Dimensions of ant diversity on a small tropical island

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Abstract. 1. Recent appreciation of the multidimensional nature of biodiversity has prompted biologists to examine the taxonomic, functional, and phylogenetic attributes of natural communities. Simultaneous consideration of such multiple diversity dimensions provides valuable insights into various community assembly processes.

2. We studied the alpha and beta components of ant diversity on a simple island landscape dominated by adjacent but abiotically distinct evergreen (humid & dense canopy) and littoral (dry & sparse canopy) forest habitats. We sought to (i) describe and examine interrelationships of ant diversity dimensions, and (ii) identify potential processes structuring ant communities by comparing the diversity patterns of observed and randomly generated communities.

3. We found that the drier littoral habitat had lower ant species richness and non-random community composition, but had similar functional diversity as evergreen forests. This result is in contrast with previous studies comparing intact and human-altered habitats that reported severe loss of ant functional diversity with reduced richness. In our study, the functional similarity between habitats was maintained because communities in littoral forests were functionally overdispersed than expected by chance. We suggest that competition and/or thermal tolerance of ants may drive overdispersion of littoral ant communities.

4. At the small spatial scale of our island, phylogenetic diversity was a poor predictor of habitat differences despite significant phylogenetic signal in functional traits and non-random functional diversity patterns. Our work highlights the need for a broad range of studies comparing multidimensional diversity in adjacent habitats that would provide a baseline for interpreting community-level changes due to anthropogenic pressures.

Key words. Andaman Islands, community assembly, competition, Formicidae, functional diversity.

Introduction

A primary goal of ecology is to document biodiversity patterns and understand the processes that generate them. Much of our current understanding of such patterns is based on taxonomic diversity – mainly estimated using species richness and turnover – across environmental gradients and experimental manipulations. However, it is now well recognised that biodiversity is a multidimensional construct (Naeem *et al.*, 2016), and focusing only on taxonomic diversity gives us an incomplete picture of the dynamics of ecological communities (Stevens & Gavilanez, 2015). Consequently, great strides have recently been made to develop a more holistic framework of biodiversity that incorporates diversity estimates based on evolutionary relationships (phylogenetic diversity) and

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functional or morphological attributes of species (functional diversity) (e.g. Webb *et al.*, 2002; Pavoine & Bonsall, 2011). As these additional dimensions carry useful information about ecological and evolutionary variability among species (Petchey & Gaston, 2006; Cavender-Bares *et al.*, 2009), their simultaneous consideration provides useful insights into the relative importance of ecological and evolutionary processes that shape different components of biodiversity. Such information on spatial patterns of multiple dimensions of biodiversity and their underlying processes is crucial to predict responses of natural communities and design effective efforts for biodiversity conservation, in a time of global environmental change.

Comparisons of functional and/or phylogenetic dispersion of observed communities with randomly generated communities of the same species richness from the regional pool of species provide insight into the relative roles of various deterministic and stochastic processes in structuring communities. Communities assembled via random selection from the regional pool are expected to show non-linear positive and asymptotic relationships ("null" expectation) between functional/phylogenetic diversity and taxonomic diversity (Kluge & Kessler, 2011). If functional/phylogenetic dispersion of observed communities is higher than the null expectation, it indicates a strong role of deterministic processes inducing increasing niche dissimilarity among coexisting species (e.g. inter-specific competition and niche partitioning) (Macarthur & Levins, 1967; Mayfield & Levine, 2010). On the other hand, lower phylogenetic/functional dispersion than null expectation suggests that abiotic or biotic filtering may play a strong role in structuring communities (e.g. environmental filtering or competitive exclusion by a set of dominant species) (Weiher & Keddy, 1995; Mayfield & Levine, 2010). Observed dispersion patterns consistent with null expectations suggest a dominant role of stochastic processes (e.g. ecological drift) in structuring communities (Hubbell, 2001).

While several recent studies have leveraged a multidimensional approach to better understand plant and vertebrate biodiversity patterns (Webb, 2000; Cadotte *et al.*, 2009; Swenson & Enquist, 2009; Safi *et al.*, 2011; Cisneros *et al.*, 2014; Klingbeil & Willig, 2016), relatively few studies have focused on insect biodiversity. Therefore, for the most diverse and abundant group of all animals, we still lack a general understanding of how different dimensions of diversity vary across landscapes, with each other, and with levels of disturbance. Among insects, ants are particularly diverse, characterised by high levels of biotic interactions and sensitivity to environment (Hölldobler & Wilson, 1990). They are also an environmentally important group, often considered "ecosystem engineers", as they perform key ecological functions such as soil aeration and seed dispersal (Folgarait, 1998). As such, ants are an ideal taxon in which to explore multiple diversity dimensions and study community assembly processes.

Recent biodiversity studies incorporating quantitative trait data and/or phylogenetic relationships of ants have focused on ant functional/phylogenetic diversity patterns along broad environmental gradients of climate, elevation, or productivity, at the regional biogeographic scale (e.g. Machac *et al.*, 2011; Arnan *et al.*, 2014, 2015, 2017; Smith *et al.*, 2014; Werenkraut *et al.*, 2015; Liu *et al.*, 2017). Local-scale studies examining differences across ant diversity dimensions are rare and mostly limited to comparisons of intact and human-modified habitats (e.g. Arnan *et al.*, 2018; Bihn *et al.*, 2010; Liu *et al.*, 2016; Martello *et al.*, 2018; but see Blaimer *et al.* (2015) for differences in phylogenetic structure of ant communities between dry and humid forests of Madagascar). These local-scale studies have revealed a strong decrease in ant functional diversity with reduced species richness in human-modified habitats, with low functional redundancy of ant communities. However, the relationship between species richness and functional as well as phylogenetic diversity of ant communities in naturally different habitats is not well understood.

