



## RESEARCH PAPER

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# Island area, not isolation, drives taxonomic, phylogenetic and functional diversity of ants on land-bridge islands

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**Abstract**

**Aim:** To explore the impact of island area and isolation on multiple dimensions of ant biodiversity (taxonomic, phylogenetic and functional diversity) and the underlying processes of community assembly on islands.

**Location:** Thousand Island Lake, Zhejiang, China, created by dam construction in 1959.

**Taxon:** Ants.

**Methods:** We sampled ants on 33 islands, built a species-level phylogenetic tree and measured five morphological traits of all species collected to estimate taxonomic, phylogenetic and functional diversity. We used multiple linear regression models and null models to examine the relationships between diversity metrics and island variables (area and isolation).

**Results:** We recorded 97 ant species on the study islands. We verified positive diversity–area relationships for species richness, phylogenetic diversity and functional diversity. However, although functional and phylogenetic community structure were indistinguishable from random communities, phylogenetic structure tended to be clustered, whereas functional structure tended to be overdispersed. Additionally, we found the structure of ant communities shifted from phylogenetic and functional clustering on smaller islands to phylogenetic and functional overdispersion on larger islands.

**Main conclusions:** Our results support the hypothesis that environmental filtering is the dominant process structuring ant communities on smaller islands, and that competitive exclusion becomes more important on larger islands. Thus, island area acts as an important filter even though ant community structure on the study islands was indistinguishable from random communities. Moreover, our results show that environmental filtering influences phylogenetic community structure of ants, whereas competitive exclusion influences functional community structure of ants. These findings highlight the need to examine both phylogenetic and functional diversity in order to understand the mechanisms that govern the assembly of natural communities on islands.

**KEYWORDS**

ants, community structure, competitive exclusion, environmental filtering, island biogeography, morphological traits, phylogeny, Thousand Island Lake

## 1 | INTRODUCTION

Inspired by his travels and ant collecting in the South Pacific, Edward O. Wilson worked closely with Robert H. MacArthur to elucidate the classic Theory of Island Biogeography (hereafter, TIB; MacArthur & Wilson, 1967), a general model to explain the number of species on islands. TIB posits an equilibrium model of ecological communities, through a colonization–extinction dynamic which implicitly assumes that species are equally different from each other and are randomly sampled from a regional pool (MacArthur & Wilson, 1967). Although TIB briefly considered the importance of traits (such as dispersal ability; table 8 on page 81 in MacArthur & Wilson, 1967), the verbal model did not consider that species have different evolutionary backgrounds and possess distinct functional roles (i.e. phylogenetic diversity and functional diversity). Recent work has begun to incorporate the functional and phylogenetic dimensions of species into TIB (e.g. Jacquet, Mouillot, Kulbicki, & Gravel, 2017; Ottaviani et al., 2020 for the functional dimension; Pyron & Burbrink, 2014; Weigelt et al., 2015 for the phylogenetic dimension). However, efforts to understand the drivers of community assembly on islands that consider simultaneously both the phylogenetic and functional differences among species are limited (Patiño et al., 2017; but see Si et al., 2017; Ross, Friedman, Janicki, & Economo, 2019). Here, we use TIB to assess the phylogenetic and functional community structure of the ant fauna on an island archipelago in subtropical China.

Phylogenetic diversity captures the evolutionary relationships among species and represents a comprehensive estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares, Kozak, Fine, & Kembel, 2009). In contrast, functional diversity provides insights into niche differences between species because traits used to measure functional diversity often incorporate a wide range of functional roles that a species might play in a community (Petchey & Gaston, 2002). If functional traits affect colonization–extinction dynamics on islands, these traits may then influence co-occurrence patterns among island faunas (Whittaker et al., 2014). In general, closely related taxa are likely to be more ecologically similar, and one might expect that phylogenetic diversity could therefore serve as a proxy for functional diversity (Graham, Parra, Rahbek, & McGuire, 2009). However, the phylogenetic pattern does not always reflect the functional pattern (Sobral & Cianciaruso, 2016). This disparity can be the case when the selected functional traits do not have a strong phylogenetic signal (Cadotte, Carboni, Si, & Tatsumi, 2019), which may vary among different taxa and spatial scales (Krasnov, Poulin, & Mouillot, 2011). Thus, considering both the phylogenetic and functional structure of communities should help us understand the relative importance of the different mechanisms shaping community structure on islands (Sobral & Cianciaruso, 2016).

