




Nonlinear thresholds in the effects of island area on functional diversity in woody plant communities

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Funding information

National Natural Science Foundation of China, Grant/Award Number: 31930073, 31870401, 31901211, 31361123001 and 31570524; International Collaborative Project of National Key R & D Plan, Grant/Award Number: 2018YFE0112800; Project of Zhejiang Provincial Natural Science Foundation of China, Grant/Award Number: LY21C030006; Central Universities, Grant/Award Number: 2019QNA6002; University of Florida Foundation

Handling Editor: Kun-Fang Cao

Abstract

1. Threshold nonlinearities in the relationship between island area and species richness can result in dramatic declines in richness with a seemingly small decline in area near the threshold. What is not known, is whether threshold declines in richness are also accompanied by nonlinear changes in functional trait space and non-random shifts of trait group composition in response to declining area.
2. Plant species richness was recorded, and four functional diversity (FD) indices calculated based on 12 traits for 76 tree species in 5,082 plots (5 × 5 m) on 29 islands in the Thousand Island Lake region, Zhejiang, China. We tested for threshold nonlinearities in richness and FD relationships using segmented regression, with randomized resampling using a null model to account for potential sampling artefacts. We clustered tree species into trait groupings based on trait dissimilarity, and used multinomial segmented models to test whether threshold area effects on FD were associated with shifts in trait group composition.
3. Species richness and three of the four FD indices showed significant threshold nonlinearities with declining island area below a threshold of ca 1.16–6.88 ha. K-means clustering identified two trait groups, reflecting species at the ‘fast’ versus ‘slow’ ends of the trait spectrum. Significant area thresholds in trait group composition were driven by increasing relative richness, but decreasing relative abundance, of species with resource-conservation traits on islands below the threshold.
4. *Synthesis.* We found a threshold collapse in richness on islands below c. 1 ha, resulting in a significant decrease in functional trait space (functional richness) and an increase in the degree of niche differentiation among species in the community (functional divergence) on small islands. Threshold effects were associated with non-random re-assembly of trait group composition, favouring the relative richness of species at the ‘slow’ resource-conservation end of the trait spectrum, but the relative abundance of a few species with ‘fast’ resource-acquisition traits. These results suggest that disturbance-driven dynamics potentially drive a functional shift in the ecosystem state at a critical threshold. We show that a minimum critical habitat area is required to maintain functional diversity in woody plant communities.

KEYWORDS

functional diversity, habitat area, habitat loss, ISAR, plant community assembly, small island effect, threshold, trait group

1 | INTRODUCTION

The island species–area relationship (ISAR) has been one of the cornerstones of predicting species loss rates following habitat loss and fragmentation (Matthews et al., 2014; Whittaker & Fernández-Palacios, 2007). Most applications of the ISAR to declining habitat area have implicitly assumed a uniform exponent of the SAR (MacArthur & Wilson, 1967), although though scale dependence in the form of the ISAR has long been recognized across area gradients from local to regional scales (Rosenzweig, 1995; Triantis et al., 2012). In particular, there has been great interest in potential ‘threshold’ nonlinearities in the ISAR, such as the small island effect, in which richness–area relationships vary below and above the threshold, forming a ‘break point’ in the SAR curve (noted in MacArthur & Wilson, 1967; see Matthews et al., 2014; Schrader et al., 2019; Wang et al., 2018). Understanding area thresholds can lead to better predictions of minimum habitat requirements to mitigate biodiversity loss, and thus help to improve environmental management and conservation strategies in fragmented habitats with varying patch areas (Groffman et al., 2006).

Threshold effects of island area have been investigated largely in relation to a decline in species richness, largely for animal assemblages rather than plant communities (e.g. Estavillo et al., 2013), and not for life-history strategies or functional trait distributions of the species that are lost versus those that persist within remnant communities. This is surprising, as species attributes can give crucial insight into the relative prospects for growth, reproduction and survival among species, providing a mechanistic link to species performance along environmental gradients (Reich, 2014; Violle et al., 2007).

