



Evaluating the conservation value of sacred forests for ant taxonomic, functional and phylogenetic diversity in highly degraded landscapes

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ABSTRACT

Land use changes and accelerating deforestation rates impact biodiversity on a global scale. While it is well established that the loss of primary forests is devastating, considerably less is understood about the conservation value of sacred forests (e.g. Feng shui woods in China) as local biodiversity reservoirs in human influenced landscapes. When these forests were assessed, the focus was generally on floral diversity, while faunal aspects were neglected. Here we address this knowledge gap by evaluating several dimensions of faunal biodiversity in Hong Kong Feng shui woods. We compare taxonomic, phylogenetic and functional elements of the leaf litter dwelling ant fauna collected over five years among Feng shui woods and two woody habitats corresponding to two distinct successional stages. Ant assemblages in Feng shui woods presented higher species richness that were more resilient to invasions by tramp species, and encompassed specialist species with a distinct set of traits. Phylogenetic diversity was similar in Feng shui and successional woods, while functional diversity was clustered in early successional habitats. The scarcity of tramp species and presence of specialists in Feng shui woods despite their close proximity to human settlements highlights their conservation value for native species in highly degraded landscapes. Our results provide much needed insight on the faunal biodiversity of Feng shui woods. We highlight the conservation value and urgent need for a better protection of these widely overlooked sacred forests in highly disturbed landscapes.

1. Introduction

Global biodiversity has suffered major declines in recent decades. Declines in species and biomass are attributed to the anthropogenic impact on the environment, and are linked to climate change, biological invasions and most notably to large-scale land use changes that lead to habitat loss (Dirzo et al., 2014; Joppa et al., 2016; Sala et al., 2000; Seibold et al., 2019; Wagner, 2020). A high diversity of species is vital for ecosystem functioning, the provision of ecosystem services, such as primary production and nutrient cycling, and for ecosystem resilience in the face of disturbances (Chapin et al., 2000; Hooper et al., 2012; Oliver et al., 2015). Areas with high biodiversity value, foremost primary or old-growth forests, have, however, substantially decreased during the last half century (Betts et al., 2017; Curtis et al., 2018; Hansen et al., 2013). Their high biodiversity value is lost with particularly pronounced severity in tropical and subtropical regions, and there is little hope for improvement in the near future given the low levels of protection they receive (Betts et al., 2017; Curtis et al., 2018). In addition, the biological value observed within primary forests is unrivalled by secondary re-

growth forests even after several decades (Alroy, 2017; Sayer et al., 2017; Whitworth et al., 2018). The continuing loss of native forests has prompted an increased interest in evaluating remnant old-growth forests as biodiversity reservoirs in predominantly human influenced landscapes.

Remnant forests are small isolated patches of old-growth forests that persisted in anthropogenically altered landscapes. They can act as reservoirs for local biodiversity in otherwise species-poor human-influenced landscapes (Hahs et al., 2009; Nooten et al., 2018) and their seedbanks can be used as sources for propagating new forests (Aerts et al., 2016; Hu et al., 2011; Merkonnen et al., 2019; Wassie and Teketay, 2006). A particular type of cultural old-growth woods – sacred groves – could persist in largely deforested landscapes in many regions of the world due to cultural and spiritual reasons (Bhagwat and Rutte, 2006). Yet, these areas have a high ecological value, providing ecosystem services and valuable habitat for regional biodiversity (Aerts et al., 2016; Bhagwat and Rutte, 2006; Chen et al., 2018; Marafa, 2003). For instance, church forests in Ethiopia preserve floral biodiversity in a largely barren landscape by harbouring a substantial proportion of tree

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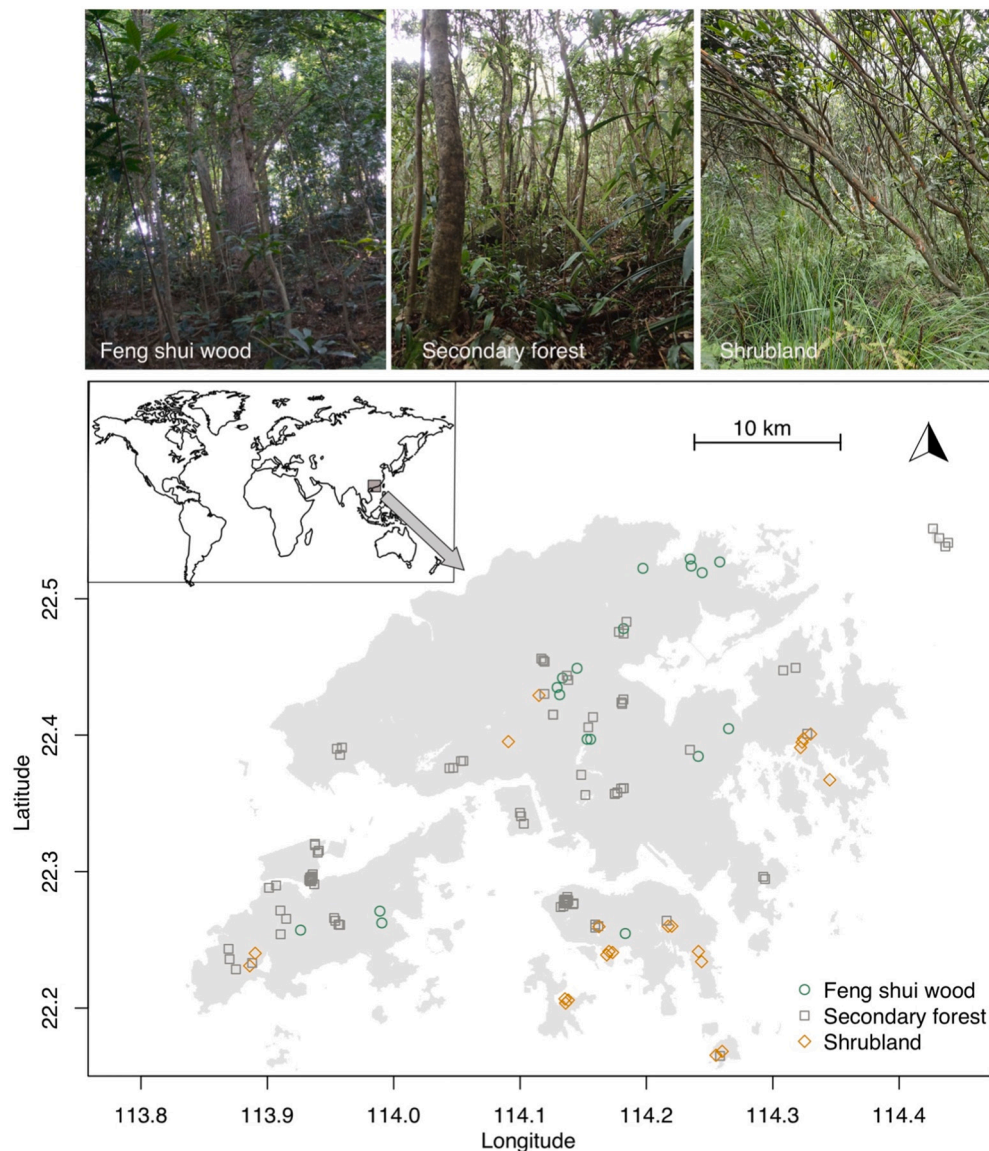