To address this gap and infer potential processes underlying ant community assembly, we assess how the alpha and beta components of taxonomic, functional, and phylogenetic diversity of ant communities vary on a small (~110 km^2) and relatively simple island landscape dominated by two adjacent habitats (evergreen and littoral forests) that vary considerably in their abiotic structure. Havelock, our study island, is situated in the biodiversity-rich Andaman Islands archipelago in the Bay of Bengal. The littoral (coastal) forests are distributed along the coast, have primarily sandy soil, sparse canopy, face stronger winds, and are drier than the inland humid evergreen forests that have typical tropical rainforest soil, dense canopy cover, and a relatively stable environment. Our study island thus provides a useful model system with contrasting habitats for testing hypotheses about community assembly in ants from a multidimensional perspective.

The main objectives of our study were to: (i) describe and examine interrelationships of ant diversity dimensions, and (ii) compare observed diversity patterns with randomly generated communities to test multiple hypotheses of community assembly. Specifically, we test the following hypotheses about the relationship between species richness and functional/phylogenetic diversity of ant communities: (i) If stochastic processes such as ecological drift are dominant, we expect functional diversity to be similar to that of random communities of equal species richness. (ii) If inter-specific competition/niche partitioning plays an important role in structuring communities, we expect functional diversity to be higher than random expectation due to increasing niche dissimilarity among coexisting species. (iii) If communities are primarily structured by abiotic/biotic filtering, we expect coexisting species to be very similar to each other and thus lower functional diversity than random expectations. We expect patterns of phylogenetic diversity to mirror

functional diversity if traits show a strong phylogenetic signal.

Materials and methods

Study location

We conducted an island-wide survey of ants on Havelock Island in the Andaman Islands archipelago in the Bay of Bengal, from November 2015 to January 2016 (Fig. 1). This tropical archipelago has humid, warm climate (average temperature range 23–31 °C; humidity 70–90%) and experiences heavy rainfall (up to 3000 mm annually) from southwest and northeast monsoons. Havelock, our focal island, has an area of about 113 km^2, out of which ~80% is forested (Work Plan, Andaman Forest Department). The main forest types on the island are (semi) evergreen forest, tidal swamp forest (mangroves), and littoral forest (coastal forest). Littoral forests, distributed along the coast, have more open canopy, are drier, and face stronger winds compared to the inland evergreen forests. These two habitat types are distributed adjacent to each other. We sampled ants in these two habitats and excluded the mangrove habitat because ants do not use it for nesting. In order to document broad differences in local environment in the two habitats, we recorded the following variables at each sampling point: ambient temperature, soil temperature, relative humidity, and canopy cover. For each transect, we calculated the average of the five values for each variable.

Sampling of ants

We collected ants inhabiting leaf litter from 22 transects in evergreen forest and 12 transects in littoral forest (sampling locations shown in Fig. 1), the number of transects being approximately proportional to the area occupied by each habitat. Each 80-m-long transect was laid in the middle of the forest, as far away from forest trails as possible. Starting at 0 m, we collected leaf-litter samples from five points, spaced 20 m apart. At each point, we collected four leaf-litter samples using a quadrat of 50 cm^2 such that the total area per point added up to 1 m^2. We combined the five samples per transect and treated it as a sampling unit (community/assemblage/site) for statistical analyses. We used standard Winkler extraction process for 48 h to extract ants from the leaf litter (Agosti *et al.*, 2000). In Winkler extraction, samples of leaf litter are agitated in a bag with a coarse mesh to obtain finer "siftate" that contains all the litter arthropods. The siftate is then suspended in "Winkler" sacks in a finer mesh and hung for 48 h to passively extract arthropods at the bottom of the sack which holds a cup containing 80% ethanol.