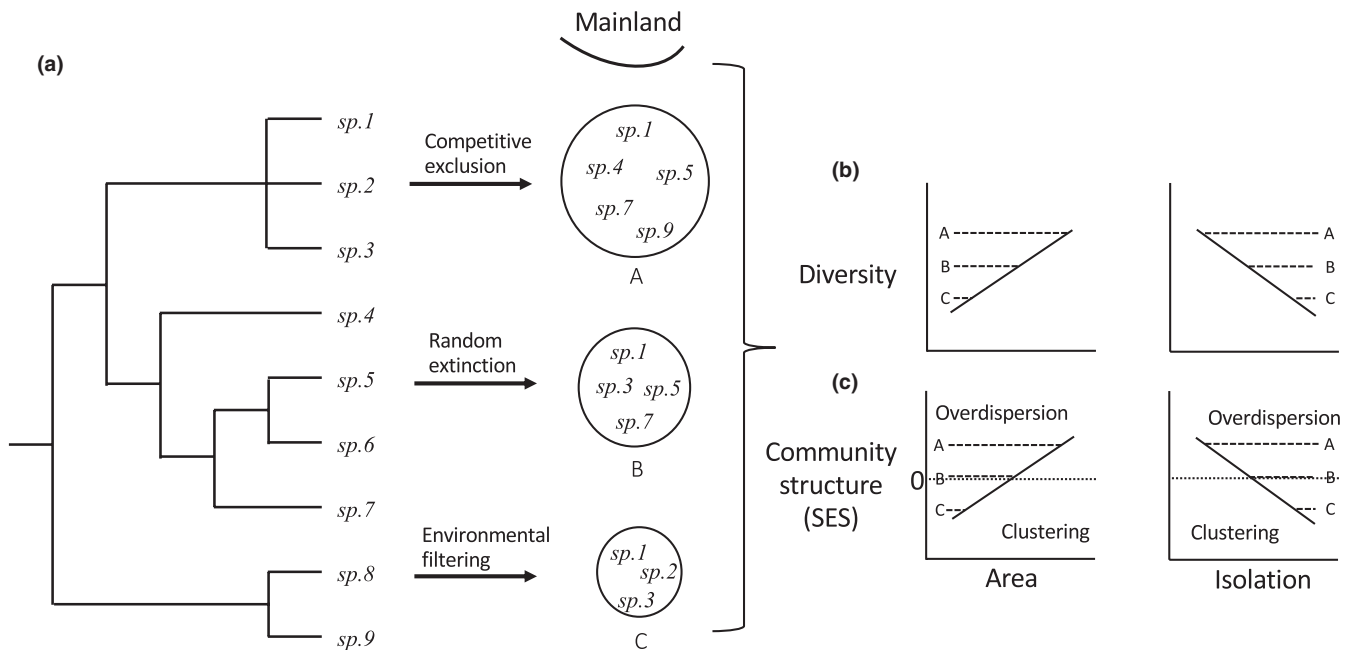
Under the equilibrium model of TIB, species richness (SR) is expected to increase with island area and decrease with isolation (figure 8 on page 22 in MacArthur & Wilson, 1967). Similarly, we might expect phylogenetic and functional diversity to also increase with

island area and decrease with isolation because each additional species in a community will potentially add more phylogenetic or functional information (Si et al., 2017; Whittaker et al., 2014). However, even though the positive diversity–area and negative diversity–isolation relationships could be intuitively predicted, the processes that drive functional and phylogenetic structure on different islands may be distinct. Community assembly on islands may be driven by a variety of processes, including environmental filtering, competitive exclusion and random extinction (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Figure 1a).

On smaller islands, abiotic conditions are often more extreme and homogeneous than on larger islands, such that species that are not well-adapted to those conditions can face higher extinction pressure (Liu et al., 2019). Where this occurs, one may expect environmental filtering to play an important role in shaping communities, favouring a subset of species that share similar functional traits (e.g. generalist diet or thermal tolerance; Figure 1a) that promote success in these conditions (Kraft et al., 2015). Under these circumstances, functional community structure is therefore expected to be clustered. Furthermore, if those clustered traits are also evolutionarily conserved, the community will likely also show phylogenetic clustering (Figure 1c). Conversely, larger islands with diverse habitats can provide a wide range of niches that might allow species from different lineages and/or that possess distinct functional traits to co-occur. Where this is true, interspecific competition among closely related species might be expected to be greater than environmental filtering (Cavender-Bares et al., 2009; Sobral & Cianciaruso, 2016), resulting in close relatives being competitively excluded from the community (Figure 1a). Consequently, the coexistence of species on large islands is predicted to show a high degree of functional and/or phylogenetic overdispersion (Figure 1c).

Similar to the effect of island area, the isolation of islands may also influence the assembly of communities (Jones, Bunnefeld, Jump, Peres, & Dent, 2016). For example, only species with strong dispersal abilities may have the opportunity to colonize remote islands (Moore, Robinson, Lovette, & Robinson, 2008), leading to a clustered community structure on these distant islands (Figure 1a,c). Islands close to the mainland (i.e. close to the species pool) are more likely to have frequent dispersal events from taxa with a wide range of (often weaker) dispersal abilities. The subsequent colonization success of arriving species is likely to depend more on their competitive ability than on their dispersal ability. Therefore, we may expect community structure to range from phylogenetic and functional clustering on smaller and more distant islands to phylogenetic and functional overdispersion on larger and less isolated islands (Figure 1c).