Trait-based perspectives have been used to resolve the different mechanisms that might generate and maintain species co-existence within communities (Dehling et al., 2014), and underpin community assembly rules (Craven et al., 2018; McGill et al., 2006; Sonnier et al., 2014). For instance, plant functional traits can be used to reflect plant resource-use strategies along the acquisitive versus conservative, or ‘fast’ versus ‘slow’, ends of resource economy (Díaz et al., 2016). Moreover, variation in the diversity of functional traits (Petchey & Gaston, 2006) reflects the ‘dimensionality’ and distribution of attributes of species within trait space (Mason et al., 2005). Such variation has been used to quantify changes in community structure following disturbance (Mouillot et al., 2013) and to discriminate among the processes driving community re-assembly, such as environmental filtering versus competition (Mason & De Bello, 2013). In a study of seasonally wet tropical secondary forests in Central Panama, Craven et al. (2018) compared functional diversity between observed and simulated plant communities and found that functional diversity was reduced as a result of environmental filtering. The strength of this effect increased during succession

(Craven et al., 2018), providing mechanistic insight into the processes driving species co-occurrence patterns.

In systems undergoing habitat loss and the fragmentation of remaining habitat into smaller, more isolated patches, species will face impacts not only from declining population size but also from increasing disturbance and abiotic edge effects as patch size decreases (Ewers & Didham, 2006; Haddad et al., 2015). As a result, community re-assembly in small habitat remnants is likely to be associated with the filtering of species with a particular combination of traits that allow them to persist under highly disturbed conditions, which we hypothesize leads to a narrowing of trait space and an associated decrease in functional diversity (Girão et al., 2007; Sonnier et al., 2014). Trait-dependent responses of species to habitat fragmentation have been widely recognized in previous studies (Ewers & Didham, 2006; Laliberté et al., 2010). Likewise, negative effects of habitat fragmentation on components of functional diversity have been observed, such as functional richness as a measure of total trait ‘dimensionality’ of the community (Sonnier et al., 2014) and the mean functional distance between species in the community (Arellano-Rivas et al., 2018). However, few studies have addressed fragmentation effects on multiple interlinked components of functional diversity (Hatfield et al., 2018), or tested potential threshold nonlinearities in plant functional responses to declining habitat area in the ISAR (but see Whittaker et al., 2014 and Magioli et al., 2015, e.g. in animal communities).

Here, we investigate potential nonlinearities in the effect of island area on the taxonomic richness and functional diversity of re-assembling plant communities on 29 land-bridge islands recently formed following flooding by hydroelectric dam construction in the Thousand Island Lake (TIL) region of eastern China. We test for (a) potential threshold nonlinearities in the decline of species richness with decreasing island area and (b) whether threshold declines in richness are also accompanied by nonlinear changes in functional trait space and non-random re-assembly of trait group composition within woody plant communities. A null hypothesis would be that even though species richness may decline in small areas, this is random with respect to functional trait composition and diversity. We, in contrast, predict that a rapid decline in richness below an island area threshold would be associated with sudden and rapid changes in multiple measures of functional diversity, over and above stochastic effects of declining richness and abundance of individuals. The dimensionality of trait space (overall functional richness) would be expected to decline more rapidly below an area threshold than above it, due to strong correlations between functional richness and species richness (Mouchet et al., 2010). At the same time, functional differentiation among species might also be expected to decline, if strong environmental filtering in small fragments selects for species with a narrow distribution of traits (Cornwell et al., 2006; Mason et al., 2005). We expect species at the ‘slow’ end of

the trait spectrum (e.g. with higher leaf dry matter content, LDMC, and lower specific leaf area, SLA) to increase disproportionately on small islands below the threshold while species at the 'fast' end of the spectrum (e.g. with lower LDMC and higher SLA) might be expected to decrease. The reason is that such species should be better able to tolerate disturbances, which we expect are more prevalent in small islands.

2 | MATERIALS AND METHODS

2.1 | Study site and island attributes

The study was carried out on islands in the TIL region in Zhejiang Province, China (29°22'–29°50'N and 118°34'–119°15'E). The lake was formed in 1959 by the construction of a hydroelectric dam on the Xin'anjiang River, after which this valley (around 573 km²) was flooded, resulting in the formation of over 1,000 land-bridge islands (Liu et al., 2018; Yu et al., 2012). Before the construction of the dam, forests in the TIL region were clear-cut, but after damming the area was legally protected from further human disturbance (Hu et al., 2011; Liu et al., 2018). After 60 years of succession, 88.5% of island area is now covered by secondary forest dominated by Masson pine *Pinus massoniana* and mixed broad-leaved species (Liu et al., 2018, 2020). The climate in the TIL region is subtropical and influenced by the monsoon, with an average annual temperature of 17.0°C (and a minimum recorded value of –7.6°C in January and maximum recorded value of 41.8°C in July), average annual precipitation of 1,430 mm, and an average of 155 days of precipitation per year (Hu et al., 2011).

