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Life-history dimensions indicate non-random assembly processes in tropical island tree communities

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Community assembly processes on islands are often non-random. The mechanisms behind non-random assembly, however, are generally difficult to disentangle. Functional diversity in combination with a null model approach that accounts for differences in species richness among islands can be used to test for non-random assembly processes, but has been applied rarely to island communities. By linking functional diversity of trees on islands with a null model approach, we bridge this gap and test for the role of stochastic versus non-random trait-mediated assembly processes in shaping communities by studying functional diversity–area relationships. We measured 11 plant functional traits linked to species dispersal and resource acquisition strategies of 57 tree species on 40 tropical islands. We grouped traits into four life-history dimensions representing 1) dispersal ability, 2) growth strategy, 3) light acquisition and 4) nutrient acquisition. To test for non-random assembly processes, we used null models that account for differences in species richness among the islands. Our results reveal contrasting responses of the four life-history dimensions to island area. The dispersal and the growth strategy dimensions were underdispersed on smaller islands, whereas the light acquisition dimension was overdispersed. The nutrient acquisition dimension did not deviate from null expectations. With increasing island area, shifts in the strength of non-random assembly processes increased the diversity of dispersal and acquisition strategies in island communities. Our results suggest that smaller islands may be more difficult to colonize and provide more limited niche space compared to larger islands, whose tree communities are likely determined by stochastic processes and higher niche diversity. Our null model approach highlights that analyzing the functional diversity of different life-history dimensions provides a powerful framework to unravel community assembly processes on islands. These complex, non-random assembly processes are masked by measures of functional diversity that do not account for differences in species richness between islands.

Keywords: community assembly, dispersal filtering, environmental filtering, functional dispersion, functional island biogeography, functional trait space

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Introduction

Islands constitute natural experiments to test ecological and evolutionary hypotheses in spatially discrete arenas (Whittaker and Fernández-Palacios 2007). The study of islands has yielded many influential theories on the maintenance of species diversity in isolated and fragmented habitats, the most prominent being MacArthur and Wilson's equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1967). ETIB posits that species richness on islands results from a dynamic equilibrium of random colonisation and extinction events, where larger and less isolated islands support more species than smaller and more isolated ones (MacArthur and Wilson 1967).

ETIB provides a quantitative framework to study species richness patterns on islands. However, it assumes that community assembly processes on islands are neutral, calling for extended theories to examine species assembly processes on islands. Indeed, geographic and ecological factors on islands such as colonisation barriers (Carlquist 1965), niche shifts (Diamond 1970), area requirements (Schrader et al. 2019a) or biotic interactions (Carlquist 1974, Taylor et al. 2019) suggest that island floras are at least partially shaped by non-random assembly processes (Emerson and Gillespie 2008, Biddick et al. 2019). Trait-based approaches to island biogeography have been proposed to provide insights into the underlying mechanisms of island community assembly (Ottaviani et al. 2020) and to disentangle the role of random and non-random assembly processes (Jacquet et al. 2017, Si et al. 2017).

Functional traits characterise morphological, physiological or phenological features at the individual level that are linked to species' dispersal abilities and niche requirements (Díaz and Cabido 2001, Arjona et al. 2018). The diversity of functional traits in a species community, e.g. functional diversity (FD), captures key aspects of community structure, such as functional commonness and rarity (Laliberté and Legendre 2010). For islands, it has been shown that FD increases with area in a similar fashion as species richness (Ding et al. 2013, Whittaker et al. 2014). However, FD–area relationships should be interpreted with caution as FD can be affected by species richness, habitat diversity and area (Fig. 1b; Petchey and Gaston 2002, Schleuter et al. 2010, Smith et al. 2013). This suggests that measures of FD – when uncorrected for species richness, habitat diversity and/or area – may not provide further insights into insular diversity patterns or underlying assembly processes (Fig. 1a–c). Alternatively, FD corrected for species richness, habitat diversity and/or area can indicate non-random assembly processes such as competition, predator–prey interactions and herbivory or dispersal constraints (Kraft et al. 2008, Mason et al. 2013, Spasojevic et al. 2014, Cadotte and Tucker 2017).

To test for non-random assembly processes, FD is commonly compared to those of randomly generated communities (Ackerly and Cornwell 2007, Cadotte and Tucker 2017). FD can be either more similar (underdispersed) or dissimilar (overdispersed) than expected by chance (Fig. 1d–e;

Ackerly and Cornwell 2007). On small islands, Burns and Neufeld (2009) reported that plant species have more similar dispersal-related traits than plants on larger islands, as they are predominantly bird dispersed. On atolls, plants are often widely dispersed and well-adapted to coastal conditions (Stoddart 1992), likely leading to clustered dispersal syndromes and traits associated with environmental conditions
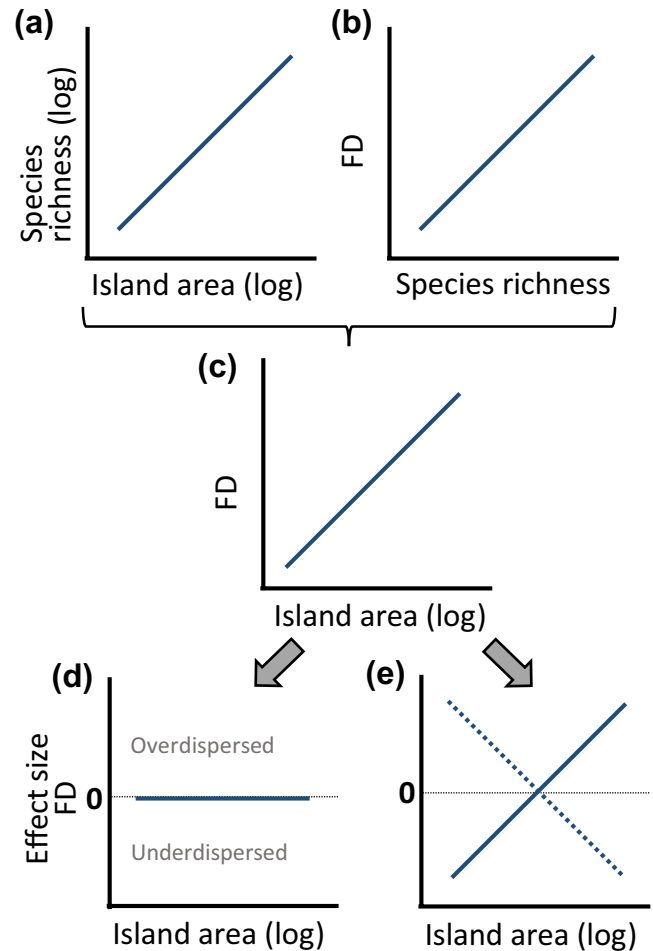