We sorted ants under a microscope in the field, stored them in 95% ethanol, and brought them back to the laboratory. In the laboratory, we point-mounted morphologically distinct species from each transect and identified them up to species level when possible, or assigned a morphospecies code. The specimens are deposited in the Research Collections Facility at the National Centre for Biological Sciences, Bangalore.
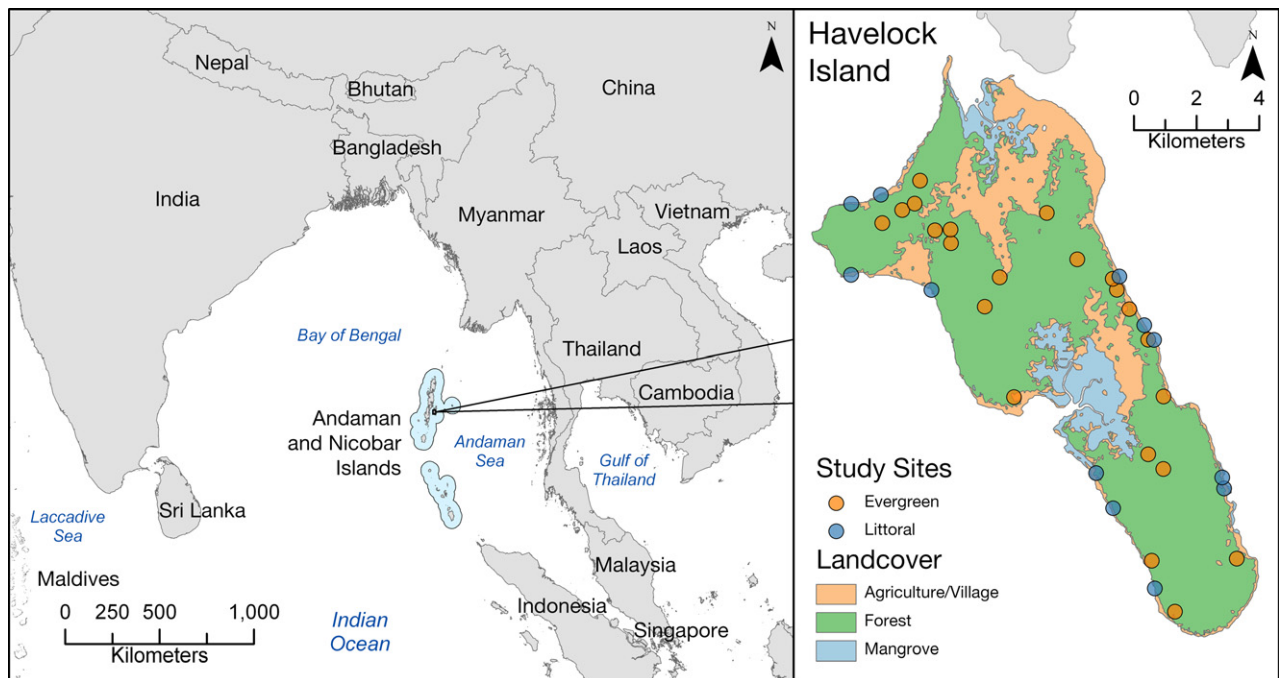
Fig. 1. Location of the Andaman and Nicobar Islands archipelago in relation to mainland India and Southeast Asia (left), and starting points of 80 m transects surveyed on Havelock Island (right).

Functional traits

In order to quantify functional diversity relevant to the assembly of ant communities, we measured traits related to species niche, mainly resource and microhabitat use. We measured morphological traits for which direct relationships with foraging strategies, diet, and microhabitat preference have been previously demonstrated (Gibb *et al*., 2015). For each species we measured traits of up to five individuals selected from different transects in order to maximise intra-specific variation. For ant species with polymorphic castes, we measured only minor workers. We measured the following traits for each species: (i) *Weber's length:* Weber's or mesosomal length, a commonly used indicator of body size in ants, was measured as the maximum diagonal length from the anterodorsal margin of the pronotum to the posterior edge of the propodeum. Body size is one of the most important traits of all organisms, related to resource use, metabolic characteristics, and other important life-history traits and has been shown to be important in ant community assembly (Fayle *et al*., 2015; Pawar, 2015). (ii) *Relative mandible length:* Mandible length varies in relation to diet, indicating the kinds of food resources utilised (Weiser & Kaspari, 2006). We measured this trait as the ratio of straight-line distance from the basal margin of the mandible to the tip, to Weber's length. (iii) *Relative leg length:* Leg length in ants is related to foraging efficiency and speed, and varies in relation to habitat complexity (Feener *et al*., 1988). It was measured as the ratio of the summed length of hind femur and hind tibia to mesosomal length. (iv) *Relative eye length:* Eye size is related to activity period, food searching, and navigation in general (Weiser & Kaspari, 2006), and was measured as the ratio of the longest eye diameter to mesosoma length.

Taxonomic diversity of ant communities

As ants are social insects and the unit of abundance for a species is the number of colonies, counts of individual ants do not reflect a meaningful measure of abundance (Gotelli *et al*., 2011). Estimation of colony number for each species is nearly impossible in tropical forests. All the analyses are thus based on species presence–absence data among sites.

We recorded taxonomic alpha diversity as the number of ant species found per site. Taxonomic beta diversity, the variation in species composition from site to site, was estimated using a modified version of the Raup-Crick pairwise dissimilarity metric (β_{rc}) based on Chase *et al.* (2011). Compared to other beta-diversity metrics, β_{rc} is robust to stochastic variation in local (alpha) diversity and as a result offers beta-diversity estimates that are independent of alpha diversity (Chase *et al*., 2011). By incorporating a null model approach, for a pair of communities (e.g. C1 and C2), the metric calculates the probability of sharing the same or higher number of species

between two communities, by repeatedly drawing the same number of species as C1 and C2 from the regional pool. The probability values are then scaled to range from -1 to 1 indicating whether dissimilarity between pairs of communities is higher than (approaching 1), similar to (close to 0), or lower than (approaching -1) that expected by chance (see Chase *et al*., 2011, for details).

We calculated taxonomic beta diversity for community pairs within each habitat (a 22×22 pairwise matrix for evergreen communities and 12×12 matrix for littoral communities) as well as for pairs between the two habitats (a 22×12 pairwise matrix). For calculating β_{rc}, appropriately delineating the regional pool is crucial. Due to the small size of the island and absence of obvious dispersal barriers, ants could potentially colonise all sites across Havelock Island. Hence, we defined our regional pool as all the species collected from all our sampling sites. To test whether β_{rc} of communities within a habitat differed significantly from the null expectation, i.e. 0, we used the non-parametric Wilcoxon's signed-rank test. We used the Mann–Whitney test to compare beta diversity between habitat groups.

