities of Hong Kong. For instance, if ecosystem functions

556 mainly respond to the functional identities of the ant communities (i.e., selection effects),

557 they may be impacted significantly by the altered CWMs of invaded communities.

558 Alternatively, functional homogenization and the decline of functionally unique species in

559 invaded communities could impact ecosystem functions driven by functional

560 complementarity. Ecosystem functions may also respond to both functional identity and

561 complementarity across different spatial and temporal scales (Isbell et al., 2018). Whatever

562 the case, the present findings show *S. invicta* invasions in Hong Kong to have significant

563 impacts on the functional structure of ant communities, which may also affect ecosystem-

564 wide changes.

565

566 **Implications for understanding and managing invasions**

567 Using data on the traits of individuals we have shown that an alien invasive species alters – in

568 a selective, non-random manner – the functional properties of native communities that may

569 influence ecosystem processes. Crucially, our findings further suggest that such impacts may

570 unfold in the absence of similar changes in both taxonomic and functional richness. Thus,

571 assessments exclusively using taxonomic measures of diversity, or indices that only describe

572 trait variety, may fail to detect various consequences of invasions for the structure and

573 function of ecological communities. These other ecologically significant consequences of

574 invasion (e.g., functional clustering and homogenization) can be uncovered by investigating

575 patterns in the diversity and distribution of traits at the species, community, and landscape

576 levels. Future work using such comprehensive functional approaches may not only improve

577 the management of invasive species, but also help to identify other alien species driving

578 'cryptic impacts' on ecosystem-relevant community structure amid modest taxonomic

579 change.

580

Authors' Contributions

582   M.K.L.W., B.G. and O.T.L. designed the study. M.K.L.W. conducted fieldwork, analysed the

583   data and wrote the first draft of the manuscript. All authors contributed substantially to

584   manuscript revisions.

585

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