Fig. 1. Sampling locations across Hong Kong. Showing 140 sites in three habitats types: Feng shui woods (18), Secondary forest (100), and shrubland (22).

species native to tropical northeast Africa (Aerts et al., 2016; Merkonnen et al., 2019; Wassie and Teketay, 2006). In India, more than one hundred thousand sacred groves are refuges for the biological diversity of many taxa, including medicinal plants, birds and fungi (Bhagwat et al., 2005; Ormsby and Bhagwat, 2010). Across southeast Asia, Feng shui woods prevailed in widely deforested landscapes for reasons of the Chinese geomancy (Liu et al., 2019), where they harbour considerable plant diversity in the eastern Himalayas (Salick et al., 2007), in China (Chen et al., 2018; Hu et al., 2011) and Hong Kong (Dudgeon and Corlett, 2004; Zhuang and Corlett, 1997). Despite their ecological uniqueness and protection by cultural traditions, many of these sites face considerable threats, including anthropogenic disturbance, pollution and invasive species (Bhagwat and Rutte, 2006; Cardelus et al., 2019; Chen et al., 2018; Osuri et al., 2014). Centuries of close proximity to human settlements may have favoured exchanges of species and the implantation of exotic species. Intentional introductions have occurred for plants, especially trees (Aerts et al., 2016; Cardelus et al., 2019; Zhuang and Corlett, 1997). The question arises whether similar patterns can be observed in the case of unintentional introductions of species from other taxa. The high conservation value and general lack of protection of these remnant forests necessitates an evaluation beyond

species richness to capture the different dimensions of biodiversity.

Biodiversity is multidimensional and includes taxonomic, phylogenetic, and functional aspects (Lyashevskaya and Farnsworth, 2012; Naeem et al., 2016). The most commonly used single metric for assessing biodiversity is species richness. However, this simplest of all indices performs poorly as a single surrogate and does not accurately capture the three aspects of biodiversity (Lyashevskaya and Farnsworth, 2012). Studies that use two or more dimensions of biodiversity are currently surprisingly small despite the increased recognition of their significance. When two or more dimensions are assessed, they can yield contrary results, as was the case for plants, birds and insects. Species richness of birds, but not functional diversity, decreased along a successional gradient (Sayer et al., 2017). Phylogenetic diversity of tree saplings was positively related to forest age, while functional diversity showed the opposite trend (Muscarella et al., 2016). Ants declined in taxonomic and functional diversity, but not phylogenetic diversity along a habitat conversion gradient (Liu et al., 2016), and showed no change in taxonomic diversity but in functional diversity along an invasion gradient (Wong et al., 2020). Such contrary results highlight the importance of assessing biodiversity using multiple metrics encompassing functional, phylogenetic and taxonomic elements.

Ants are increasingly used for biodiversity surveys, due to their omnipresence in virtually every terrestrial ecosystem, significant contributions to ecological functioning and sensitivity to disturbances (Andersen and Majer, 2004; Folgarait, 1998; Hölldobler and Wilson, 1990; Underwood and Fisher, 2006). They perform vital ecosystem services, including pollination, pest control and decomposition (Folgarait, 1998; Hölldobler and Wilson, 1990; Philpott and Armbrrecht, 2006). Here, we use ants to evaluate the biodiversity value of cultural old-growth remnant woods, by employing multiple techniques, involving species and traits, to capture the multidimensional aspects of biodiversity. The ant fauna is compared among old-growth and secondary re-growth wooded habitats at species and community level, using taxonomic species richness and diversity, phylogenetic diversity and functional trait distribution and diversity. The following questions are addressed: 1) Is taxonomic and phylogenetic diversity higher in old-growth habitats? 2) Is this corroborated by the distribution and diversity of functional traits? 3) Do old-growth cultural woods harbour more exotic species? Based on previous literature, we anticipate that old-growth forests will be taxonomically more diverse (Alroy, 2017; Sayer et al., 2017; Whitworth et al., 2018), and that functional diversity will bolster this pattern (Rajasri et al., 2017). We expect that phylogenetic diversity will support the functional and taxonomic patterns, although this has not yet been assessed in sacred groves. Further, we expect that cultural old-growth woods will harbour more exotic species due to their close proximity to humans and the intentional introduction of exotic plants.

2. Methods

2.1. Study area

The study was carried out in Hong Kong, southeast Asia (22°09'–11°37'N, 113°50'–114°30'E). The climate is sub-tropical, with hot, wet summers (mean during summer months 28.8 °C) and cool, dry winters (15.8 °C) (Dudgeon and Corlett, 2004). Hong Kong comprises part of the Chinese mainland and several large islands, its topography is rugged, with elevational differences of up to 950 m (Zhuang and Corlett, 1997). A total of 140 sites were selected to represent old-growth cultural woods, i.e. Feng shui forest stands ($n = 18$), and secondary re-growth forests with different succession stages ($n = 100$ and $n = 22$ respectively; Fig. 1): (I) Feng shui woods date back further than 70 years and may be as old as 400 years; (II) secondary forests are the dominant vegetation form across Hong Kong as a result of the continuing large-scale deforestation until the early 1950s; (III) shrublands are generated by more recent hill fires during the last decade or two (Dudgeon and Corlett, 2004; Zhuang and Corlett, 1997).