For the purposes of this study, we selected 29 islands ranging from 0.08 to 1,154 ha (Table S1; Figure S1), all of which have permanent long-term vegetation monitoring plots (Liu et al., 2020). These islands span a range of areas, shapes and distances from the mainland, and have low human disturbance. Island area was determined using a Geographic Information System (ArcGIS 9.3) based on areal extent at a lake water level of 108 m a.s.l. (generally corresponding to the edge of forest cover; Hu et al., 2011). We focus on island area in particular, because distance from the mainland has been shown previously to have negligible effects on plant communities in this study system (reviewed in Wilson et al., 2016).

2.2 | Trait selection

We measured 12 functional traits that are associated with resource-use strategies in plants: leaf area (LA), leaf thickness (LT), LDMC, SLA, leaf chlorophyll content (Chloro), leaf stomatal density (StoD), leaf carbon concentration (LCC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), plant maximum height (MH), wood density (WD) and seed mass (SM). Specifically, LA mediates the trade-off between an ability to intercept a large amount of light per leaf and the ability to take advantage of light-rich micro-patches (Pérez-Harguindeguy et al., 2013), which is important for energy and hydraulic balance of a plant (Westoby et al., 2002). This trait

varies at the community level along major environmental gradients (Ackerly et al., 2002; Westoby et al., 2002). LT is associated with the trade-off between leaf photosynthetic rate and construction cost (Niinemets, 2001) and the ability of a plant to cope with environmental stress (Pérez-Harguindeguy et al., 2013). LDMC can be an indicator of both soil fertility and maximal plant growth rate (Hodgson et al., 2011). High SLA and Chloro (a proxy for photosynthesis rate; Murchie & Horton, 1997) are associated with fast-growth species while species with low SLA tend to have higher survival rates (Adler et al., 2013). StoD is a determinant of leaf diffusive conductance: plants with higher StoD have greater flexibility of CO₂ and water fluxes between leaves and the atmosphere (Franks et al., 2015), permitting greater leaf photosynthetic capacity (Tanaka et al., 2013). LCC, LNC and LPC are calculated, respectively, as the ratio of total carbon, nitrogen and phosphorus to leaf dry mass, which are indicators of leaf quality and associated with leaf construction cost and photosynthetic rate (Penning de Vries et al., 1974; Wright et al., 2004). MH corresponds to the ability of a species to compete for light resources, and is closely associated with growth form and potential lifespan of a plant (Díaz et al., 2016). WD is associated with water transport and storage capacity of woody tissues, and it has been shown to be negatively correlated with growth rate and tree mortality (Chave et al., 2009). SM is associated with species dispersal strategy and seedling survival ability versus colonization ability in space and time (Díaz et al., 2016).

2.3 | Data collection

We carried out a census of woody plants (stem diameter at breast height, DBH ≥ 1 cm) on each study island in 2009–2010. On smaller islands (≤1 ha), contiguous 5 m × 5 m plots were arrayed across as much of the island as possible, but irregularities in island shape precluded a total census of the island (Table S1). As island size increased the proportion of total area that could be sampled decreased (Table S1). On islands >1 ha, 5 m × 5 m contiguous plots were established in two or three transects, which traversed the edge and interior habitat of an island (Hu et al., 2019; Liu et al., 2020). The total number of plots on each larger island depended on island area and shape. The number of 5 m × 5 m plots per island varied from 7 on the smallest island to 598 on the largest island (5,082 plots across all islands; Table S1). Variation in sampling effort across islands was accounted for in statistical analyses (as described below).