Ants (Hymenoptera: Formicidae) were an early model for testing the classic TIB (Cole, 1983; MacArthur & Wilson, 1967), and they are an ideal taxon for assessing biodiversity patterns and community assembly on islands. They are highly diverse and abundant (Hölldobler & Wilson, 1990) and play a wide range of ecological roles, including soil movement, decomposition and seed dispersal (Toro, Ribbons, & Pardini, 2012). However, to date, only a few studies have examined ant community structure from multiple dimensions (Donoso, 2014;



**FIGURE 1** Models of phylogenetic and functional community structure and the effects of island area and isolation. We illustrate (a) a hypothetical phylogenetic (or functional) tree and three potential mechanisms shaping the ant communities on three different islands (A, B and C). Circles indicate islands, and the size and position of each island indicate the island area and distance to the mainland at the top. We also illustrate (b) the predicted patterns of diversity and (c) community structure (as measured by the standardized effective size; SES) of ant species as a function of island area and isolation. According to the Theory of Island Biogeography, taxonomic, phylogenetic and functional diversity should increase with island area and decrease with island isolation. Communities on smaller and more remote islands may be highly clustered because the subset of species either shares similar functional traits or similar evolutionary histories (a). Conversely, communities on larger and less isolated islands may be overdispersed because these islands provide more potential habitats and niches, and closely related species would compete for resources, resulting in close relatives being competitively excluded from the community. Additionally, we may expect a shift from clustering to overdispersion as increasing island area and decreasing isolation (c)

Liu, Guénard, Blanchard, Peng, & Economo, 2016). Recent work has examined ant phylogenetic and functional diversity along elevational gradients (Machac, Janda, Dunn, & Sanders, 2011; Smith, Hallwachs, & Janzen, 2014), among habitats types (Fichaux et al., 2019; Liu et al., 2016) or along climatic gradients (Gibb et al., 2018; Liu, Dudley, Xu, & Economo, 2018). To the best of our knowledge, no study has examined how the phylogenetic and functional diversity of ant communities vary among islands.

Reservoir islands (or land-bridge islands) are an ideal platform for testing mechanisms of community assembly because the islands are formed simultaneously by dam construction and the water matrix clearly shows the edge of islands (Weigelt et al., 2015). In this study, we took advantage of a reservoir island system, the Thousand Island Lake (TIL) located in subtropical China, to examine how island area and isolation influence multiple dimensions of ant biodiversity and community structure. Specifically, we sampled ants on 33 islands that differed in area and isolation, developed a proposed species-level phylogeny of all ant species in our study system to overcome the shortcomings of only considering the genus-level data in previous studies (Donoso, 2014; Liu et al., 2016; Machac et al., 2011) and measured morphological traits for each species. In this study, we predicted that (a) positive diversity–area and negative diversity–isolation relationships would be found for each dimension of biodiversity (Figure 1a,b) and (b) environmental filtering would be

the dominant process in structuring ant assemblages on smaller and more isolated islands but that competitive exclusion would become more important on larger and less isolated islands (Figure 1a,c).

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and island selection

This study was carried out in TIL, a land-bridge island system located in Zhejiang Province, southeastern China (29°22'–29°50'N, 118°34'–119°15'E), formed in 1959 by the construction of a dam. The lake area is approximately 580 km<sup>2</sup> and includes more than 1,000 islands (each of which was previously a hilltop before flooding). The region is in the subtropical zone and has a typical subtropical monsoon climate with significant seasonal changes. The average annual temperature is 17.0°C. Daily temperature ranges from –7.6°C in January to 41.8°C in July. The annual precipitation is 1,430 mm, mainly concentrated in the rainy season between April and June (Si, Pimm, Russell, & Ding, 2014). The dominant vegetation on the islands is secondary forest, mostly of *Pinus massoniana* (Liu et al., 2019).

We selected 33 islands representative of the range in island area and isolation that occurs among most islands in the archipelago (Figure 2; Table S1). Island area and isolation (measured as the

shortest shore-to-shore distance to the mainland) were calculated in ArcGIS 10.4 (<https://support.esri.com/zh-cn/products/desktop/arcgis-desktop/arcmap/10-4-1>) for a water level of 100 m a.s.l.

## 2.2 | Data collection

### 2.2.1 | Ant sampling

On each island, we set up between one and nine transect lines, proportional to the natural logarithm of island area (e.g. one transect on islands <3 ha, nine transects on the largest island; Table S1). Transect length was up to 200 m (on larger islands). On smaller islands <200 m long, the transect was laid parallel to the longest axis. Transects on the same island were separated by at least 400 m to minimize sampling the same ant colonies. Each transect was sampled using pitfall traps, hand collection and Winkler extraction in a random order (Agosti, Majer, Alonso, & Schultz, 2000; see Appendix S1 for sampling details).

All ant specimens were identified to species level when possible, or to morphospecies. Specimens are preserved in the College of Life Sciences, Zhejiang University, China.

### 2.2.2 | Phylogenetic construction

A phylogeny was constructed using BEAST v. 1.10.4 (Drummond & Rambaut, 2007), based on three nuclear genes (18S, 28S and wingless; see Appendix S1 for more details). The resulting tree was visualized with FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/>) and used for all

subsequent analyses (Figure S2). All sequences were newly identified in the present study and were deposited in GenBank with accession numbers MN159606–MN159908 (Table S3).