2.2. Ant sampling

The leaf litter dwelling ant fauna was collected using Winkler sifter (Bestelmeyer et al., 2000). At each site, $4 \times 1 \text{ m}^2$ of leaf litter including top humus layer were collected from each corner of a 20x20 m area and sifted through a mesh bag with 0.6 cm mesh width. The 4 m^2 of leaf litter were subsequently dried in mini-Winkler bags for 72 h. To achieve a more complete arthropod extraction, the leaf litter in Winkler was emptied and refilled after 48 h, as described in Guénard and Lucky (2011). This method is suitable for comparisons among sampling sites with a wide variety of environmental variables, as it standardises the sampling area and extraction rate of arthropods. Sampling was conducted in five consecutive years (2014–2019) during dry days and at least one day after rain. Secondary forest sites were sampled over a 5 years' period, shrublands over a 3 years' period and Feng shui woods over a 2 years' period (Table S1), with each site sampled once. Ants were sorted and point mounted for species level identification using taxonomic literature. Undescribed species received morphospecies codes and were cross-referenced with the reference collection at our lab. In

addition, ants were classified into native and tramp species, based on current literature and expert knowledge (Leong et al., 2017). Here we use 'tramp species' rather than 'exotic species' due to the uncertainty regarding the origin of exotic species within Asia. Tramp species can be defined as species with a particular set of life history traits and association with human disturbance and spread (Hölldobler and Wilson, 1990; Passera, 1994). From a conservation perspective, tramp species can thus inform on the quality of a particular habitat due to their high affinity with heavily disturbed habitats.

2.3. Functional traits

We randomly selected five workers (minors for polymorphic species) per species to measure nine commonly used morphometric traits (Table S2). Traits were selected in accordance with earlier studies, where they had shown ecological relevance (Lee and Guénard, 2019; Nooten et al., 2019; Silva and Brandão, 2010; Weiser and Kaspari, 2006). We used Weber's length as a proxy for body size (Weber, 1938), femur length, antenna scape length, mandible width and length, clypeus length, eye length and head width and length (Table S2). The latter is less informative for dietary adaptations than overall head shape (Holley et al., 2016; Kaspari, 1993; Sarty et al., 2006), thus we analysed these measurements in form of a cephalic index (CI), calculated as: $CI = 100 \text{ HW} / \text{HL}$. All traits were normalised to body size by dividing through Weber's length (WL), thus obtaining relative trait values. Measurements were conducted using standardised procedures with the Leica Application Suite V4 Software to the nearest of 0.01 mm.

2.4. Data analyses

Ant species richness, diversity and sampling coverage at the three habitats were calculated using the standardised method of Hill numbers via incidence-based rarefaction and extrapolation (Chao et al., 2014; Chao and Jost, 2012) in *iNEXT* (Hsieh et al., 2016) in R v3.6.0 (R Development Core Team, 2019). We further compared singletons and doubletons, i.e. species occurring with 1 or 2 individuals and common and unique species. To account for the uneven number of sampling sites in the three habitats, we used relative species richness (i.e., number of species per site / by total species * 100) for all, native and tramp ants, and the proportions thereof for comparisons between habitat types. Generalized linear models based on negative binomial distributions for over dispersed data were used (glm.nb) (Zuur et al., 2010).

Community composition across the different habitats was analysed using incidence-based data in the multivariate extension of generalized linear models (manyglm) with negative binomial distribution (Warton et al., 2012) in *mvabund* (Wang et al., 2012). The multivariate Wald χ^2 test statistic was used to evaluate differences between habitats. We visualised the data with a Bayesian ordination approach in *boral* (Hui, 2016; Hui et al., 2015), which complements the manyglm analysis. A model-based approach for unconstrained ordination based on latent variable models (LVMs) was used that visualizes sites and indicator species on a low-dimensional plot and includes latent variables that account for residual correlation between species (Hui, 2016). Significance level is set at $\alpha = 0.05$ for all tests.

Phylogenetic diversity was assessed by constructing a community phylogeny. We used a published phylogenetic tree covering >14,000 ant species from (Economo et al., 2018) as a baseline, and added species collected in this study but not contained in the tree using 'add.species.to.genus' in *phytools* (Revell, 2012), and removed surplus species using 'drop.tip' in *ape* (Paradis and Schliep, 2018). The modified tree contained 170 ant species from 52 genera and nine subfamilies. Phylogenetic alpha diversity was assessed using two metrics: Faith's PD (Faith, 1992) and mean pairwise distance (MPD; Webb et al., 2002). Faith's PD calculates phylogenetic diversity based on branch lengths in a phylogenetic tree (Faith, 1992). MPD detects phylogenetic over-dispersion or clustering in a community, by comparing average branch length of each

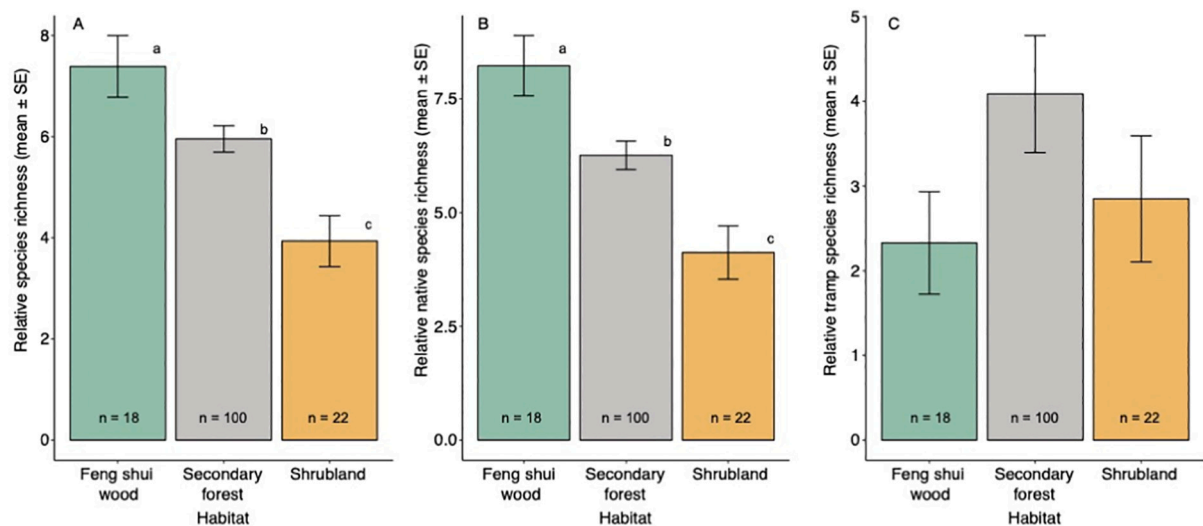


Fig. 2. Species richness for (A) all, (B) native and (C) tramp ants at three habitats. Showing mean \pm SE across sampling sites, small letters indicate statistical significance, n shows number of sites.

species (Webb, 2000; Webb et al., 2002). The two metrics were compared between assemblages using a standardised null model approach in *picante* (Kembel et al., 2010). First, null model communities were generated by randomizing the community matrix using 'independent swap' (1000 randomizations) and the R code provided by Swenson (2014). Then, the observed communities were compared to the randomized ones using standardised effect sizes (SES). Negative SES values indicate phylogenetic clustering (i.e. species are closer related than expected) and positive SES values overdispersion. Lastly, statistically significant divergence of the observed SES values from the randomized ones, and differences between habitats were evaluated using a two-sided Wilcoxon signed rank test (Bernard-Verdier et al., 2012; Lee and Guénard, 2019).