Community phylogenies and phylogenetic signal

Due to the lack of a species-level ant-wide phylogeny, we used 100 trees from posterior sets of ant-wide phylogenies (Economo *et al*., 2018). These trees are similar in features to other ant-wide phylogenies (Moreau *et al*., 2006; Moreau & Bell, 2013) but are updated to include the latest molecular data (Brady *et al*., 2014; Ward *et al*., 2015) to maximise coverage of genera. Similar to other efforts in, e.g. mammalian phylogenetics (Kuhn *et al*., 2011), these tree sets retain relationships between subfamilies and genera but structures within trees follow a random branching pattern to resolve polytomies. These trees are thus expected to collectively integrate over phylogenetic uncertainty. The trees were constructed to match global species richness in each genus such that the phylogenetic distance between two species within a genus reflects the average divergence between species of that genus, but the positions of individual species within genera varied randomly across trees. We pruned the trees to retain only the species found in our sampling, and assigned undescribed species randomly within their respective genera. Analyses of alpha and betaphylogenetic diversity as well as phylogenetic signal were performed on all the 100 trees and the average value was reported for all the results.

To evaluate the degree to which measured traits showed a phylogenetic signal, we used Blomberg's K (Blomberg *et al*., 2003) and Pagel's λ (Pagel, 1999) metrics. These metrics use a Brownian model of trait evolution to evaluate whether the observed distribution of trait values differs from expectations under the Brownian model. For both metrics, values close to 1 indicate trait evolution consistent with the Brownian model and that traits exhibit phylogenetic signal; values close to 0 indicate no

phylogenetic signal. We used the phylosig function from the R package *phytools* to compute phylogenetic signals as well as their statistical significance (Revell, 2012). We computed phylogenetic signal for each trait using our set of 100 trees.

Functional and phylogenetic diversity of ant communities

We used two types of metrics to explore functional and phylogenetic alpha diversity of ant communities. To examine total phylogenetic/functional diversity, which reflects the phylogenetic/functional space occupied by a given community, we used Faith's PD (Faith, 1992) and the analogous Petchey and Gaston's FD metric (Petchey & Gaston, 2006) that sum branch lengths connecting coexisting species in a given community on a phylogenetic tree or functional dendrogram ("richness" metric, sensu Tucker *et al.*, 2017). To understand functional/phylogenetic (un)relatedness of coexisting species in a community, we used mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) metrics ["divergence" metrics, sensu Tucker *et al.*, (2017)]. While MPD is a basal measure of pairwise functional/phylogenetic distance among all species within a community, MNTD is a more terminal metric in that it measures the distance between each species and its closest neighbour on a dendrogram/tree that co-occurs in the same community (Webb *et al.*, 2002). We report results from the richness metric in the main text and from divergence metrics in the Supplementary Material as the results of richness and divergence metrics were generally consistent with each other. In addition to examining functional diversity based on all traits considered together, we also analysed functional dispersion of ant communities in each habitat using body size alone.

For phylogenetic diversity calculations, we converted our tree sets into distance matrices using the function cophenetic from R package *stats*. For functional diversity, we first calculated z-standardised trait values for all species (so that no single trait dominates the trait distance matrix) and converted them into a Euclidean distance matrix. This distance matrix was then used to calculate functional alpha-diversity metrics mentioned above. To generate the functional trait dendrogram, we clustered ant species according to their functional distances using the "WPGMA" method (cophenetic correlation 0.80). The choice of methods for constructing trait distance matrix and performing hierarchical clustering was made using the R script and procedure from Mouchet *et al.* (2008) in order to maximise cophenetic correlation between the original species distances and the distances estimated from hierarchical clustering.

In order to examine the degree to which observed community patterns deviated from random assembly of communities and thus evaluate preferential assembly of more similar or more dissimilar species for a given richness, we calculated standardised effect sizes (SES) for all the diversity metrics. For alpha diversity, we randomised the species presence–absence matrix to create null expectations as we were interested in understanding the impact of species interactions, mediated through co-occurrence, on composition of local assemblages. To do this, we used the "independent swap" null model that randomises co-occurrence of species by shuffling elements of the species-by-site matrix while maintaining the overall frequency of each species as well as species richness of each site (Gotelli, 2001). For alpha diversity, this is preferable to shuffling tips of phylogeny/dendrogram because it preserves the abundance of different traits in the system and focuses on whether they co-occur, whereas preserving the community matrix and shuffling phylogeny/dendrogram tips would destroy information about trait abundance. We compared our observed ant communities with 999 randomly generated communities using the formula SES = (Obs–Mean$_{\text{null}})$/S.D.$_{\text{null}}$; where Obs = metric value for observed communities; Mean$_{\text{null}}$ = mean metric value of null distributions; and S.D.$_{\text{null}}$ = standard deviation of metric value for null distributions. Standardised effect sizes of MPD and MNTD are equivalent to net related index (NRI) and nearest taxon index (NTI). We multiplied NRI and NTI by -1 to indicate overdispersion for positive values and underdispersion for negative values.

We followed Swenson (2014) to calculate functional and phylogenetic beta diversity, using a presence–absence weighted pairwise distance metric (D_{pw}) that indicates overall dissimilarity between pairs of communities. For a given pair of communities, D_{pw} is the functional or phylogenetic distance between all species from one community to all species in the second community, based on a functional or phylogenetic distance matrix. Standardised effect sizes of beta diversities were calculated using the same formula mentioned above. We intended to keep spatial structure (co-occurrence of species) of the community matrix intact in order to evaluate the degree to which environment or space affect turnover in functional traits or phylogeny. Therefore, we chose to randomise taxa in trees/ dendrogram for phylogenetic/functional beta diversity, rather than randomising species co-occurrence, so that the spatial arrangement of the communities remains fixed. If the observed spatial structure of communities is not constrained, it might result in higher bias towards finding lower than expected turnover (Swenson, 2014). To generate null communities, we randomly shuffled column names, i.e. species identity, of the functional and phylogenetic distance matrices 999 times.