Figure 1. Conceptual framework to integrate functional diversity (FD) into classical island biogeography theory and test for non-random assembly processes along gradients in island area. (a) The equilibrium theory of island biogeography predicts that species richness increases with island area. (b) FD normally increases with species richness, as both are strongly correlated. (c) Consequently, FD can be expected to increase with island area. An increase in FD with island area alone, however, is uninformative about community assembly and non-random assembly processes on islands. Using a null model approach to account for species richness effects on FD, the extent to which island area influences FD patterns can be examined. When the effect size is not correlated with island area (d), communities can be regarded as a random subsample of a larger species pool without non-random processes shaping these communities. (e) When the effect sizes increase (solid line) or decrease (dashed line) with island area, FD is either under- or overdispersed for certain communities. That would be a strong signal of non-random community assembly processes.

on atolls. Overdispersion on islands, in turn, can occur when high competition for limited resources among species leads to niche differentiation (MacArthur and Levins 1967, Astor et al. 2014), or when predation or herbivory are absent (Schoener and Toft 1983), allowing many functionally different species to coexist (Swenson 2013, Cadotte and Tucker 2017). Testing for non-random assembly mechanisms, therefore, has the potential to reveal new insights into the community structure of insular biota and into the mechanisms underlying FD–area relationships.

Here, we investigate the underlying mechanisms of the FD–area relationship by using a null model approach that tests for non-random assembly of island communities. We apply this approach to functional traits of trees on 40 small tropical islands that vary in size by three orders of magnitude. We first investigate how species richness and abundance affect FD on islands directly. We then focus on life-history dimensions related to dispersal and niche partitioning of growth strategy dimension as well as light and nutrient acquisition, to test for non-random assembly processes. We expect that FD – also when grouped into life-history dimensions – will increase with island area, as more functionally different species may co-occur on larger than on smaller islands. We assume that smaller islands may be more difficult to colonize, provide fewer habitats and impose stronger environmental filters to species establishment. Consequently, only species with special adaptations may establish on smaller islands. We thus expect null models to reveal that FD of communities on smaller islands will be underdispersed for all traits as well

as for the species' trait combinations grouped into life-history dimensions. In contrast, we expect FD for all traits and divided into life-history dimensions to be neutral or overdispersed on larger islands. This may be explained by larger islands imposing weaker dispersal filters for colonisation and providing greater habitat diversity, and more favourable environments, thus allowing more species with unique trait combinations to co-exist and increasing FD.

Material and methods

Study area

We studied 40 tropical islands ranging in size from 6 m² to 11 806 m² located in a bay of Gam Island in the Raja Ampat Archipelago, Indonesia (Fig. 2a). Climate in the region is wet tropical and lacks a pronounced seasonality with mean annual precipitation of 2768 mm and a mean annual temperature of 27.4°C (nearest weather station Sorong/Jefman, ca 50 km apart; <http://www.worldclimate.com>, 2019). All islands consist of coralline substrate, belong to the same limestone plateau and are of similar age. Therefore, differences in elevation and topographic heterogeneity across islands were very small, ranging for elevation between ca one to eight m a.s.l. Woody vegetation dominates on all islands. Mineral soil was absent and the only soil present consisted of organic matter. We calculated island area (m²) by georeferencing island shapes from satellite images (World Imagery, ESRI 2017)
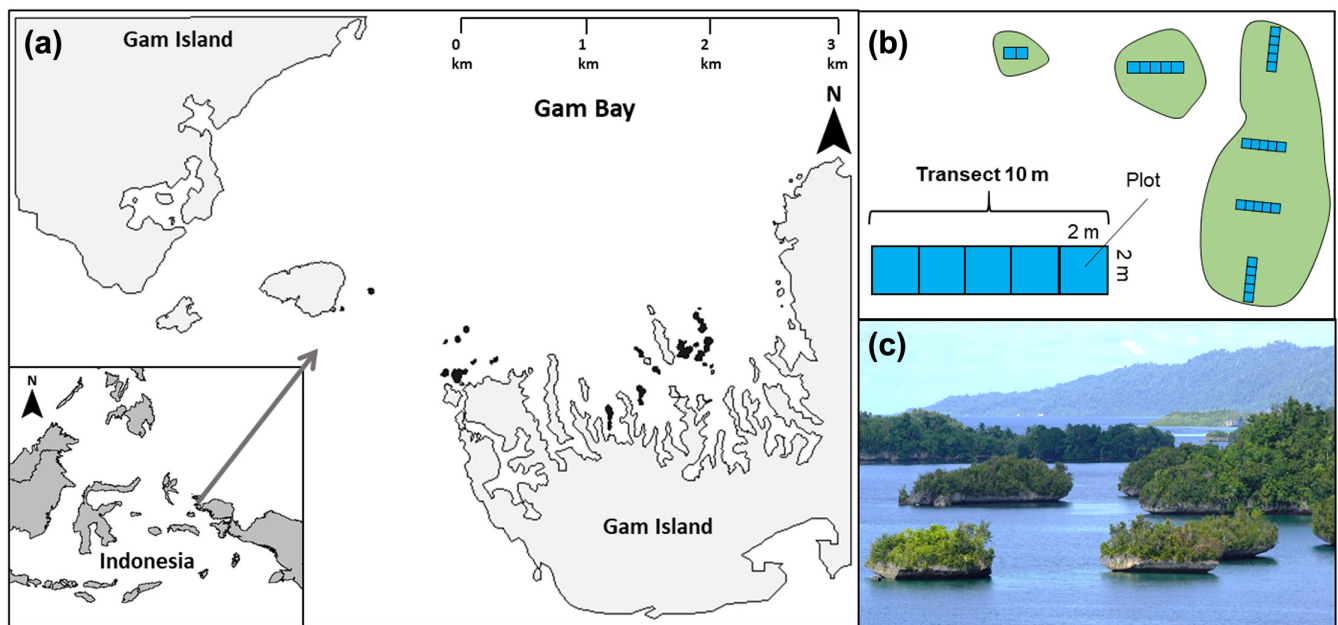