Functional traits were assessed at species and community level. Species level comparisons between habitats were conducted using single traits in glms based on gamma distribution. At the community level, functional trait diversity was assessed for each habitat using a set of single and multiple trait metrics. For single trait metrics, we calculated trait range, based on differences in highest and lowest trait values, and trait variance, based on standard deviation among trait values (Swenson, 2014). Multiple trait metrics were calculated as functional richness (FRic), mean nearest-neighbour distance (MNND) and standard deviation of nearest-neighbour distance (SDND). These measures compare the functional trait space between communities and evaluate whether they are comprised of functionally similar species, by comparing species pairs (MNND and SDND) and convex hull volume (FRic) (Swenson, 2014). FRic was calculated using 'dbFD' in *FD* (Laliberté and Legendre, 2010), MNND was calculated using 'mntd' in *picante* (Kembel et al., 2010), and SDND was calculated following the R code in Swenson (2014). Functional trait diversity metrics were then compared using the same approach as described for phylogenetic alpha diversity assessments, by using a standardised null model approach in *picante* (Kembel et al., 2010): first, expected values for each trait metric were calculated using 1000 randomizations to obtain a functional diversity baseline (i.e., "zero" or null expectation). Then, observed trait metric values were compared to expected ones using standardised effect sizes (SES). Negative SES values indicate trait convergence, i.e., traits of co-occurring species are more similar when expected. Positive SES values indicate traits divergence, i.e., traits are overdispersed and show a wider variation than expected. Statistical significance of observed vs. null expectation SES values and differences between habitats were compared using a two-sided Wilcoxon signed rank test (Bernard-Verdier et al., 2012; Lee and Guénard, 2019).

Table 1

Summary of generalized linear models (glm) for richness of (A) all, (B) native and (C) tramp ant species at three habitats. Shown are the model coefficient (Estimate), standard error (SE), z ratio, p value ($\Pr(>|z|)$) of the χ^2 -Statistic and Pseudo- R^2 .

Contrast	Estimate	SE	z ratio	$\Pr(> z)$	Pseudo- R^2
(A) All ant species					
Intercept	7.389	0.602	12.278	<0.0001	0.12
Feng shui wood - sec. forest	1.430	0.654	2.188	0.073	
Feng shui wood - shrubland	3.450	0.811	4.255	0.000	
Sec. forest - shrubland	2.020	0.602	3.359	0.002	
(B) Native ant species					
Intercept	8.228	0.714	11.531	<0.0001	0.12
Feng shui wood - sec. forest	1.970	0.776	2.539	0.030	
Feng shui wood - shrubland	4.110	0.962	4.267	0.000	
Sec. forest - shrubland	2.140	0.714	2.993	0.008	
(C) Tramp ant species					
Intercept	0.845	0.528	1.600	0.110	0.008
Feng shui wood - sec. forest	-0.563	0.572	-0.983	0.587	
Feng shui wood - shrubland	-0.202	0.709	-0.285	0.956	
Sec. forest - shrubland	0.360	0.523	0.689	0.770	

3. Results

3.1. Species richness, taxonomic diversity and frequency

A total of 20,947 individual ants from 170 species (including 23 tramp species) in 52 genera were collected across 140 sampling sites (Table S3). The leaf litter dwelling ant fauna was more diverse and species rich (i.e. absolute number of species) at secondary forests than at Feng shui woods and shrublands (Table S4, Fig. S1A). Nearly half of the species at Feng shui woods were singletons, while secondary forests harboured the highest proportion of unique species. Sampling coverage was reaching asymptote at secondary forests, but not at the other two habitats (Fig. S1B). Relative species richness (i.e. number of species at a site divided by total species * 100) differed significantly among habitats (Wald $\chi^2 = 19.06$, $P < 0.0001$; df 136,2; Fig. 2A; Table 1A). Feng shui

Table 2

Summary of negative binomial generalized linear models (glm.nb) for the proportion of (A) native and (B) tramp ant species at three habitats. Shown are the model coefficient (Estimate), standard error (SE), z value, p value (Pr(>|z|) of the χ^2 -Statistic and Pseudo- R^2 (R^2).

Contrast	Estimate	SE	z value	Pr(> z)	Pseudo- R^2
(A) Native					
Intercept	4.564	0.069	65.903	<0.0001	0.01
Feng shui wood - sec. forest	0.073	0.075	0.968	0.597	
Feng shui wood - shrubland	0.121	0.094	1.296	0.398	
Sec. forest - shrubland	0.049	0.070	0.695	0.766	
(B) Tramp					
Intercept	1.396	0.117	11.902	<0.0001	0.61
Feng shui wood - sec. forest	-0.983	0.121	-8.106	<0.0001	
Feng shui wood - shrubland	-1.313	0.130	-10.132	<0.0001	
Sec. forest - shrubland	-0.330	0.063	-5.243	<0.0001	

woods harboured on average twice as many species than shrublands, and one third more than secondary forests (Fig. 2A). The same trend was observed for relative richness of native species (Wald $\chi^2 = 18.5$, $P < 0.0001$; df 136,2; Fig. 2B; Table 1B). On the other hand, relative richness of tramp species was the lowest in Feng shui woods, but this trend was not significant (Wald $\chi^2 = 1.2$, $P = 0.56$; df 136,2; Fig. 2C; Table 1C). The majority of species were native across all sites, with highest proportions observed in Feng shui woods (95%) and lowest in shrublands (84%; Fig. S2A). The proportion of tramp species per site was significantly lower in Feng shui woods (average 4%) and the highest in shrublands (average 15%) (Wald $\chi^2 = 131.9$; $P < 0.0001$; df 136,2; Fig. S2B; Table 2).