To interpret overall trends in SES values for a group of communities, we tested if SES values of the group are significantly different from 0 by using a Wilcoxon's signed-rank test (Horner-Devine *et al.*, 2007).

To visualise whether the distribution of the communities from the two habitats was separated in their taxonomic, functional, or phylogenetic structure, we performed non-metric multidimensional scaling (NMDS) using the function monoMDS from R package *vegan*. We used dissimilarity matrix from taxonomic diversity

analysis and SES of dissimilarity matrices obtained from functional and phylogenetic diversity analyses as inputs for the NMDS analyses.

All the analyses mentioned above were conducted in the R computing environment (R Development Core Team, 2016), using the packages *picante*, *vegan,* and *ape* (Paradis *et al*., 2004; Oksanen *et al*., 2007; Kembel *et al*., 2010).

Results

Our sampling yielded a total of 50 species of ants belonging to 25 genera. Of these, 46 species from 22 genera were found in evergreen forests while 33 species from 20 genera were found in littoral forests (Fig. 2). Most of the species we found were native ants except very low occurrences of the exotic *Anoplolepis gracilipes*, *Strumigenys emmae*, and *Strumigenys membranifera* (Table S1).

Taxonomic diversity

Average ant species richness was significantly lower in littoral communities [9 $\pm$ 4 (mean $\pm$ S.D.)] compared to evergreen communities (13 $\pm$ 4) (Fig. 2). Taxonomic beta diversity (β_{rc}) of communities within each habitat was very similar. β_{rc} of communities across the two habitats was significantly higher than β_{rc} of communities within each habitat type ($P < 0.001$, Mann–Whitney test; Fig. 3). Consequently, the NMDS analysis showed separation in ant community composition between the two habitats (Fig. 3). Beta diversity of communities within each habitat was significantly lower than expected under random community assembly ($P < 0.001$; Wilcoxon's signed-rank test), while for community pairs across the two habitats it was consistent with null model expectations ($P > 0.25$; Wilcoxon's signed-rank test).

Functional diversity

We did not observe a significant difference in the absolute functional diversity between habitats (Fig. 2). When compared with null model expectations, littoral communities showed a positive deviation from null expectations in both dendrogram- and distance-based metrics (i.e. SES > 0; $P < 0.01$ (FD$_{SES}$), $P < 0.01$ (MPD$_{SES}$), $P > 0.1$ (MNTD$_{SES}$); Wilcoxon's signed-rank test; Figure 2 and Figure S2), while communities in evergreen forests were either consistent with null expectation or exhibited negative deviation (i.e. SES < 0; $P > 0.30$ (FD$_{SES}$), $P < 0.01$ (MPD$_{SES}$), $P < 0.025$ (MNTD$_{SES}$); Wilcoxon's signed-rank test). There was also a significant difference in SES values of FD between the two habitats ($P < 0.004$, Mann–Whitney test; Fig. 2). Patterns of body size dispersion (Figure S2E & F, supplementary material) of evergreen and littoral communities were similar to the results

discussed above in which all traits were considered together.

Functional beta diversities (D_{pw}) of community pairs within both habitats as well as across the two habitats were lower than the null model expectation, i.e. SES < 0 ($P < 0.001$; Wilcoxon's signed-rank test; Figure 3). We did not observe separation in functional structure of communities in the two habitats based on the NMDS analysis (Fig. 3). However, SES values of functional beta diversity of littoral ant communities were significantly different from evergreen forest communities ($P < 0.001$; Mann–Whitney test; Figure 3), and they were much more closer to the null expectation.

Phylogenetic signal and diversity

All the traits we measured exhibited significant phylogenetic signal in both the Blomberg's K and Pagel's λ metrics and both the metrics were generally consistent with each other (Fig. 4). Summary statistics from phylogenetic signal analyses are reported in Table S2 in supplementary material. We found significant decrease in absolute phylogenetic diversity in littoral forests, as expected with lower species richness (Fig. 2). However, this decrease was consistent with expectations under random community assembly (Fig. 2). These results suggest that species forming local communities were random with respect to their position on the phylogeny.

Phylogenetic beta diversity (D_{pw}) of communities within as well as across the two habitats showed trends of negative deviation from null expectations, similar to functional beta diversity (Fig. 3). Although this deviation was generally very small, communities within evergreen forest and across the two habitats had beta diversity significantly different from null expectations, i.e. SES < 0 ($P < 0.01$; Wilcoxon's signed-rank test). Phylogenetic beta diversity within littoral habitat communities was not significantly different from null expectations ($P > 0.08$). We did not observe separation of communities in the two habitats in our NMDS plot of phylogenetic beta diversity (Fig. 3).