Figure 2. Map of the study region and schematic representation of the study design. (a) Location of 40 islands studied (largest sampled islands highlighted in dark grey; note that the smallest islands cannot be shown at this scale) in Gam Bay in the Raja Ampat Archipelago, Indonesia (coordinates: 0°30′47″S, 130°34′48″E; coordinates for all sampled islands are available in Supporting information). (b) Species richness and number of stems were recorded in plots (2 × 2 m) and transects (10 × 2 m). Number of transects placed on an island depended on island area, whereas larger islands received more transects. On islands smaller than the area of a single transect, we placed as many plots as possible on each island. (c) Gam Bay with some of the islands studied (photo credit: JS).

in ArcGIS (v. 10.3). We only included islands that had not been subject to recent anthropogenic disturbances, limiting the maximum island size to ca 12 000 m². Island isolation did not have strong effects on species richness patterns and functional diversity (Schrader et al. 2019b; Supporting information for effect of island isolation on FD). All islands share a common origin, ontogeny and have very similar ecological conditions. For these reasons, we exclusively focus on island area in our analyses (Supporting information for details of island environmental properties).

Field sampling and functional trait measurements

Botanical field surveys and trait measurements were performed between June 2016 and February 2018. We established transects of 2 × 10 m comprised of five 2 × 2 m plots (Fig. 2b). The number of transects on an island was approximately proportional to island size and ranged from one to six transects (for scaling relationship of sampling area and island area, Supporting information). For the ten islands whose area was < 10 m², we placed as many plots as possible on the island. Larger islands had two transects oriented towards the island centre. The interior was covered by a varying number of transects (depending on the island size) ranging from one to four transects. Distance between transects was held constant within each island. Following this method, we ensured that relevant microhabitats along island edges and interiors were sampled. We recorded all woody plants rooted within the transects with diameter at breast height ≥ 2 cm. We then pooled both species incidences and abundances for all species recorded on each island respectively, resulting in species incidence and abundance matrices used for all subsequent analyses. Soil depth was recorded in all plots at five locations with equal distance to each other (33 cm) and spaced along the central axis of the transect (for detailed description see Schrader et al. 2019b, 2020). Soil fertility is a good proxy for habitat quality, affecting species richness on these islands (Schrader et al. 2019b), and is widely known to also influence species trait combinations (Lebrija-Trejos et al. 2010, Hulshof and Spasojevic 2020).

We studied 11 plant functional traits that represent major dimensions in plant form and function (Westoby 1998, Reich 2014, Díaz et al. 2016). These traits included leaf area, leaf mass per area (LMA), chlorophyll content, leaf N, C:N, C:P and N:P, wood density, plant maximum height and fruit and seed mass. The number of individuals sampled ranged from one to ten individuals from multiple islands, depending on the distribution and rarity of a species. All measurements were aggregated into species' mean trait values (Table 1, Supporting information). For logistical reasons, our trait sampling focused on reliably capturing interspecific trait variation (Lavorel et al. 2008, Baraloto et al. 2010) as it is usually larger in magnitude than intra-specific trait variation (Albert et al. 2010, Thomas et al. 2020).

We measured leaf traits on ten mature and sun-exposed leaves from several individuals per species when available. We calculated leaf mass per area (LMA; g cm⁻²) by calculating

Table 1. Traits, ranges of trait values, number of species sampled and trait classification into four life-history dimensions. LMA: leaf mass per area. Note that tree height was used for both dispersal and the growth strategy. For definitions of the studied traits and references for life-history dimensions, see Methods; for information on species–trait matrix, Supporting information.

Trait and unit	Range	No of species	Life-history dimension
Fruit mass (g)	0.01–20.03	44	Dispersal
Seed mass (g)	0.00004–5.07	51*	Dispersal
Height (m)	1.5–15.8	57	Dispersal; growth strategy
Wood density (g cm⁻³)	0.29–0.99	53	Growth strategy
LMA (g cm⁻²)	0.52–2.6	56	Growth strategy
Leaf area (cm²)	1.78–126.66	56	Light acquisition
Chlorophyll (µm cm⁻²)	19.45–114.55	52	Light acquisition
Leaf N (%)	0.63–2.79	56	Light acquisition
Leaf C:N (ratio)	18.10–86.46	56	Nutrient acquisition
Leaf C:P (ratio)	43.52–421.27	56	Nutrient acquisition
Leaf N:P (ratio)	0.98–13.41	56	Nutrient acquisition

* Seed mass data for 13 species were obtained from the KEW Seed Information Database (<http://data.kew.org/sid/>).

leaf area (cm²) using Leaf-IT (Schrader et al. 2017) and by using a digital balance (± 0.001) for measuring dry leaf mass. Leaves were oven-dried at 80°C for 48 h. We measured leaf chlorophyll content using a chlorophyll-meter (Konica Minolta, SPAD – 502DI Plus), and converted the SPAD measurements to chlorophyll concentrations (µm cm⁻²) using the correlation $Chl = 117.1 \times SPAD / 148.84 - SPAD$ (Coste et al. 2010).