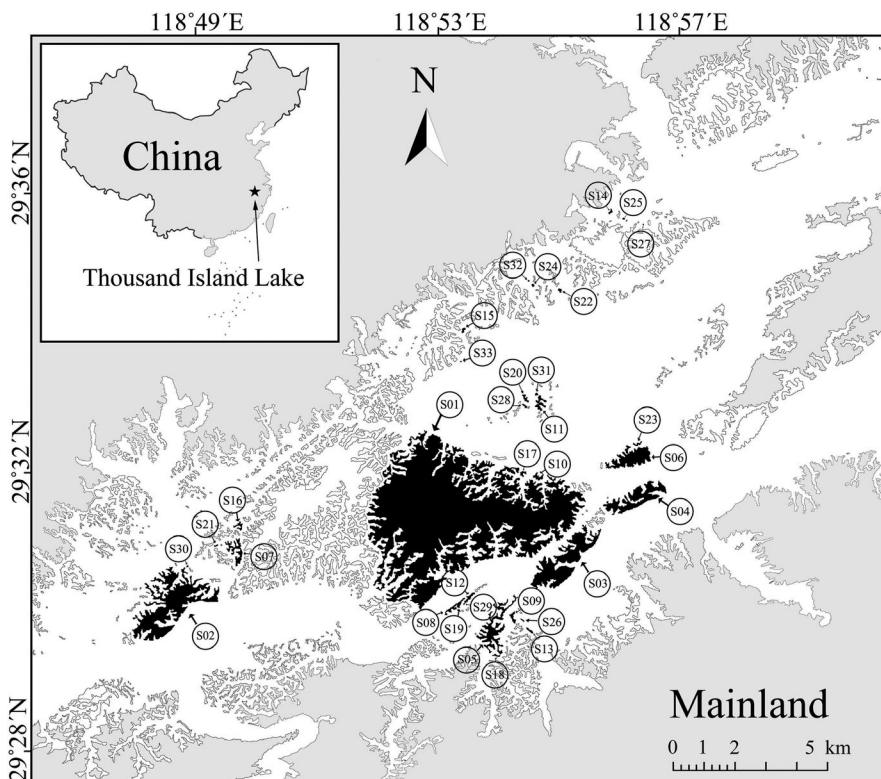
### 2.2.3 | Selection of morphological traits

We chose five morphological traits related to ant diet, habitat preferences and foraging strategies: Weber's length (AL), relative eye width (ED), relative leg length (LL), relative mandible length (ML) and relative scape length (SL). By focusing on morphological traits, we inevitably ignored some important aspects of ant ecology, such as nest preference or thermal tolerance (Arnan, Arcoverde, Pie, Ribeiro-Neto, & Leal, 2018). However, direct links between morphological traits and functions have been observed in ants (Table S4). See Appendix S1 for measurement of morphological traits.

## 2.3 | Data analyses

### 2.3.1 | Diversity metrics

To test our first prediction, we calculated three dimensions of biodiversity for which we tested for a positive diversity–area and a negative diversity–isolation relationships. For the taxonomic diversity metric, we used SR, calculated by pooling all ant individuals and species sampled by the three methods (pitfall traps, hand collection and Winkler extraction). For the phylogenetic diversity metrics, we calculated Faith's phylogenetic diversity (hereafter, PD; the sum of the branch length of



**FIGURE 2** The 33 study islands (in black) in the Thousand Island Lake region, Zhejiang, China (modified from Si et al., 2014). Islands are labelled as a function of decreasing areas from S01 to S33



species within a community) and the mean pairwise distance (MPD; Faith, 1992; Webb, Ackerly, McPeck, & Donoghue, 2002). PD and MPD were calculated using the *pd* and *mpd* functions in the 'picante' package in R (Kembel et al., 2010). For comparison with phylogenetic diversity metrics, we calculated Petchey and Gaston's functional diversity (hereafter, FD; total branch length of the functional dendrogram that species are clustered in trait space) and the functional equivalent of MPD (hereafter FD\_MPD; Arnan et al., 2018; Petchey & Gaston, 2002). The functional trait-based dendrogram was generated with a Gower dissimilarity distance matrix from the scaled and centred trait values, applying the unweighted pair group method with arithmetic mean (UPGMA). FD was calculated using *alpha* function in the 'BAT' package in R (Cardoso, Rigal, & Carvalho, 2015) and FD\_MPD was calculated using the same R functions as MPD, except that the trait-based dendrogram rather than phylogenetic tree was used.

### 2.3.2 | Community structure and null models

To test our second prediction that environmental filtering dominated ant community structure on smaller and more isolated islands compared to competitive exclusion on larger and less isolated islands, we used a 'shuffling tip' null modelling approach. This method tested whether the observed phylogenetic and functional diversity metrics differed from communities assembled at random relative to the observed phylogenetic or functional tree. We randomly shuffled the names of the species on the tips of the two trees 999 times but retained the structure of the phylogenetic or functional tree (Swenson, 2014). Next, we calculated the standardized effect sizes (SES) of the phylogenetic and functional diversity metrics (i.e. *sesMPD* and *sesFD\_MPD*) to estimate ant community structure, as follows:

$$SES = (\text{Obs} - \text{Mean}_{\text{null}}) / \text{SD}_{\text{null}}$$

where Obs is the observed phylogenetic or functional diversity on each island, and  $\text{Mean}_{\text{null}}$  and  $\text{SD}_{\text{null}}$  are the values of the mean and standard deviation of 999 randomized communities for phylogenetic or functional diversity on each island. SES is a metric of the randomness of community structure: positive values of SES indicate community overdispersion, and negative values indicate community clustering (Webb et al., 2002). Values greater than 1.96 or less than -1.96 indicate significantly community clustering or overdispersion ( $\alpha = 0.05$ ).