Discussion

Our study of multiple ant biodiversity dimensions on a simple island system revealed incongruent patterns of these dimensions in the humid and dry forest habitats on the island. By simultaneously considering three dimensions of ant biodiversity, we found that functional diversity was similar despite significant differences in species richness across habitats, a result that contradicts previous studies that compared this relationship in intact vs. human-modified habitats. Moreover, we detected functional overdispersion of ant communities in the littoral forests, suggesting a plausible role of inter-specific competition or thermal tolerance in structuring these communities. Finally, at the small spatial scale of our study island,
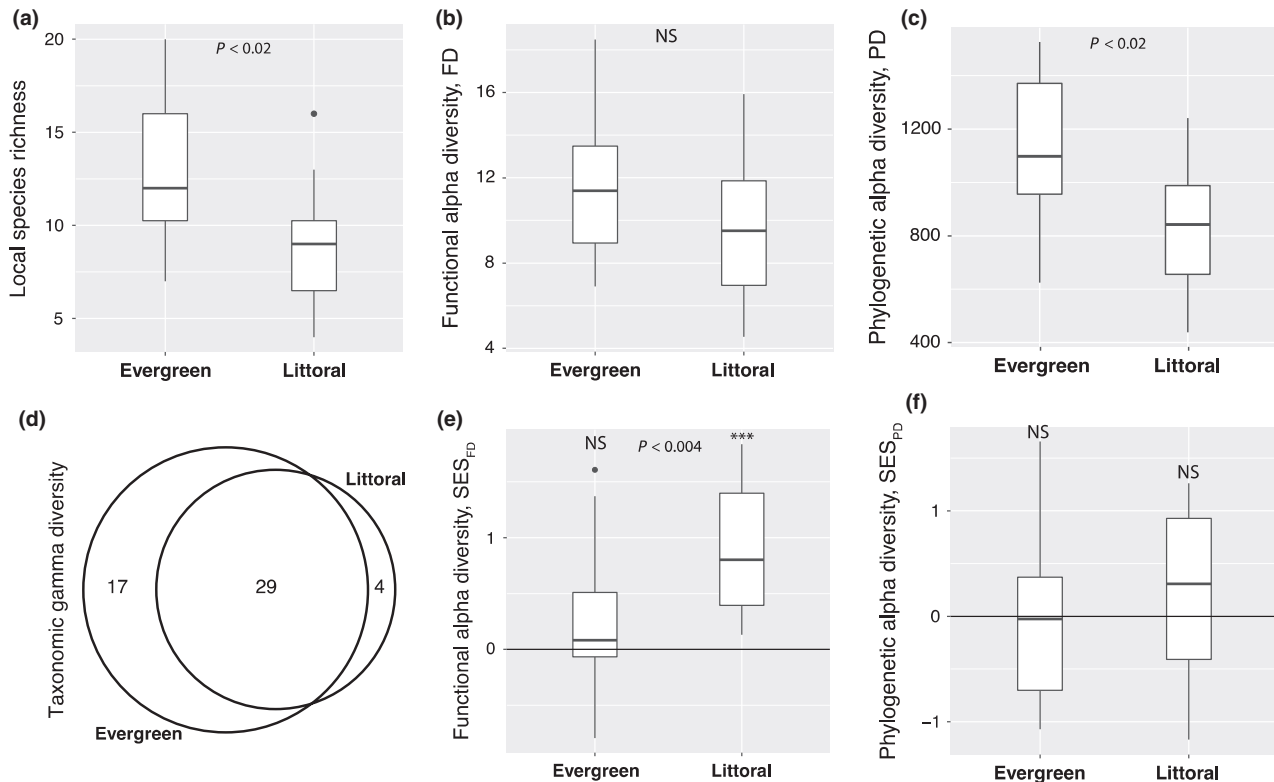
Fig. 2. Alpha and gamma diversities of ant communities in evergreen and littoral forests. (a) Local species richness, (b) absolute functional diversity (FD), (c) absolute phylogenetic diversity (PD), and (d) gamma diversity. After correcting for species richness, littoral ant communities showed overdispersion in functional diversity while evergreen communities were consistent with null expectations (e, scaled by SES_{FD}) and phylogenetic diversity of communities in both the habitats was consistent with null expectations (f, scaled by SES_{PD}). Asterisks indicate statistical significance from null model expectations, i.e. SES> or <0 (***$P < 0.001$, NS, non-significant; Wilcoxon's signed-rank test). *P*-values between box plots indicate statistical significance for differences in values between the habitats (Mann–Whitney test).

we found that phylogenetic diversity is a poor predictor of habitat differences, compared to taxonomic or functional diversity. These patterns provide insight into the processes governing community assembly of ants on this small island ecosystem and highlight the utility of multidimensional approach to study biodiversity patterns.

Overall, species richness was consistently lower in littoral forest communities than the larger evergreen forest habitat. While the smaller littoral habitat communities were composed of subsets of species from the larger evergreen forest habitat, the community-level divergence in species composition (as seen in the NMDS and taxonomic beta-diversity analyses) of the two habitats indicates that the littoral forest assemblages were not random subsets of the evergreen forest species. Considering significant differences in the abiotic environments of the habitats (Figure S1), these results suggest that the littoral forest ant fauna on the whole was filtered by the environment. Our result of lower species richness in the drier littoral habitat was similar to a recent study that compared ant species richness in humid vs. dry forests of Madagascar (Blaimer *et al.*, 2015), which also found lower richness in dry forests.

The difference in ant species richness in the two habitats, however, does not mirror patterns of functional diversity, which was relatively similar across the two habitats. This relative similarity was reached because the littoral ant fauna, albeit filtered from the evergreen forest fauna, was composed of local communities that were much more functionally overdispersed than the evergreen forest communities. In other words, species are packing niche space in the evergreen habitat more tightly than in the littoral habitat. Thus, although the overall trait morphospace occupied by communities in the two habitats was similar, the more speciose communities in evergreen forests were composed of species close to each other in the trait morphospace whereas littoral communities were composed of fewer species that were far apart from each other. This result was consistent across both dendrogram-based and pairwise distance metrics of functional diversity. It implies that community assembly is not random with respect to traits and suggests a significant role of deterministic processes in structuring local communities.