For leaf nutrient analyses, all leaf samples of each species were pooled, oven-dried at 80°C for 48 h, and then grinded. We determined leaf nitrogen and carbon concentration (mg g⁻¹) by automated dry combustion (Elementar, Vario EL Cube). We measured leaf phosphorus concentration (mg g⁻¹) using inductively coupled plasma-atomic emission spectrometer (iCAP 6300 Duo VIEW ICP Spectrometer, Thermo Fischer Scientific GmbH, Dreieich, Germany).

We measured wood density (g cm⁻³) as the volume of the main stem without branches divided by its oven-dry weight. To this end, we cut the main stems into cylinders of two cm length and removed all green parts and the bark. We dried samples at 100°C for 48 h. We used two mature individuals per species for measuring wood density as more extensive sampling was not possible.

We calculated maximum tree height (m) as the mean height of the three tallest individuals of each species (following King et al. 2006).

We measured the dry fruit and seed mass (g) of 44 and 38 species, respectively, aiming for at least ten fruits per species, which was difficult for some species when fruiting was scarce (number of fruits sampled per species ranged from 1 to 40; mean = 11.6). Fruits and seeds were oven-dried at 80°C for

72 h. For the 13 species for which we were unable to collect data in the field, we used seed mass data from the Kew Seed Information Database (SID; <http://data.kew.org/sid>; accessed July 2018). For eight species absent in SID or not identified to species level, we used genus-level means from SID. Trait data are available in Supporting information and in Schrader et al. (2020).

As trait data were missing for 32 (5%) of the 627 species–trait combinations (one trait value missing for LMA, leaf area, leaf N, Leaf C:N, C:P, N:P; three for wood density; four for chlorophyll; six for seed mass; 13 for fruit mass), we applied trait imputation to estimate missing trait data by using multivariate imputation using chained equations in the R-package 'mice' 3.4.0 with the function 'mice' (Van Buuren and Groothuis-Oudshoorn 2011). We used predictive mean matching as recommended for numerical data (Van Buuren and Groothuis-Oudshoorn 2011) and repeated the imputation five times. We log-transformed leaf area and seed and fruit mass to reduce skew.

We grouped the 11 traits into four life-history dimensions that capture important plant strategies for colonisation and establishment on islands (Table 1 for details and Supporting information for trait correlation matrix and Supporting information for clustering of life-history dimensions in trait space). Grouping of traits into life-history dimensions allows for in-depth analyses of community assembly processes (Kohli et al. 2018), which can vary non-uniformly along an environmental gradient that may not be captured by total measures of FD (Spasojevic and Suding 2012). The four life-history dimensions, each represented by three traits (note that tree height was used in two life-history dimensions), were:

1. Dispersal ability: island colonisation greatly depends on species' dispersal abilities (Carlquist 1974). Seed and fruit mass determine long-distance dispersal, as lighter and smaller seeds are more easily dispersed over longer distances and fruits are often transported by birds between islands (Burns 2005, Arjona et al. 2018). Additionally, tree height increases dispersal distance, especially for shorter distances (Thomson et al. 2011).
2. Growth strategy: plant growth strategies depend on environmental conditions and differ greatly between species. The growth strategy dimension characterises species strategies of resource uptake, growth and tissue turnover and includes components of the fast–slow continuum like wood density and LMA. Species with a fast growth strategy tend to have fast resource uptake and tissue turnover rates, while slow species have slower resource uptake, growth and tissue turnover rates (Reich 2014, Díaz et al. 2016, Craven et al. 2018). In this study, we use plant height, LMA and wood density to represent the growth strategy dimension following Wright et al. (2004), Reich (2014) and Díaz et al. (2016).
3. Light acquisition: light availability can differ greatly with island size, with plants on smaller islands being more exposed to light than plants on larger islands where denser forest canopies and lower edge-to-core ratios may decrease light availability. Chlorophyll content, leaf N and leaf area respond strongly to light availability (Valladares et al. 2000, Wright et al. 2004, Díaz et al. 2016), and were used to represent the light acquisition dimension in this study.
4. Nutrient availability: smaller islands may have less available nutrients, as they may have less developed soil and are subject to frequent disturbances due to wave action (Whittaker 1995; Supporting information and Fig. 3–5). By contrast, nutrients and soils on larger islands can accumulate more easily as they are less disturbed. Thus, we used leaf C:N, C:P and N:P to represent the nutrient availability dimension (Wassen et al. 2005, Pérez-Harguindeguy et al. 2013).

Data analysis

For each island, we calculated FD as functional dispersion (FDis) using all traits and the four life-history dimensions separately in the R package 'FD' 1.0-12 (Laliberté and Legendre 2010). FDis is the species' mean distance from the community centroid, accounts for relative abundances, and is recommended when testing for species assembly processes (Schleuter et al. 2010, Mason et al. 2013, Legras et al. 2020). In our island system, only a few species were very abundant while most species were rare (Fig. 2 in Schrader et al. 2020a). Both common and rare species may add novel trait combinations to a community and affect FD (Mouillot et al. 2013, Violle et al. 2017). To test whether FD could be affected by common and rare species alike, we calculated FDis for incidence ($FDis_{inc}$) and abundance data ($FDis_{abun}$). We used the number of individuals recorded in all plots on an island to calculate species abundance.

As we were specifically interested in effects of island area on FDis patterns, we accounted for varying forest structure among islands, which can affect FD (Lohbeck et al. 2014, Craven et al. 2015). Forest structure – expressed as tree basal area per ha (m^2 ha^{-1}) – exhibited a moderate positive and significant correlation with island area (Pearson correlation = 0.45, p < 0.05), indicating that forests on large islands have higher aboveground biomass than on smaller ones. In our island system, differences in tree basal area also affected FDis patterns among islands (Supporting information). Therefore, we minimized the importance of forest structure in our models to isolate the effects of island area on FDis by calculating partial residuals of a linear model with FDis as a response variable and island area (log-transformed) and tree basal area as predictor variables. Island isolation did not exhibit strong effects on FDis and was excluded from all analyses (Supporting information for scaling relationship of island isolation with effect size of FDis).