### 2.3.3 | Sampling completeness and efforts

To test the completeness of sampling on the larger islands with a total transect length  $\geq 200$  m (Table S1), we calculated species' frequency (how many times a species was captured in the pitfall traps or Winkler extraction) and abundance (total number of individuals captured by hand collection) for each island. The sampling completeness curves were calculated using the *iNEXT* function in the 'iNEXT' package in R (Hsieh, Ma, & Chao, 2016).

To test whether differences in sampling effort among islands influenced the observed relationship between diversity metrics and island variables, we generated a null distribution of data by taking 1,000 subsets of the data for each island. For each subset, we randomly selected data according to the minimum number of samples per sampling method. Specifically, for each run, we randomly chose four pitfall traps, two samples of Winkler extraction, and pooled 40 m lengths of transect trails for each island. Then, we calculated SR, PD, FD, MPD and FD\_MPD derived from the 1,000 runs and checked if the relationships between these rarefied diversity metrics and the island variables were identical with the observed relationship. To further reduce the effect of sampling effort, we tested our hypotheses at both the island scale and the transect scale.

### 2.3.4 | Phylogenetic signal

To examine the phylogenetic signal of each trait, we used two indices: Blomberg's *K* (Blomberg, Garland, & Ives, 2003) and Pagel's  $\lambda$  (Pagel, 1999). For both indices, larger values indicate a stronger phylogenetic signal (for  $\lambda$ , values close to 1, and for Blomberg's *K*, values  $>1$ ).

### 2.3.5 | Effect of island area and isolation on diversity metrics and community structure

We  $\log_{10}$ -transformed island area to normalize model residuals. Island area was not correlated with isolation (Pearson:  $r = -.23$ ,  $p = .20$ ). At the island scale, we used multiple linear regression models to examine the relationships between the diversity metrics and island area and between the diversity metrics and isolation.

At the transect scale, we used linear mixed-effects regression models, setting island identity as a random effect, to regress the diversity metrics against island area and isolation. All analyses were conducted in R version 3.5.1 (R Core Team, 2018).

## 3 | RESULTS

A total of 91,011 individual ants were captured across the 33 islands, belonging to 97 species in 44 genera and eight subfamilies. *Pheidole nodus* ( $n = 23,999$ ) and *Carebara vespillo* ( $n = 20,202$ ) were the most abundant species. We captured 81 species by pitfall trap, 84 species by hand collection and 66 species by Winkler extraction (Figure S3). SR ranged from 11 to 68 species per island (mean = 30) and from 11 to 44 per transect (mean = 29).

The sampling completeness curves showed that the pitfall traps, Winkler extractions and hand collections were sufficient to characterize assemblage richness on the study islands (Figures S4–S6). After controlling for sampling effort across islands, we found that the rarefied diversity metrics increased with island area and decreased with isolation, consistent with the observed results (see results below, Tables S5–S7).

All morphological traits had relatively strong phylogenetic signals (Table S8), indicating that the traits were phylogenetically conserved.

### 3.1 | Effects of island area and isolation on three dimensions of diversity

All the diversity metrics showed a similar trend, in line with our first prediction: they all increased with island area and decreased with isolation (Figures 3 and 4). At both the island and transect scales, SR significantly increased with island area (island scale:  $t = 14.90$ ,  $p < .001$ , Figure 3a; Table S6; transect scale:  $t = 12.39$ ,  $p < .001$ , Figure 3a; Table S7). PD and FD were both strongly correlated with SR (Pearson:  $r > .7$ , Tables S9 and S10), and also increased with island area regardless of the scale (island scale: PD,  $t = 11.50$ ,  $p < .001$ , Figure 3b; Table S6; FD,  $t = 11.49$ ,  $p < .001$ , Figure 3c; Table S6; transect scale: PD,  $t = 4.69$ ,  $p < .001$ , Figure 3b; Table S7; FD,  $t = 4.69$ ,  $p < .001$ , Figure 3c; Table S7). MPD significantly increased with island area at the island scale ( $t = 2.84$ ,  $p = .008$ , Figure 4a; Table S5) but not at the transect scale ( $t = 2.30$ ,  $p = .25$ , Table S7). Conversely, FD\_MPD was not significantly affected by island area at the island scale ( $t = 0.71$ ,  $p = .48$ , Table S6), but increased with island area significantly at the transect scale ( $t = 2.879$ ,  $p = .006$ , Figure 4b; Table S7). Also leading some support to our first