3.2. Community composition and phylogenetic diversity

Community composition differed significantly between the three

habitats (Wald $\chi^2 = 13.22$; $P = 0.003$; df 136,2; Table S3, Table S5). Differences were largely driven by variations in the occurrences of frequent species: e.g., in Feng shui woods occurrences of *Pheidole noda/tumida*, *Hypoponera psw-cn01* and *Ectomomyrmex leeuwenhoekii* were significantly higher, but presence of *Technomyrmex horni* were reduced. Shrubbylands had fewer occurrences of *Strumigenys* species (*S. sauteri*, *S. canina* and *S. rallahrhina*), and more *Tapinoma melanocephalum* (tramp species). Some unique species in secondary forests contributed significantly to compositional differences between habitats, these include *Camponotus* sp. cf. *irritans hongkongensis*, *Monomorium chinense*, *P. tibodana* and the tramp species *Tetramorium lanuginosum* and *P. parva*, (Fig. 3). None of the ant communities diverged significantly from randomized ones for any of the two phylogenetic alpha diversity measures, nor was there a significant difference between habitats (Fig. S3).

3.3. Species level functional traits

Ant body size varied 18-fold, ranging from 0.29–5.32 mm. Ants in Feng shui woods (0.91 ± 0.04 mm) were on average similar sized to those in secondary forests (mean \pm SE, 0.90 ± 0.02 mm), and 7% larger than in shrublands (0.84 ± 0.05 mm), but not significantly so (Wald $\chi^2 = 0.91$; $P = 0.63$; Fig. S4A). Four of the eight morphometric traits were significantly different among the three habitats: Relative leg length varied 3-fold (0.46–1.29 mm). Feng shui woods harboured on average significantly shorter legged ants (by 5%) than shrublands (Wald $\chi^2 = 6.4$; $P = 0.04$; Fig. 4A; Table 3A). Cephalic index (CI) varied 2.5-fold (47–121) and ants in Feng shui woods had significantly (by 4%) larger CI (i.e. wider heads) than in shrublands (Wald $\chi^2 = 6.9$; $P = 0.03$; Fig. 4B; Table 3B). Relative antennae scape length varied 3-fold (0.33–1.10 mm), and ants in Feng shui woods had significantly shorter (by 5%) antennae scapes than in shrublands (Wald $\chi^2 = 8.5$; $P = 0.01$; Fig. 4C; Table 3C). Relative eye length varied 30-fold (0.01–0.30 mm). Ants in Feng shui woods had on average significantly smaller eyes (by 5%) than in secondary forests, and by 16%, than in shrublands (Wald $\chi^2 = 22.3$; $P < 0.0001$; Fig. 4D; Table 3D). No significant differences were found for relative clypeus length, mandible width and length (Fig. S4B–D).

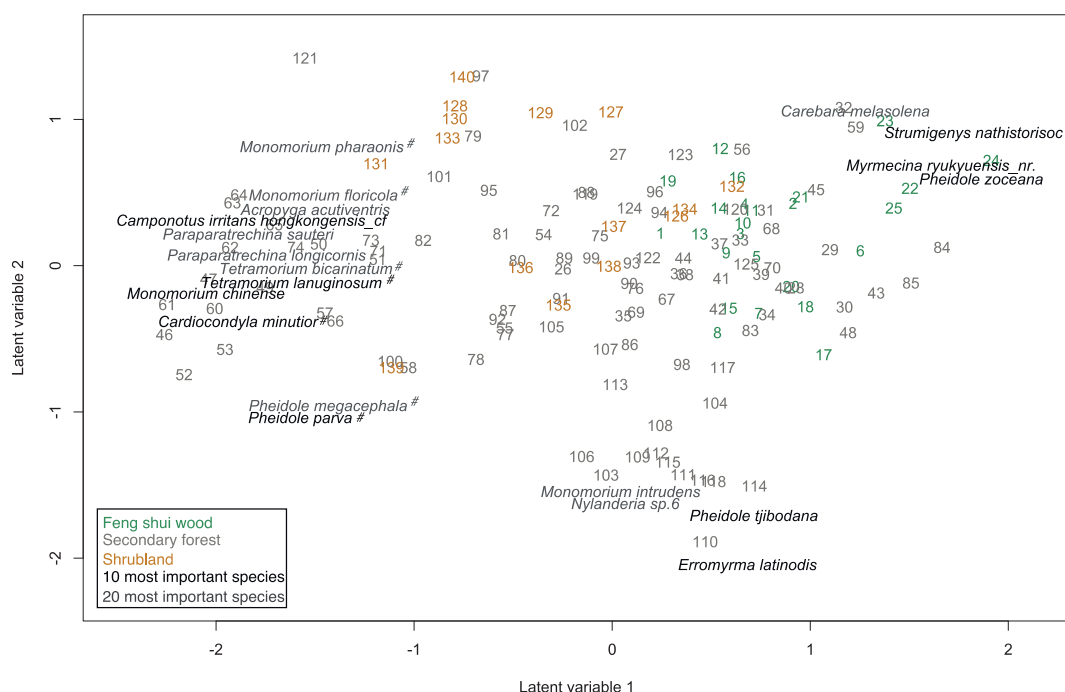


Fig. 3. Unconstrained ordination based on latent variable models (LVMs) for ant community composition at three habitats. Showing numbered sites and the most important 20 species. # indicates tramp species.