We constructed two different null models to test whether observed FDis varied from the random expectation that island area had no direct effect on FDis (Mason et al. 2013). We used two null models, because ecological processes derived from random expectations can differ considerably among null models (Götzenberger et al. 2016).
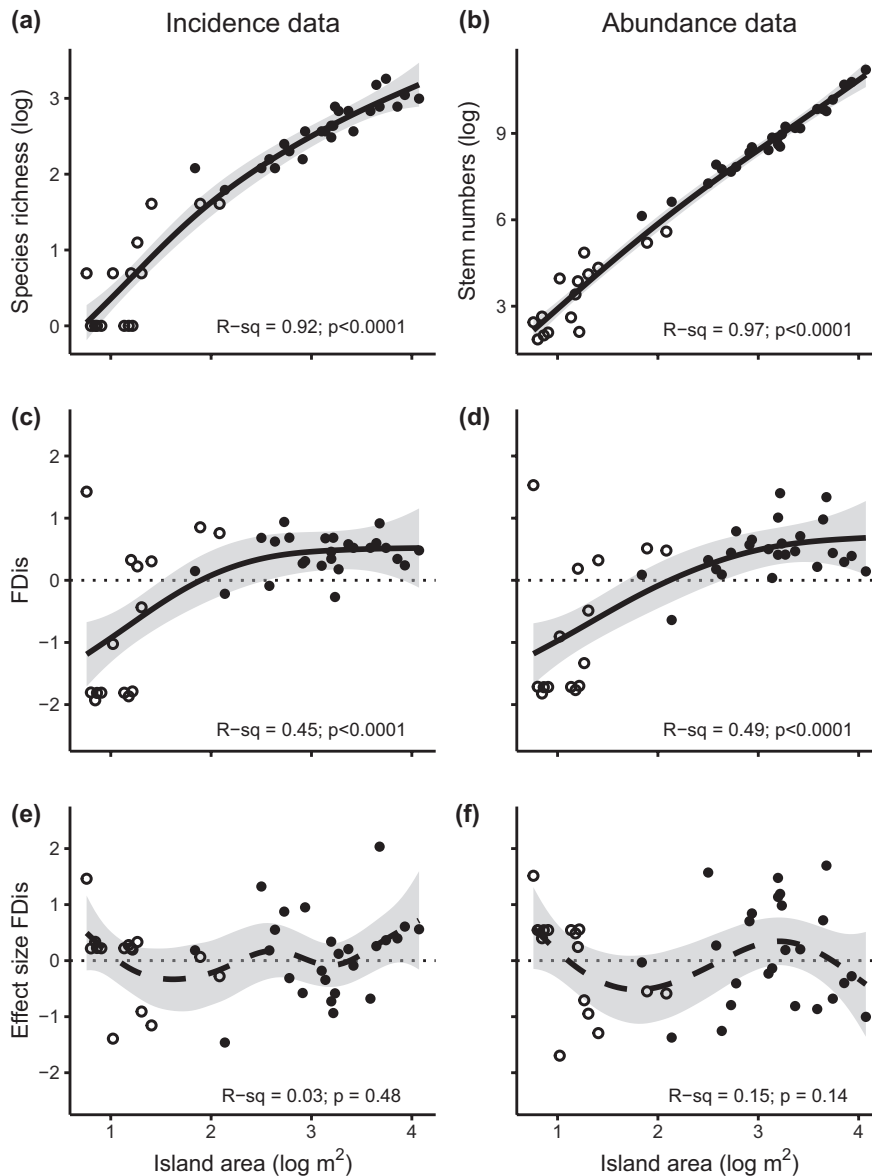
Figure 3. Spatial scaling of species richness, abundance and functional dispersion (FDis) of trees on 40 tropical islands. (a) Species richness and (b) number of stems increase with island area. (c–d) FDis increased with area for both incidence and abundance data. (e–f) Effect size of FDis between observed and randomly created communities using incidence and abundance data. Regression lines indicate partial fits of island area after accounting for tree basal area, which can result in negative FDis values in (c) and (d). White circles indicate islands where soil was absent, and black circles where soil was present. 95% confidence intervals are displayed by grey bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p < 0.05$) are indicated by solid black lines and show that the response variable scales significantly with island area. Non-significant smoothed fixed effects are indicated by dashed lines.

For the first null model, we randomly assigned species to each island while keeping species richness constant, which is suitable to detect non-randomly assembly processes (Götzenberger et al. 2016). For the second null model, we held species frequency and species richness constant. Both null models were repeated 1000 times. For constructing the null models, we used the function 'randomizeMatrix' and the command 'richness' for the first null model and the command 'independentswap' for the second null model within the R package 'picante' v. 1.7 (Kembel et al. 2010).

Results of both null models were strongly positively correlated (Supporting information). As we were primarily interested in detecting non-random assembly processes among islands, we used the first null model for all subsequent analyses.