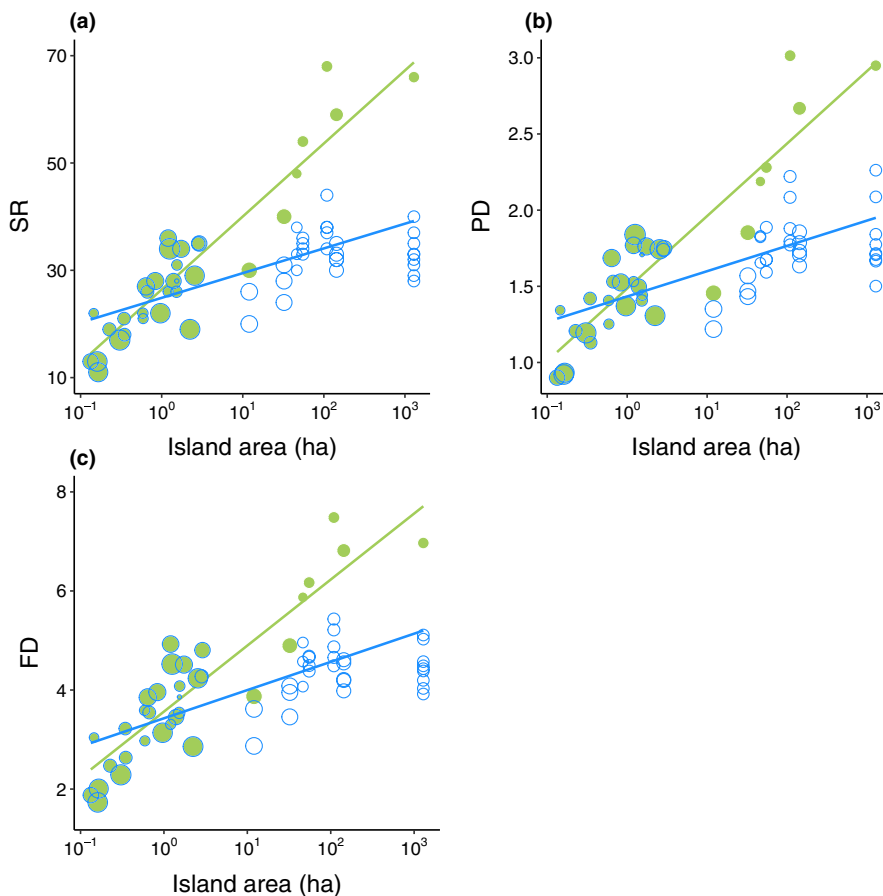
prediction, all diversity metrics decreased with isolation, but none were significant.

### 3.2 | Effects of island area and isolation on phylogenetic and functional community structure

Overall, the values of phylogenetic and functional community structure (sesMPD and sesFD\_MPD) were between  $-1.96$  and  $1.96$  (Figure 4c,d), indicating that the ant communities were neither significantly clustered nor significantly overdispersed. In other words, the ant communities could not be distinguished statistically from random assemblages.

Despite this lack of difference, some patterns were apparent. The values of the phylogenetic community structure (sesMPD) were lower than zero for most islands (Figure 4c), suggesting phylogenetic clustering. The exception to this pattern occurred on some of the larger islands (e.g. islands S01 and S02), where communities tended to be overdispersed (Figure 4c). In contrast to phylogenetic community structure, values of functional community structure (sesFD\_MPD) were higher than zero on most islands (Figure 4d), suggesting overdispersion.

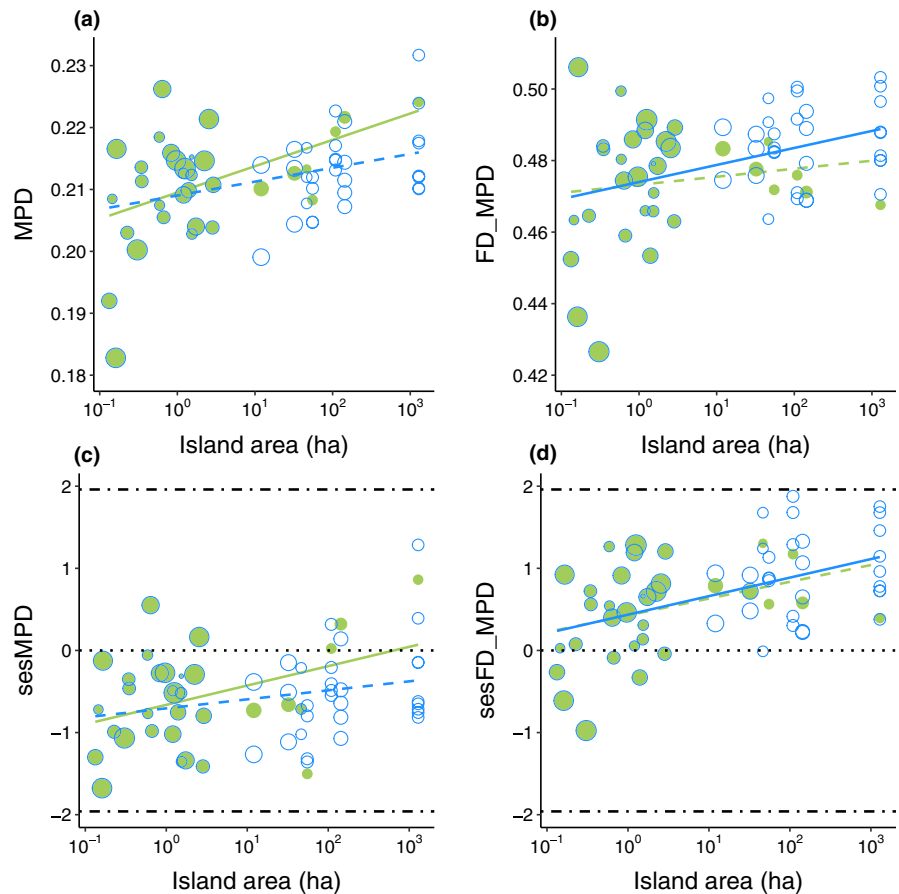
Interestingly, measures of both phylogenetic and functional community structure indicated that ant communities became less closely related on larger islands, although neither varied systematically as