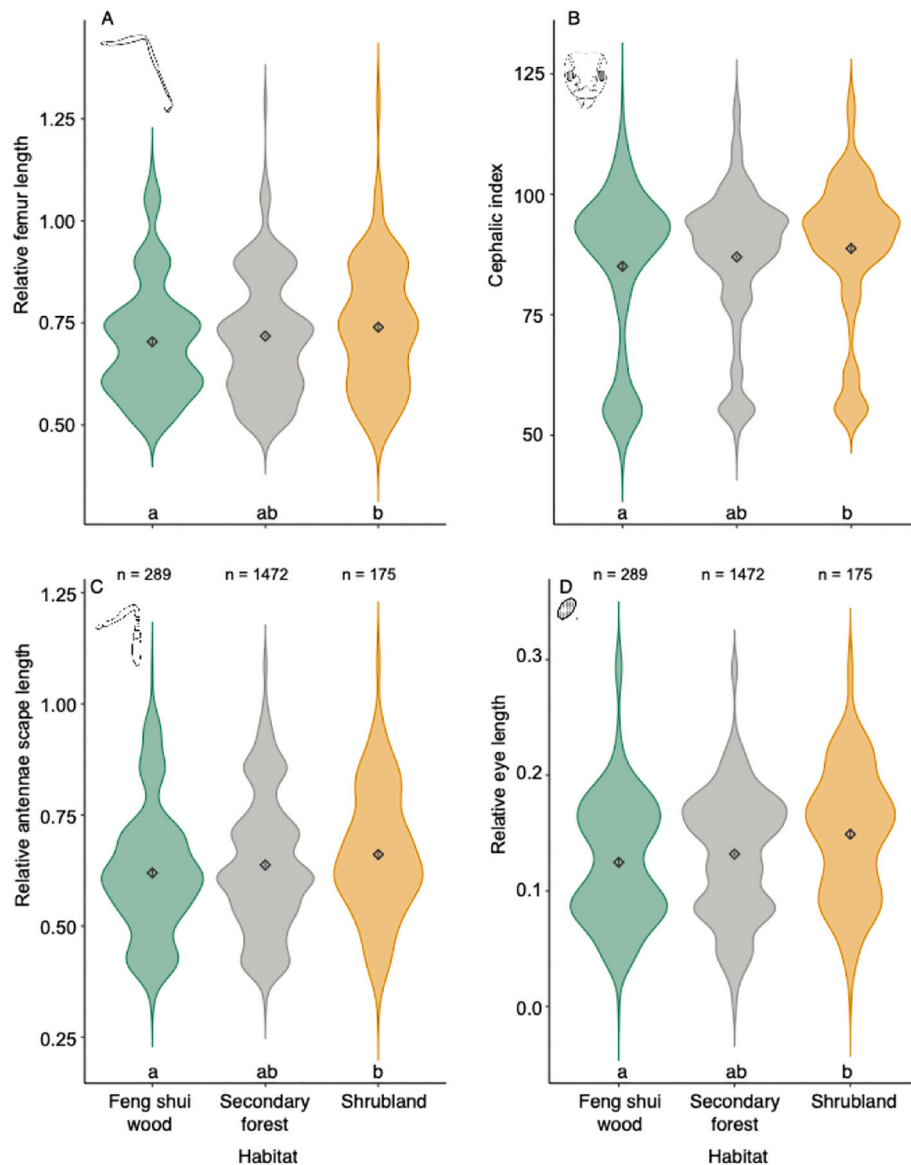


Fig. 4. Violin plots showing kernel probability density plots of four ant functional traits at three habitats, (A) relative femur length, (B) cephalic index, (C) relative antennae scape length and (D) relative eye length. Black bars show mean \pm SE, n shows sample sizes, small letters indicate statistical significance.

3.4. Community level functional traits

Single trait metrics, estimated as variance and range, deviated significantly from the null expectation for four of eight traits. In Feng shui woods, communities consisted of ants with significantly higher CI variance than expected ($P = 0.043$), and lower range and variance of relative mandible length ($P < 0.05$; Fig. 5). In shrublands, communities were comprised of ants with significantly narrower variance and range than expected, for relative clypeus ($P = 0.038$ and 0.0294 , respectively) and mandible length ($P = 0.005$; Fig. 5). Trait variance and range differed significantly between shrublands and the other habitats for three of eight traits. In shrublands, ants had significantly narrower relative clypeus length, mandible length and width ($p < 0.01$), and CI ($P = 0.031$; Fig. 5). Multiple trait metrics diverged significantly from the null expectations in three instances. Shrubland ant communities occupied a significantly smaller functional trait space (FRic: $P = 0.038$) with lower filling density (MNND: $P = 0.048$; Fig. 6), while ant communities in secondary forests had a significantly more evenly filled functional trait space (SDND: $P = 0.049$; Fig. 6).

4. Discussion

The dramatic reduction of primary forest habitats and diminishing biodiversity over the last decades has highlighted the need for evaluating the conservation value of cultural old-growth woods within highly disturbed landscapes. Here, we assessed the biodiversity value of Feng shui woods using the leaf litter dwelling ant fauna collected over five years. Complementary metrics were used to compare taxonomic, phylogenetic and functional diversity of ant assemblages among old-growth and two types of re-growth woody habitats along a succession stage. Overall, ant assemblages in Feng shui woods presented higher species richness at local scale and were more resilient to invasions by tramp species than the other two habitats. Functional traits also differed between habitats, with Feng shui woods harbouring ants with smaller eyes, narrower heads and shorter appendages. While phylogenetic diversity was similar among the three habitats, functional diversity for some traits was higher in Feng shui woods than in re-growth habitats.

Table 3

Summary of generalized linear models (glms) for (A) relative femur length (B) cephalic index, (C) relative antennae scape length and (D) relative eye length at three habitats. Shown are the model coefficient (Estimate), standard error (SE), *t* value, *p* value ($\Pr(>|t|)$) of the χ^2 -Statistic, df 2037,2.

Contrast	Estimate	SE	t value	$\Pr(> t)$
(A) Relative femur length				
Intercept	1.4204	0.0170	83.4840	<0.0001
Feng shui wood - sec. forest	0.0269	0.0186	1.4520	0.3144
Feng shui wood - shrubland	0.0682	0.0269	2.535	0.0302
Sec. forest – shrubland	0.0412	0.0221	1.866	0.1485
(B) Cephalic index				
Intercept	0.0118	0.0001	97.4500	<0.0001
Feng shui wood - sec. forest	0.0003	0.0001	1.9800	0.1172
Feng shui wood - shrubland	0.0005	0.0002	2.5600	0.0283
Sec. forest – shrubland	0.0002	0.0002	1.4580	0.3116
(C) Relative antennae scape length				
Intercept	1.6144	0.0223	72.5660	<0.0001
Feng shui wood - sec. forest	0.0454	0.0242	1.874	0.1463
Feng shui wood - shrubland	0.1016	0.0348	2.917	0.0099
Sec. forest – shrubland	0.0562	0.0285	1.975	0.1185
(D) Relative eye length				
Intercept	0.1247	0.0032	39.0490	<0.0001
Feng shui wood - sec. forest	−0.0072	0.0035	−2.0490	0.1006
Feng shui wood - shrubland	−0.0243	0.0052	−4.6700	0.0001
Sec. forest – shrubland	−0.0171	0.0043	−3.9450	0.0002

4.1. Are Feng shui woods biodiversity reservoirs for local species?

Taxonomic species richness, when standardised for sampling effort, was higher in Feng shui woods than in successional habitats. This supports the significance of old-growth woods in having higher biodiversity value than secondary re-growth forests (Alroy, 2017; Sayer et al., 2017; Whitworth et al., 2018). Remnant woods can be biodiversity hotspots in human influenced landscapes for many different taxa, including plants (Aerts et al., 2016; Hu et al., 2011; Nooten et al., 2018; Salick et al., 2007), ants (Nooten et al., 2019; Yates and Andrew, 2011), moths (Lintott et al., 2014) and birds (Bhagwat et al., 2005). Here, the presence of predator specialists like *Strumigenys*, *Carebara*, and *Ectomomyrmex* (Hölldobler and Wilson, 1990) add unique conservation value to Feng shui woods. This corroborates the importance of Feng shui woods in Hong Kong (Dudgeon and Corlett, 2004) and highlights their conservation value not only for rainforest trees but also for the local insect fauna.