Next, we calculated effect sizes of FDis for both incidence and abundance data for all traits and each life-history dimension using probit-transformed p-values (Lhotsky et al. 2016) because FDis of the random communities was not normally distributed. To calculate p-values, we used
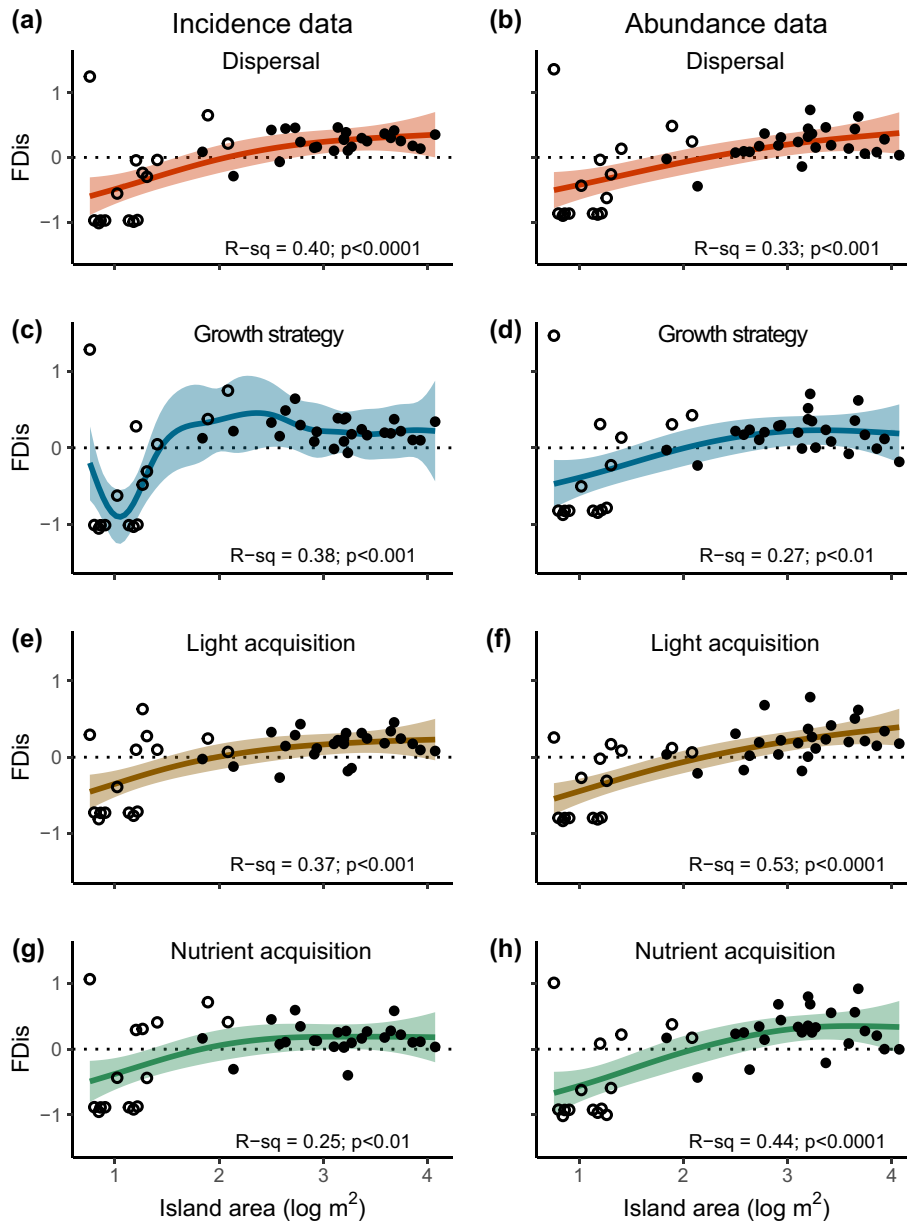
Figure 4. Spatial scaling of functional dispersion (FDis) divided into four life-history dimensions for incidence (left panels) and abundance (right panels) data of 40 insular tree communities. FDis increases for all life-history dimensions with island area. Regression lines indicate partial fits of island area after accounting for tree basal area, which can lead to negative FDis values. White circles indicate islands where soil was absent, and black circles where soil was present. 95% confidence intervals are indicated by coloured bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects (p < 0.05) are indicated by solid lines and show that FDis increases significantly with island area. Grouping of traits into life-history dimensions is shown in Table 1.

the equation proposed by Bernard-Verdier et al. (2012):

$$P = \frac{\text{number(null} < \text{observed)} + \text{number(null} = \text{observed)} / 2}{\text{number randomised communities} + 1}.$$

p-values where then probit-transformed to calculate effect sizes following Lhotsky et al. (2016). Dispersion of effect sizes of FDis can indicate non-random community assembly (Kraft et al. 2008, Mason et al. 2013). Underdispersed effect sizes can be attributed to ecological processes that lead to communities sharing similar traits such as dispersal and

environmental filtering, whereas overdispersed effect sizes indicate processes that lead to trait dissimilarities such as competition, facilitation and niche differentiation (Kraft et al. 2008, Cadotte and Tucker 2017). Evenly dispersed effect sizes of FDis hint towards random assembly processes.