**FIGURE 3** The effect of island area on (a) species richness (SR), (b) Faith's phylogenetic diversity (PD) and (c) Petchey and Gaston's functional diversity (FD) of ant communities at the island scale (green filled circles and lines) and the transect scale (blue open circles and lines) on 33 study islands in the Thousand Island Lake, China. The green and blue lines represent the predicted values of SR, PD and FD for island area (solid lines indicate significant relationships at  $\alpha = 0.05$ ) that were obtained by holding isolation constant at the mean value. Larger circles represent more isolated islands [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** The effect of island area on (a) the mean pairwise distance (MPD), (b) the functional equivalent of the mean pairwise distance (FD\_MPD), (c) the standardized effect size of MPD (sesMPD) and (d) the standardized effect size of FD\_MPD (sesFD\_MPD) of ants communities at the island scale (green filled circles and lines) and the transect scale (blue open circles and lines) on 33 study islands in the Thousand Island Lake, China. The green and blue lines represent the predicted values of MPD, FD\_MPD, sesMPD and sesFD\_MPD for island area (solid lines indicate significant relationships at  $\alpha = 0.05$ ) that were obtained by holding isolation constant at the mean value. Larger circles represent more isolated islands. Black dash-dotted lines indicate the threshold of  $\pm 1.96$  SES for significantly non-random values in (c) and (d) at  $\alpha = 0.05$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



a function of isolation (Tables S6 and S7). Specifically, sesMPD significantly increased with island area at the island scale but not at the transect scale ( $t = 2.185$ ,  $p = .037$ , Figure 4c; Table S6), whereas sesFD\_MPD significantly increased with island area at the transect scale but not at the island scale ( $t = 3.709$ ,  $p < .001$ , Figure 4d; Table S7). Importantly, these significant relationships between sesMPD and sesFD\_MPD and island area at different scales were identical with the observed patterns of MPD and FD\_MPD, indicating that the island area still affected community assembly even though ant community structure on the islands was indistinguishable from random communities.

## 4 | DISCUSSION

In this study, we analysed the response of ant communities to island area and isolation using three dimensions of biodiversity (taxonomic, phylogenetic and functional diversity) in a subtropical island archipelago system. Our results indicated that island area, not isolation, is the main driver of ant biodiversity and community structure on our study islands (Tables S6 and S7). These results supported the following predictions: (a) positive diversity–area relationships for the three dimensions of biodiversity and (b) environmental filtering is the dominant process in structuring ant assemblages on smaller islands, whereas competitive exclusion becomes more important on

larger islands. Moreover, we found that communities tended to be phylogenetically clustered but functionally overdispersed on islands. This result suggested that distinct mechanisms may influence phylogenetic and functional community structure.

The positive species–area relationship is widely observed, acknowledged and studied in biogeography (Matthews, Rígal, Triantis, & Whittaker, 2019). Larger islands host more species due to more diverse habitat types, higher ecosystem productivity and higher quality of resources (Wardle, Hörnberg, Zackrisson, Kalela-Brundin, & Coomes, 2003). Previous studies in our system have found positive species–area relationships for plant, bird, snake and small mammal communities as well (Wilson et al., 2016). Our results for ant communities are broadly consistent with these findings. However, although such species–area relationships have been intensively examined, phylogenetic–area and functional–area relationships have been less reported (but see Ross et al., 2019; Si et al., 2017; Whittaker et al., 2014). In our study, phylogenetic and functional diversity (PD, MPD, FD and FD\_MPD) were both positively related to the island area, consistent with results from other studies (Ross et al., 2019; Si et al., 2017). Larger islands supported higher SR, as well as higher functional and phylogenetic diversity. Notably, the slopes of the diversity–area relationships of SR, PD and FD were steeper at the island scale than at the transect scale (Figure 3), indicating turnover of ant species among transects on larger islands.



Ant communities in our study islands tended to be phylogenetically clustered (Figure 4c). Such a clustering pattern would be expected if environmental filtering was the dominant process structuring the ant communities. In general, theory suggests that phylogenetic clustering is more likely to occur when conditions are relatively extreme because fewer organisms possess the traits required to survive and these organisms are more likely to be more closely related (Machac et al., 2011; Smith et al., 2014). Environmental filtering has also been suggested to be common, if not universal, on islands. For example, Carvajal-Endara, Hendry, Emery, and Davies, (2017) found that floras on the Galápagos Islands were strongly influenced by environmental filtering. Similarly, Si et al. (2017) found that environmental filtering shaped bird communities on all but the largest island in the Thousand Island lake system. If environmental filtering was mediated by functional traits with strong phylogenetic signals, we would also expect functional trait clustering to occur. In our study, all functional traits exhibited a significant phylogenetic signal, in line with results from other studies of ants (Arnan et al., 2018; Donoso, 2014). However, rather than clustering, we found that the functional structure of the ant communities tended to be overdispersed (Figure 4d). These contrasting results are reconcilable if interspecific competition dominates the assembly of the functional trait community.