4.2. Fewer tramp species in Feng shui woods

Ant assemblages in Feng shui woods had the highest proportion of native species and surprisingly few ($3\times$ less) tramp species. This scarcity of tramp species is somewhat counterintuitive. Indeed, Feng shui woods are not randomly distributed but are usually found in lowland and at the edge of century-old human settlements (Zhuang and Corlett, 1997). In regions like Hong Kong, marked by important commercial activities and the planting of exotic tree species in Feng shui woods, one could expect that tramp ants would have had plenty of time to set foot in those habitats. Their relatively small size (<14 ha) (Zhuang and Corlett, 1997) may have offered potential edge effect, usually perceived as more prone to invasions (Bolger, 2007). However, our results show the opposite. This is encouraging from a conservation perspective as it shows that historically human activities did not necessarily trigger an increase in tramp species, or alternately that some habitats act as potential barrier to their spread. Even in other parts of the world, highly fragmented old-growth forests in anthropogenically altered landscapes can harbour a high proportion of native and few exotic species, as is the case for plant species in remnant woods in Australia (Nooten et al., 2018), church forests in Ethiopia (Merkonnen et al., 2019) and Chinese Feng shui woods (Hu et al., 2011). This emphasizes the importance of these sites as refuges for native species.

4.3. Ants with shorter appendages in Feng shui woods

Ants in Feng shui woods had relatively smaller eyes, narrower heads and shorter legs and antennae scapes, while shrublands harboured longer legged ants with larger eyes and longer antennae scapes. This may indicate that ant assemblages in Feng shui woods are predominantly composed of species with a leaf litter foraging lifestyle, which may be largely absent in the young re-growth habitat. Feng shui woods may have retained more of this specialist fauna associated with the better topsoil layer than the two woody re-growth habitats. As the leaf litter and humus layer has been severely eroded and washed away due to the prolonged long-term deforestation across Hong Kong since the 16th or 17th centuries (Dudgeon and Corlett, 2004). The presence of a leaf litter ant community is beneficial as these facilitate nutrient cycling and decomposition and thus can minimise the spread of diseases through rotten carcasses (Del Toro et al., 2012; McGlynn and Poirson, 2012). A shift in species traits when comparing old- with re-growth habitats was also evident for other taxa. Forest tree communities were dominated by species with small seeds in early succession and shifted towards species with large seeds in mature habitats (Muscarella et al., 2016), and seed dispersing rainforest birds were larger in pristine than in successional forest habitats (Emer et al., 2018).

4.4. Phylogenetic and functional diversity in Feng shui woods

Both, phylogenetic and functional diversity in Feng shui woods did not diverge from randomized or expected communities. This might indicate that these leaf litter ant communities underly stochastic assembly processes at both dimensions. Furthermore, these phylogenetically and functionally even communities might also provide some level of resistance to disturbances, which is evident by the reduced number of tramp species in Feng shui woods. There was no difference in phylogenetic diversity between the three habitat types. A potential explanation for the lack of differences could be the resolution of the phylogenetic tree being at the genus and not species level, which may be insufficient to capture differences across natural habitats. Functional diversity in shrublands, the youngest successional habitat, however was clustered. These communities occupied a smaller trait space (low FRic value) with lower filling density (low MNND value). It is possible that a more generalist set of ant species occupies shrublands, and that leaf litter specific species with their unique set of traits are not yet recruited. Elsewhere, functional diversity was lower in primary or old-growth than in secondary forests, for birds (Sayer et al., 2017) and trees (Muscarella et al., 2016), but not for ants (Bihn et al., 2010). This reinforces the need to protect cultural old-growth forests as these provide refuges for native species across the species-poor human-influenced landscape.

The present study, as any, has its limitations. The sample size of Feng shui woods and shrublands is smaller when compared to secondary forests. Given that the sampling coverage in both habitats (Feng Shui woods and shrublands) does not reach asymptote, these might be under-sampled possibly incurring a sampling bias. It should be noted, however that the 20 most common species occur in all habitats, with secondary forests presenting more singletons and doubletons for more rarely collected species. Increasing sampling effort would have increased the probability to get more rare species (Gotelli and Colwell, 2001), but not necessarily more tramp species which usually are more common and widespread, and thus strengthening our outcome. Another point of consideration is the classification of species into tramp species which may evolve in the future and leads to new consideration on the magnitude in the settlement of these species within the different habitats studied here. In this study a number of species were given morphospecies code due to their uncertain taxonomy and presence of several species complex (e.g. *Dolichoderus sibiricus* complex, *Diacamma* sp.). Many of these species belong to genera which are either not known to get established into new regions (e.g. *Carebara*, *Myrmecina*) or are poor invaders generally (e.g. *Crematogaster*). While our taxonomic and