We did not assume a linear relationship between FDis and island area, and thus fitted generalised additive models (GAM) with a Gaussian distribution using the package 'mgcv' 1.8-28 (Wood 2001).
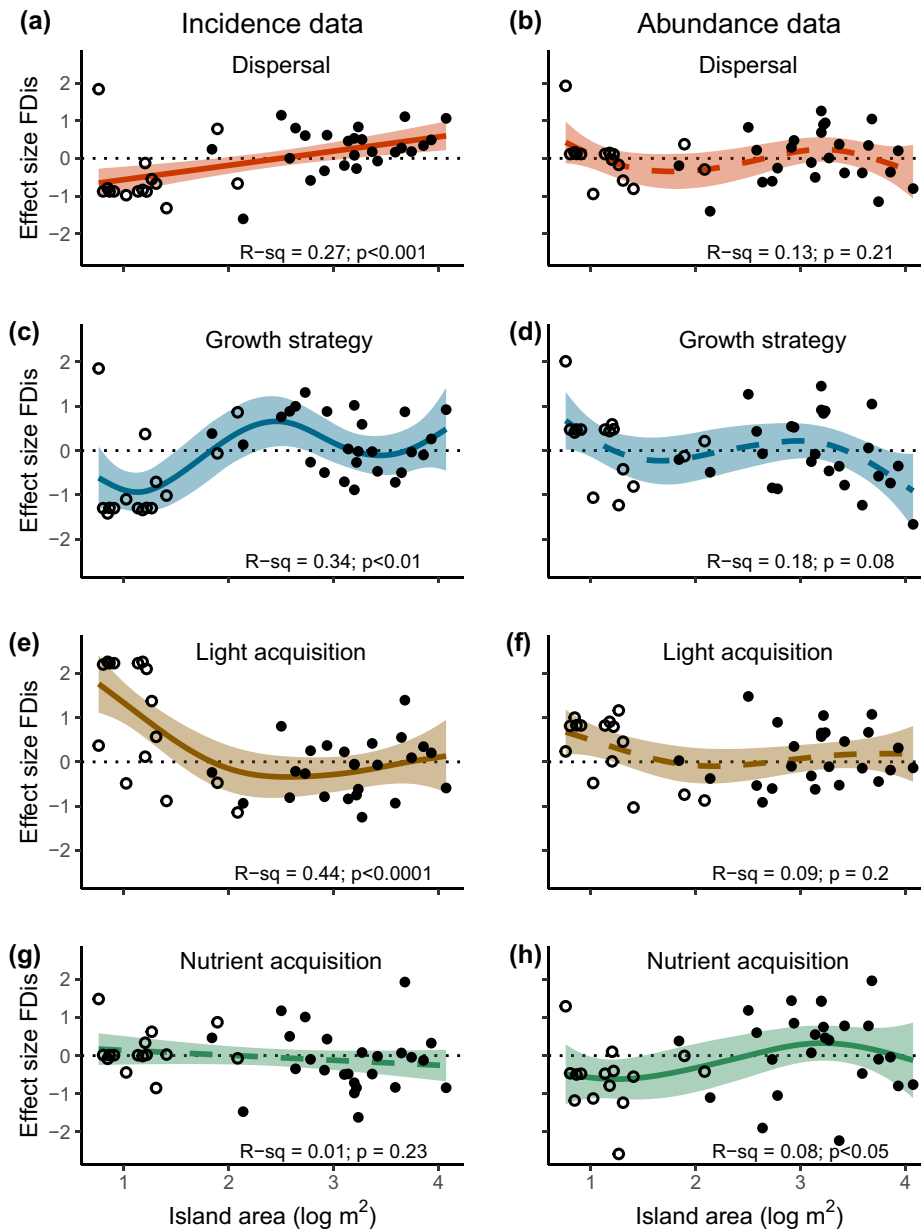
Figure 5. Spatial scaling of the effect size of functional dispersion (FDis) calculated between observed and randomly created communities in four life-history dimensions based on species incidences (left panels) and abundances (right panels) of 40 insular tree communities. Positive effect sizes indicate that the observed FDis on the island was greater than expected by chance and negative effect size indicate that the observed FDis was lower than expected by chance. Regression fits indicate partial fits of island area after accounting for tree basal area. White circles indicate islands where soil was absent, and black circles where soil was present. 95% confidence intervals are indicated by coloured bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p < 0.05$) are indicated by solid lines and show that the effect size of FDis increases significantly with island area and non-significant smoothed fixed effects are indicated by dashed lines. Grouping of traits into life-history dimensions are shown in Table 1.

To evaluate whether common and rare species have unique trait combinations, we calculated functional uniqueness using the package 'funrar' (Grenié et al. 2017). Functional uniqueness describes the functional distance or functional dissimilarity of a species to its functionally nearest neighbour and indicates the degree to which a focal species has no functional equivalent species (Violle et al. 2017).

To visualise the trait space occupied by all species and by the four life-history dimensions, we performed a principal component analysis (PCA) using the function 'prcomp' on trait variables scaled to unit variance. Trait spaces are useful to indicate functional variation between species (Díaz et al. 2016).

All statistical analyses were performed using R ver. 3.4.4 (<www.r-project.org>).

Results

From the 40 sampled islands, we recorded a total of 2215 individuals (range = 1–188; mean = 55) and 57 species (range = 1–27; mean = 6.5). Species richness increased in a linear fashion with island area (Fig. 3a), mirroring the well-supported linear species–area relationship in log–log space (Triantis et al. 2012). The number of stems on an island also increased linearly with island area in log–log space (Fig. 3b).

Functional uniqueness was not correlated with species abundance, showing that functional uniqueness was evenly distributed among both common and rare species (Supporting information). The first two components of the PCA explained only 45% of trait variation, as the functional trait space was strongly partitioned by the four life-history dimensions (Supporting information). The first four dimensions explained a total of 72% of trait variation.

$FDis_{inc}$ and $FDis_{abun}$ calculated for all traits were strongly correlated (r = 0.94) and exhibited similar relationships with island area as species richness, both increasing significantly with island area (Fig. 3c–d). In contrast, effect sizes of $FDis_{inc}$ and $FDis_{abun}$ did not vary with island area, indicating that $FDis_{inc}$ and $FDis_{abun}$ were similar among islands after controlling for species richness (Fig. 3e–f).

FDis of each life-history dimension increased with island area and was highest on larger islands (Fig. 4). Effect sizes of FDis for each life-history dimension yielded contrasting results. The effect size of $FDis_{inc}$ for dispersal increased with area and shifted from underdispersed to overdispersed (Fig. 5a). However, effect sizes of $FDis_{abun}$ for dispersal did not vary significantly with island area (Fig. 5b). We also observed a similar pattern for the growth strategy (Fig. 5c–d). $FDis_{inc}$ of the light acquisition dimension showed overdispersion for smaller islands, shifting to randomly dispersed communities with increasing island area (Fig. 5e), whereas effect sizes of $FDis_{abun}$ was not influenced by island area (Fig. 5f). In contrast, effect sizes of $FDis_{inc}$ for nutrient acquisition were not significantly related to island area, but effect sizes of $FDis_{abun}$ increased with island area from underdispersed to moderately overdispersed (Fig. 5g–h).

Discussion

Our results indicate that tree communities in the studied island system are likely influenced by non-random assembly processes. Different functional trait dispersion patterns of life-history dimensions with island area suggest that these non-random assembly processes can, at least partly, be attributed to dispersal and environmental filters that act simultaneously, but with different strengths, on assembly processes. The results from the null models reveal that these patterns could not be captured by measures of FD that include all traits. We relate the shift in the strength of non-random assembly processes with island area to increases in the diversity of dispersal and resource acquisition strategies. Smaller islands may impose greater dispersal barriers and may provide fewer available niches than larger islands, possibly resulting in underdispersed communities. On larger islands, stochasticity and competition could lead to neutral or overdispersed communities.