Our results of lower-than-expected functional beta diversity of ant communities both within and between habitats suggest that functional structure is repeatable throughout
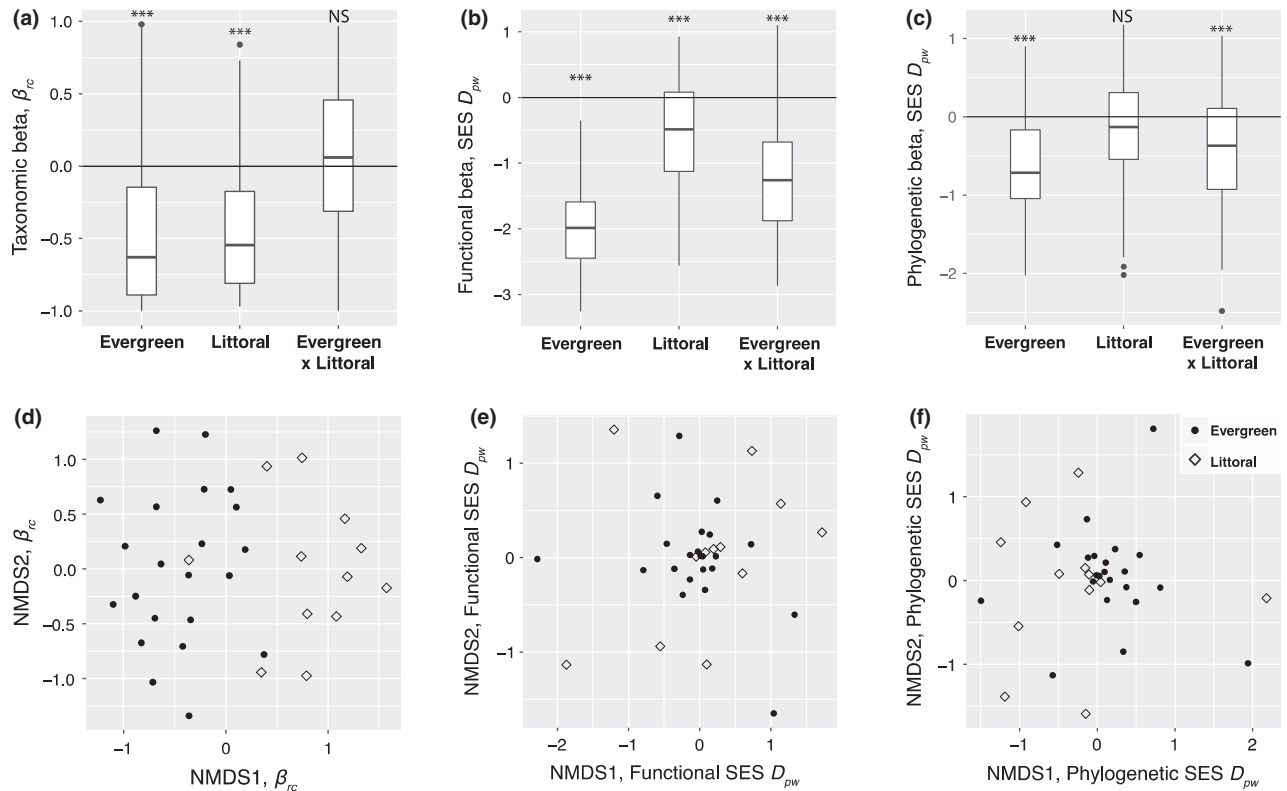
Fig. 3. Beta diversities of ant community pairs within and across habitats (evergreen × littoral). (a): Taxonomic beta diversity (β_{rc}); (b): Standardised effect size of functional beta diversity (SES D_{pw}); (c): Standardised effect size of phylogenetic beta diversity (SES D_{pw}). (d), (e), and (f): Non-metric multidimensional (NMDS) scaling of communities in the two habitats based on taxonomic (β_{rc}), functional (SES D_{pw}), and phylogenetic beta diversity (SES D_{pw})
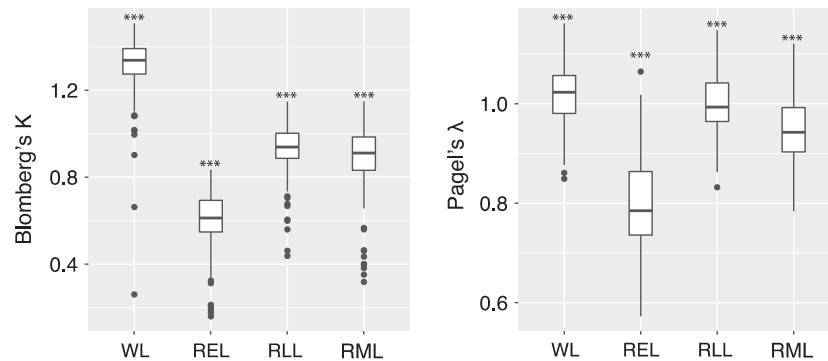
Fig. 4. Phylogenetic signal for functional traits used in the study. Phylogenetic signal was computed using the Blomberg's K (Blomberg *et al.*, 2003) and Pagel's λ (Pagel, 1999) metrics. K & λ values close to 1 indicate phylogenetic signal under Brownian model of trait evolution, whereas values close to 0 indicate no phylogenetic signal. Abbreviations of the traits are as follows: WL, Weber's length; REL, relative eye length; RLL, relative leg length; RML, relative mandible length. Asterisks on top of each box indicate statistical significance of phylogenetic signal (***$P < 0.001$).

the island and is not consistently divergent between the two habitats. However, SES of functional beta diversity of littoral communities was significantly different than evergreen forest communities and much closer to null expectation. This suggests that while repeated, functional structure in littoral habitat is more stochastic. This difference in

functional structure of communities in evergreen and littoral forests might arise due to the higher environmental heterogeneity observed in the littoral habitat.