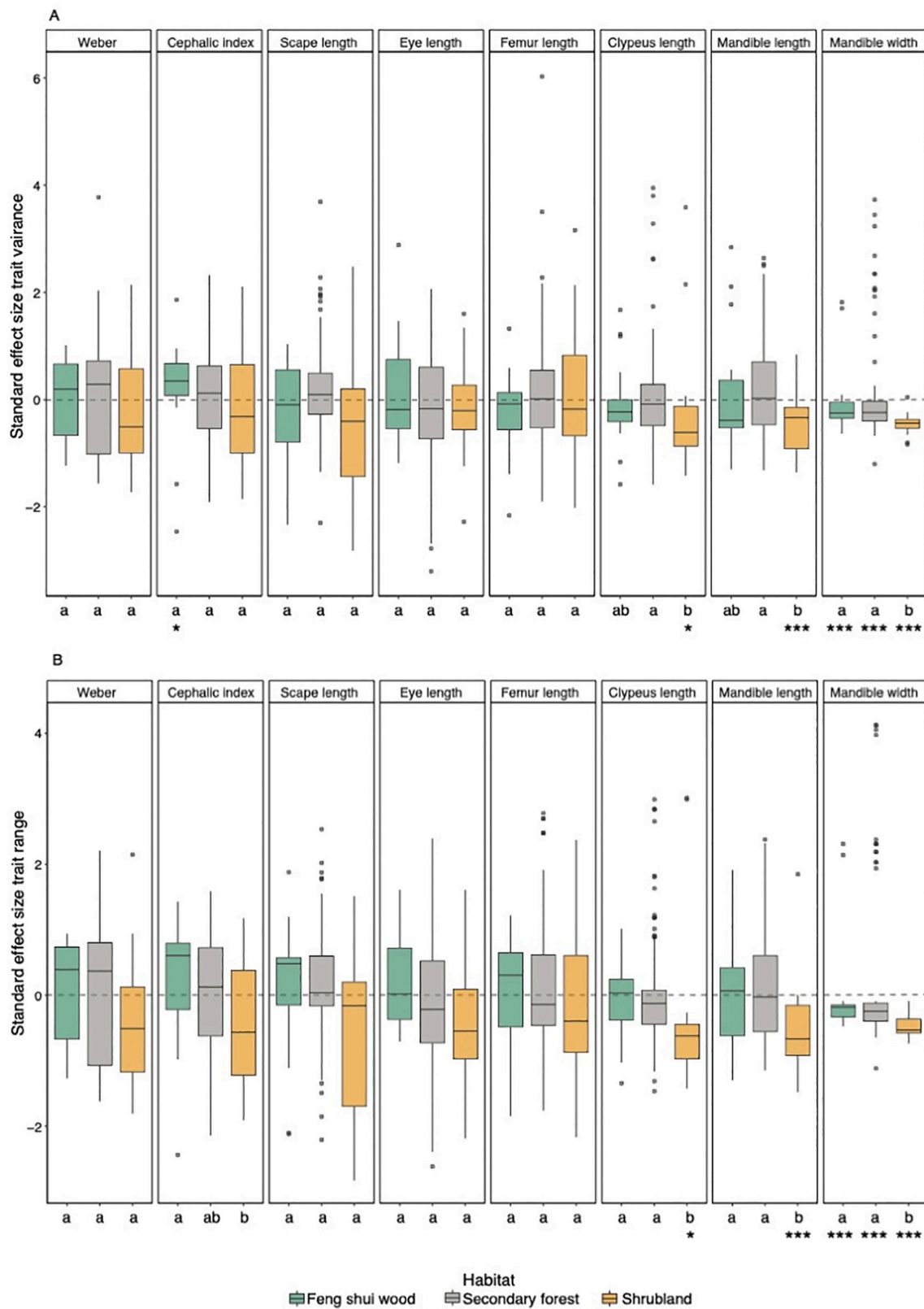


Fig. 5. Community level (A) variance and (B) range for seven functional traits of ant assemblages at three habitats (Feng shui woods, secondary forests, and shrublands). Showing standard effect sizes (SES) relative to a null model of a randomized assemblage. Null model expectation shown by dashed horizontal line. Negative SES values indicate smaller trait distribution when expected. Significant differences (Wilcoxon signed rank test) between habitats indicated by small letters, and to the null model by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

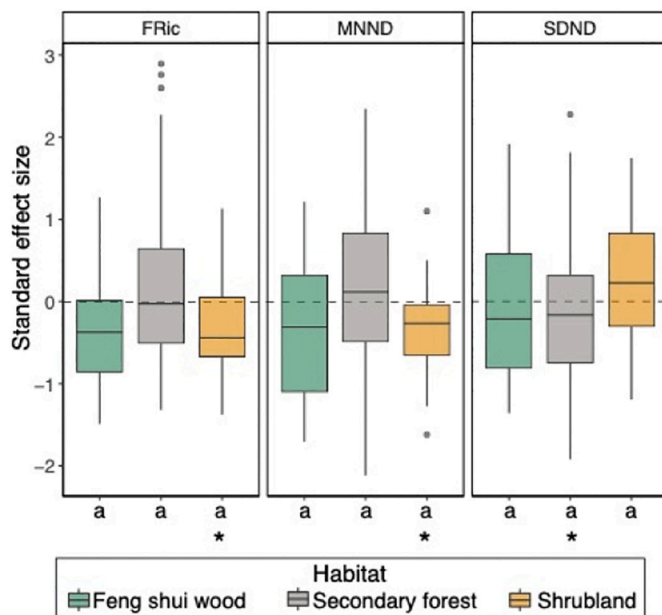


Fig. 6. Community level multiple functional trait metrics (FRic, MNND, SDND) for ant assemblages at three habitats (Feng shui woods, secondary forests, and shrublands). Standard effect sizes (SES) relative to a null model of a randomized assemblage is shown. Null model expectation indicated by dashed horizontal line. Negative SES values indicate trait clustering, positive values trait overdispersion. Significant differences (Wilcoxon signed rank test) between habitats indicated by small letters, and to the null model expectation by $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

ecological knowledge of a number of those morphospecies remain limited, we cannot fully exclude for some of these species to represent more widespread tramp species, in particular for genera such as *Hypoponera*, *Monomorium* or *Nylanderia* known to possess several tramp species. This, however, seems rather unlikely as the majority of those morphospecies are unknown from Hong Kong urban and disturbed habitats which usually host most tramp species (unpublished data). Finally, for the morphospecies belonging to genera with tramp species, it should be noted that in their majority, those were not encountered within Feng shui woods or were species poor.

5. Conclusions

Our results show that despite the relatively small size of old-growth Feng shui woods in Hong Kong, they harbour a taxonomically species rich ant fauna, that is functionally and phylogenetically diverse, and encompasses native specialist species. The scarcity of tramp species in Feng shui woods in spite of their proximity to human settlements illustrates their ecological resilience to disturbances. Our study highlights the conservation value and urgent need for a better protection of largely overlooked old-growth forest fragments in human influenced fragmented landscapes.

CRediT authorship contribution statement

Sabine S. Nooten: conceptualization, writing- original draft preparation, visualization, data curation, formal analysis. **Roger H. Lee:** writing- reviewing and editing, formal analysis, investigation. **Benoit Guénard:** conceptualization, writing- reviewing and editing, funding acquisition, supervision.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109286>.

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