Functional diversity scales with island area

Similar to previous island studies, we observed a positive FD–area relationship, resembling the well-known species (richness)–area relationship (Fig. 3a–b; Triantis et al. 2012). The shape of the FD–area relationship did not differ markedly between species incidence and abundance data. This means that both common and rare species add novel trait combinations to the respective island communities, thereby strengthening the FD–area relationship. The increase in FD with island area was also apparent for each of the four life history dimensions, although the FD–area relationship appeared to saturate for islands larger than 100–1000 m². Two mechanisms likely underpin positive FD–area relationships. First, FD was correlated with species richness (Supporting information; Petchey and Gaston 2002), suggesting that additional species add novel trait combinations to communities (Boersma et al. 2016). Therefore, an increase in FD with area is likely a consequence of increasing species richness with area, which could occur under random assembly processes on islands (Fig. 4e–f; Si et al. 2017). Second, increasing FD with island area could be attributed to greater niche diversity on larger islands. Traits are good predictors of species' niche requirements (Kraft et al. 2008, Cadotte et al. 2011), suggesting that higher FD reflects higher niche diversity (Sterck et al. 2011). Indeed, our finding that FD increases with island area supports the idea that niche diversity increases with island area (Losos and Ricklefs 2009, Chisholm et al. 2016). However, the levelling off detected for the FD–area relationship could indicate that niche diversity is finite on larger islands.

Non-random assembly processes shape island tree communities

Our results revealed that island communities are shaped by an interplay of different non-random assembly processes connected to island area, but that the strength of these processes varies with island area (Burns et al. 2010, Si et al. 2017, Schrader 2020). Isolation had no effect on assembly processes likely because the islands were clustered in the same bay and were well-connected. We could thus attribute differences in community dispersal strategies among islands to island area. Non-random assembly connected to dispersal strategies acted most strongly on small island communities, resulting in less diverse dispersal strategies than expected by chance. Plants occurring on the smallest islands often had light seeds and woody and/or winged diaspores, indicating wind or water as the main dispersal vectors. In contrast, plants on larger islands often had fleshy and colourful fruits and heavier seeds, indicating dispersal by frugivorous birds, which were important dispersal vectors in this island system. Most birds, however, preferred larger islands for perching (Schrader

unpubl.), possibly reducing dispersal of bird-dispersed plants to smaller islands. The shift in dominant dispersal vectors between smaller and larger islands may explain why FD of dispersal traits increased with island area. While wind, water and bird dispersed species could disperse readily to large islands – leading to communities with high FD of dispersal strategies – wind and water (and not birds) were prevalent dispersal vectors for colonising smaller islands, resulting in communities with similar dispersal strategies.

Environmental filters indicated contrasting patterns: trait diversity associated with the growth strategy dimension was underdispersed for smaller islands and overdispersed or randomly distributed on larger islands. The light acquisition dimension was more diverse than expected by chance for smaller islands and was randomly distributed on larger islands, while the nutrient acquisition dimension was randomly dispersed across all islands. The smallest islands in our island system had uniform habitats, lacked soil (i.e. organic matter), and were regularly exposed to waves and salt water (Schrader et al. 2019b). In particular, soil development on these islands strongly shaped community composition, as the islands were otherwise similar in terms of precipitation, elevation, shape and substrate (Schrader et al. 2019b). Deeper soil may offset stressful environmental conditions like droughts, provide more nutrients, enable facultative interactions with soil biota (e.g. mycorrhiza) and increase fine-scale environmental heterogeneity, enabling higher FD (Ackerly and Cornwell 2007, Cornwell et al. 2008). Islands with poorly developed soil may thus filter out many species from the regional pool (Liu et al. 2019), resulting in a subset of co-occurring species that share similar habitat requirements (Morrison 2011) and nutrient acquisition strategies (Cornwell et al. 2009). Indeed, shifts towards randomly or overdispersed communities usually occurred on islands that had more developed soil (Fig. 4).

Mean canopy height was lower on smaller islands than on larger ones, suggesting that here light availability was not limiting for most species. The higher solar radiation on small islands may facilitate a greater than expected diversity of leaf adaptations (Givnish 1988, Wright et al. 2004). For example, *Guettarda speciosa* L. has large leaves with low chlorophyll content, *Pemphis acidula* J.R. Forst. & G. Forst. has tiny leaves and *Bikkia gaudichaudiana* Brongn. has leaves with very high chlorophyll content, indicating that species with contrasting strategies to cope with high solar radiation can co-occur on small islands, increase FD and lead to over-dispersed communities.

We found that non-random assembly processes were differentially affected by common and rare species (Fig. 5). The effect size of $FDis_{inc}$ for dispersal, the growth strategy dimension and light acquisition increased significantly with island area, whereas $FDis_{abun}$ for the same life-history dimensions did not vary with island area. This result suggests that rare species increase the trait space of the community and occur more frequently than expected on larger islands, after accounting for species richness. Indeed, rare species had unique trait combinations and added novel trait values (Supporting information;

Mouillot et al. 2013). Common species increased trait diversity of nutrient acquisition with increasing area, possibly due to better developed soils on larger islands. This supports the idea that common species partition niche space along gradients in belowground resources (van Breugel et al. 2019) to a greater extent on larger islands.

In conclusion, we found that the assembly processes structuring tropical island plant communities have a deterministic component. Non-random assembly processes were likely connected to environmental and dispersal filtering that change in strength with island area. Tree communities on smaller islands were particularly affected by non-random assembly processes, leading to less diverse dispersal and growth strategy dimensions yet more diverse light acquisition strategies than expected by chance. Communities on larger islands, in contrast, were likely structured by niche differentiation along the dispersal and growth strategy dimensions and by random assembly processes along the nutrient and light acquisition dimensions. By zooming in on different life history dimensions, we unveiled how community assembly processes respond to islands' geographical characteristics.

Data availability statement

All data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8cz8w9gp4> (Schrader et al. 2020b).

Author contributions

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