The overdispersed nature of littoral ant communities discussed above is based on multiple traits considered together. When we analysed functional structure based on

body size alone, we found similar patterns, suggesting that constituent species in littoral assemblages were more dissimilar and spaced apart in body size than random expectations. Previous empirical and theoretical research suggests that such differences could arise due to niche differentiation in food intake or resource use, in response to competition (Basset & Angelis, 2007; Kohda *et al.*, 2008; Fayle *et al.*, 2015). These patterns beg the question: what might drive competition in littoral ant communities? It is possible that with change in the abiotic environment, food availability (e.g. density of litter arthropods such as Collembola) decreases in littoral forests. Other differences between habitats such as soil type might also induce competition, e.g. by limiting available nest sites. However, factors other than competition could also lead to overdispersion in body size. For instance, thermal tolerance of ants is known to positively correlate with body size (Kaspari *et al.*, 2015; Verble-Pearson *et al.*, 2015). It is possible that due to lower canopy cover in littoral forests, the top layer of leaf litter is much hotter and only relatively larger ants could forage there. As a result, there would be a difference in body size of ants foraging through the litter vs. those walking over it.

Even though we found differences in functional structure of communities in the two habitats and all the traits we measured showed significant phylogenetic signal, we did not detect significant differences in phylogenetic alpha diversity after accounting for differences in species richness. While a correlation is expected between functional and phylogenetic diversity when traits are conserved in the regional pool, previous studies suggest that it occurs only when traits are very strongly conserved, e.g. when Blomberg's $K > 2$ (Kraft *et al.*, 2007; Swenson, 2011). Our traits showed more modest phylogenetic signal (~0.5–1.5), and this could reflect either insufficient resolution in the phylogeny or that the traits evolve relatively rapidly and repeatedly. The latter is quite possible because generally, functional traits such as body size, eye size, and leg length are often variable in ants even among relatively closely related species. Similarly, the magnitude of deviations of phylogenetic beta diversity from null expectations was much lower compared to functional beta diversity. These results collectively indicate that at the small spatial scale of the island, community structure is better predicted by functional traits rather than phylogenetic relationships among species.

Our results of functional diversity discussed above are in contrast with previous studies that compared species richness and functional diversity of ants. For example, Bihn *et al.* (2010) reported severe loss of ant functional diversity with reduced species richness in secondary forests of Brazil. Similarly, Liu *et al.* (2016) found reduced functional diversity associated with sharp decline in species richness in rubber plantations in southern China. An important distinction between these and our study is the ecological context of the decline in species richness. While the lower species richness in littoral forests was a natural pattern, likely mediated by the abiotic environment, it was anthropogenic pressures that led to habitat loss and alteration of ant communities in both the studies

mentioned above. This difference is interesting because it suggests that the nature of reorganisation of functional structure of communities under anthropogenic pressures could be very different from how natural habitat differences or disturbances structure communities. On the other hand, our results of phylogenetic diversity were consistent with other studies that did not find significant differences between forest and rubber habitats in China (Liu *et al.*, 2016) or dry and humid forests of Madagascar (Blaimer *et al.*, 2015). These findings suggest that ant communities do not show phylogenetic responses to habitat differences at small spatial scales, although phylogenetic differences dominate community patterns across broad climatic gradients (Smith *et al.*, 2014; Liu *et al.*, 2017).

By comparing multiple dimensions of ant diversity on a small island ecosystem, our study offers insights into community assembly at a small spatial scale. The fact that functional diversity does not scale similarly with species richness in naturally different vs. human-altered habitats is interesting and could potentially have important conservation implications. Building a larger dataset of similar studies that compare adjacent habitats will help us understand if our finding is generalisable and may provide a baseline to decipher community-level changes due to anthropogenic pressures. For instance, it may be possible that this pattern manifests only on islands because the accumulation of diversity and thus total species pool is known to differ between island and mainland areas (Stuart *et al.*, 2012). Nevertheless, such an approach will build an understanding of both natural community assembly as well as human-mediated impacts on community structure of organisms.

Contribution of authors

GA, DA, and EPE conceived and designed the study. GA conducted field, laboratory work, and data analysis. DA and EPE supervised the research. GA, DA, and EPE wrote the manuscript.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of all the ant species recorded in this study with their number of occurrences in each habitat type.

Table S2. Summary statistics from the analyses of phylogenetic signal across 100 trees used in this study.

Figure S1. Environmental differences between sampled sites in the evergreen and littoral forests on Havelock Island.

Figure S2. Net related index (NRI) and nearest taxon index (NTI) values (multiplied by -1) for functional (all traits considered together) alpha diversity (A & B) and phylogenetic alpha diversity (C & D). NRI & NTI ($x - 1$) for functional alpha diversity based on body size alone (E & F).

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