A total of 76 woody plant species was recorded across the islands, and leaves, branches and fruits from all species were sampled for functional trait measurements. For each tree species, we randomly selected five individuals, and from each individual we gathered samples of 15 mature, sun exposed, healthy and intact leaves, five branches, and five fruits. Measurement of traits followed the protocol proposed by Pérez-Harguindeguy et al. (2013), with LA, LT, Chloro and fresh leaf weight measured in the laboratory within 4 hr after collection from the field. The petioles of leaves were removed before measurements were taken. Ten of the 15 collected leaves

were measured for fresh weight with an electronic balance (AL104, Mettler Toledo Co.) to the nearest 0.001 g. We measured LA (mm²) with a flatbed scanner (LA-S, Plant Image Analyses System) and LT (mm) with a micrometre. Chloro was determined with a portable chlorophyll meter (SPAD-520Plus; Konica Minolta). Finally, leaves were oven-dried at 80°C for 48–72 hr until a constant weight was reached, and the dry weights of 10 leaves were measured immediately after drying. SLA was calculated as the ratio of fresh leaf area to leaf dry weight, and LDMC was calculated as the ratio of dry weight to fresh weight. Then, oven-dried leaves were used for leaf element analyses: LCC and LNC were measured by an elemental analyzer (Vario EL III, elemental, German), and LPC was measured by a UV-Vis spectrophotometer (UV-2550, UV-Visible Spectrophotometer, Shimadzu). StoD was measured for the other five of the 15 leaves by counting the number of stomata in a field of 0.16 mm² under a light microscope (B204TR, OPTeC) with three randomly selected replicates for each leaf. MH was obtained for each species from a plant database in China (Flora of China, <http://www.iplant.cn/foc/>). WD was calculated as an area-weighted average, that is, oven-dried mass (80°C for 48–72 hr) divided by fresh volume (measured by water displacement). For each fruit, all seeds were carefully cleaned and counted; and SM was calculated as the oven-dried seed mass (80°C for 48–72 hr; Pérez-Harguindeguy et al., 2013).

2.4 | Functional diversity

We calculated four indices reflecting multiple facets of functional diversity (Mouchet et al., 2010): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv; Villéger et al., 2008) and functional dispersion (FDis; Laliberté & Legendre, 2010), which together provide complementary insights into the functional structure of species assemblages. FRic quantifies the amount of functional space occupied by the community, that is, the volume of the convex hull of the multidimensional trait space of all species in the community. We scaled FRic values as a proportion of the FRic for the reference community sampled from the largest island (for rationale, see below). FEve quantifies the regularity with which the functional space is filled by species, weighted by their abundance, as measured by the regularity of distances between species in trait space along a minimum spanning tree (Dehling et al., 2014). FEve decreases either when abundance is less evenly distributed among species, or when functional distances among species are less regular (Villéger et al., 2008). FDiv measures species deviation from the mean distance of species to the centre of gravity of trait space, weighted by abundance (Villéger et al., 2008). FDiv is thought to represent the degree of niche differentiation among species in the community and thus higher FDiv could indicate the potential for less competition (Mason et al., 2005). FDis calculates the weighted mean distance of species to the weighted centroid of the multidimensional trait space (Laliberté & Legendre, 2010). FDis is distinct from the above three indices in that it directly refers to functional dissimilarity among species in the community (Laliberté & Legendre, 2010).

Note that FEve, FDiv and FDis, by the very nature of their calculation, are not spuriously confounded with changes in species richness across ecological gradients (Laliberté & Legendre, 2010; Mouchet et al., 2010), although empirically they can covary with richness under some circumstances (Schleuter et al., 2010). Because of missing data (StoD values missing for 4 out of 76 species) we follow Legendre and Legendre (1998) in using the Gower distance metric as the basis for calculating dissimilarity in trait space. These four functional diversity indices were calculated with the *FD* package (Laliberté et al., 2014) in R 3.5.1 (R Core Team, 2020).