Conflicting patterns in phylogenetic and functional structure have also been found in other ant communities, even those with significant phylogenetic signals for functional traits (Arnan et al., 2018; Liu et al., 2016), as well as other taxa (e.g. Chun & Lee, 2017; Yang et al., 2014; for plants; Sobral & Cianciaruso, 2016 for birds). Cadotte et al. (2019) recently summarized community studies that tested the phylogenetic and functional community structure simultaneously and found that these two patterns were incongruent nearly half of the time. The simple explanation for these conflicting patterns is that the phylogenetic and functional structure of communities capture different processes. Because they are closer to the actual competition, it seems likely that functional traits better represent the extent to which competition is occurring. For example, morphological traits are known to directly influence the competitive capacity of ants (Davidson, 1977). On the other hand, phylogenetic data may capture complex relationships that better reflect environmental filtering (Cadotte et al., 2019). At this point, more studies are needed to disentangle the mechanisms governing phylogenetic and functional structure. In the meantime, it is clear that phylogenetic diversity cannot be used as a simple proxy for functional diversity. This result is an important point, in as much as phylogenetic diversity is often used as an indirect estimate of ecological diversity or similarity (Swenson, 2013). A phylogenetic approach is likely to overestimate the information relevant to one or a few traits of species. As a result, important information can be lost or missed when using phylogenetic diversity as a substitute for functional diversity (Chun & Lee, 2017). Conversely, studies using a functional trait approach often focus on traits that are easily measured, which for ants are morphological traits (Arnan et al., 2018). This strategy may ignore other 'difficult to measure' traits that are important for

ant species coexistence, such as nest site, colony size and dispersal ability. In addition, the functional trait approach also has several inherent weaknesses. For example, it typically fails to capture within-species and within-population variation that may be very relevant to coexistence (Chun & Lee, 2017; Swenson, 2013). Thus, we argue that multiple dimensions of biodiversity should be considered at the same time when assessing processes of community assembly.

Taking the measures of phylogenetic and functional structure (sesMPD and sesFD\_MPD) together, we found ant community structure on smaller islands was more likely to be clustered and that community structure on larger islands was more likely to be overdispersed. Moreover, sesMPD and sesFD\_MPD increased with increasing island area (though the statistical significance differed between transects and islands), which showed that island area (but not island isolation) acted as an important filter. For island faunas, environmental conditions on smaller islands have long been argued to be more stressful for most taxa because resources, food and habitat diversity are more scarce than on larger islands (Gravel, Massol, Canard, Mouillot, & Mouquet, 2011; Harvey & MacDougall, 2014). In this light, one might predict that only the species and lineages with traits associated with tolerance of stressful environments could persist on smaller islands (Harvey & MacDougall, 2014; Liu et al., 2019). Such an effect would lead to reduced functional and/or phylogenetic diversity on smaller islands. For example, generalized species may survive on smaller islands as they have broad diets. Indeed, we found that species on the smallest island were all generalists (Figure S2; Table S11). Ant communities on larger islands were more overdispersed potentially due to the presence of certain specialist predatory ant species. The presence of predatory species on larger islands is predicted by the trophic theory of island biogeography in which species at higher trophic levels with a narrow diet breadth are more likely to occur on larger islands (Gravel et al., 2011). For example, the army ant *Aenictus*, which preys on other ant species (Shattuck, 2008), was present only on the largest islands and is derived from a relatively ancient lineage (Figure S2). Transect versus whole-island scale analyses revealed that island area significantly influenced phylogenetic clustering at the island scale (Figure 4a,c) but affected functional overdispersion at the transect scale (Figure 4b,d). These findings could imply that assembly mechanisms are scale-dependent (Donoso, 2014; Sobral & Cianciaruso, 2016). Our results indirectly showed some evidence that environmental filtering was more important at larger scales and competition was more important at smaller scales (see also Yang et al., 2014).

We did not observe diversity–isolation relationships of ants in our study system. This result indicated that the islands were sufficiently close to the mainland to allow unimpeded dispersal among them. The most isolated island in our system was 3,547 m away from the mainland. Some ant taxa (e.g. the genus *Solenopsis*) can disperse tens of thousands of metres (Helms, 2018). However, other ant taxa (e.g. the genus *Strumigenys*) are much worse dispersers and 3,547 m might be a significant barrier. Alternatively, in the artificial archipelagic systems, rather than new colonization events on islands, remnant communities of formerly continuous habitat may undergo species loss





(i.e. relaxation) until a new equilibrium community is reached (Jones et al., 2016). In our case, ant species may have already existed on the islands since before the lake and islands were formed. Accordingly, the study islands may still be more strongly influenced by dynamics associated with persistence and extinction rather than a process of species accumulation. The extinction rate depends largely on island area (Liu et al., 2019; Si et al., 2014); as a result, we failed to find an effect of isolation on diversity and community structure.

In conclusion, we verified that island area was a better predictor than isolation of ant diversity on a subtropical island archipelago. Larger islands possessed more species and higher phylogenetic and functional diversity. The contrasting patterns between the phylogenetic and functional structure of ant communities indicated that environmental filtering dominated community structure on smaller islands, whereas competitive exclusion dominated community structure on larger islands. Our study also highlighted the extent to which the relative importance of different mechanisms of community assembly differed depending upon whether the focus was phylogenetic or functional diversity, as well as the spatial scale at which these mechanisms were considered.

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## DATA AVAILABILITY STATEMENT

Data associated with this study have been uploaded in the Dryad Digital Repository: <https://datadryad.org/stash/share/HrycR H34myN62N5YORNGMKGgAxxC6f8w3Kt-Mjg-ILU>.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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