Due to the unequal sampling effort across islands, we conducted a randomized resampling procedure to ensure that observed relationships between functional diversity and island area were not a spurious artefact of differences in sampling effort (Karadimou et al., 2016). We were specifically interested in differentiating non-random patterns of deviation in observed functional diversity from null patterns that might be expected in the absence of fragmentation and reduction in island area. Therefore, we carried out a constrained randomization of the data, using the compiled plant community composition data from all sampling plots on the largest island as our expected 'reference' species pool (53 woody plant species and 22,471 individual trees). In this case, the largest island was our best available reference state for the null draw, because we did not have 'pre-fragmentation' data available to directly test re-assembly trajectories through time, nor comparable data from the adjacent mainland forests to represent an 'unfragmented' community state. By comparison to our approach, using the entire regional pool for the random draw would violate the notion of generating null expected patterns in the absence of the ecological mechanism of interest (Gotelli & Graves, 1996), because the small-island plot samples would be contained within the 'regional pool' as well. Using the reference pool, we simulated 'null communities' based on a random draw (with replacement) of the same number of individuals as observed on each of our 29 sampled islands. The resampling process was repeated 1,000 times, generating 1,000 simulated null communities for each island. As our chosen reference species pool does not contain all species from all islands (but is larger in terms of both number of species and number of individuals compared with any single smaller island), we scaled functional diversity indices for each island as a proportion of functional diversity in the reference pool. Observed values (of richness or functional diversity indices) that fell outside the 95% confidence interval (CI) of the predicted null values were considered to deviate more (i.e. be higher or lower) than would be expected by chance alone (i.e. calculated as $(\text{observed} - \text{average}(\text{null})) / \text{standard deviation}(\text{null}))$).

2.5 | Data analysis

Initial inspection of plant community responses indicated clear non-linearity in the effect of island area on species richness and functional diversity indices. We tested for a nonlinear 'break point' in

the area relationships (based on log₁₀-transformed island area values) using segmented regression models with the package `SEGMENTED` (Muggeo, 2017) in R. For richness models, we specified a Poisson error structure (with log link function), and for functional diversity models we specified a Gaussian error structure (with identity link). Note that for ease of interpretation of the ISAR, we illustrate Poisson GLM predictions graphically using model predictions back-transformed onto a linear scaling of species richness. To determine whether the segmented model was the most parsimonious model fit to the data, we carried out a model comparison against a simple generalized linear model (GLM for Poisson models) or linear model (LM for Gaussian models), as appropriate to the data structure, using the Akaike information criterion (AIC) in the `MUMIN` package (Bartoń, 2018) in R. Poisson models were tested for over-dispersion of model residuals using the ratio of residual deviance to residual degrees of freedom, and if the residuals were over-dispersed (i.e. the ratio was much larger than 1), the quasi-Poisson model (with log link function) was used instead (Table S2). For Gaussian models, the heteroscedasticity of model residuals was tested by the Breusch–Pagan Test in the `LMTTEST` package (Zeileis & Hothorn, 2002) in R, and normality was tested by the Kolmogorov–Smirnov Normality Test with the `NORTEST` package (Gross & Ligges, 2015). If model residuals were heteroscedastic or non-normal, a log link function was specified instead (Table S3). We also used a Bayesian Information Criterion (BIC) approach for model comparison, which leads to essentially identical conclusions (see Supporting Information).

To test whether changes in functional diversity were associated with a shift in relative species composition or relative species abundances, we partitioned species into different trait groups. We used K-means partitioning in the `CLUSTER` package (Maechler et al., 2018) in R 3.5.1 to delineate trait groups within our assemblage of 76 woody plant species based on the 12 measured functional traits. We used the Gower distance metric to calculate the dissimilarity matrix in the analysis, due to missing trait data for some species (Legendre & Legendre, 1998). The number of clusters was determined using the average silhouette width criterion (Rousseeuw, 1987). Relative trait-complex differences among trait groups were visualized in a principal coordinates analysis (PCoA, the same analysis method as in the functional diversity calculation) in the R package `VEGAN` (Oksanen et al., 2019) using the Gower distance metric, and pairwise differences in mean trait values among trait groups were tested using one-way analysis of variance (ANOVA).

To test relative shifts in trait group composition across the area threshold, we applied a multinomial segmented regression model, and tested if either multiple separate breakpoints for each trait group or a single common breakpoint across all trait groups represented the most parsimonious fit to the data, as compared to a simple (multinomial) generalized linear model, as described above. The model takes the log-linear Poisson approach to multinomial analysis. In this approach, the same Poisson GLM model (with a log-link function) is used as described above for the species richness model, except species counts per trait group is used as the response variable, and 'trait group' identities are entered as an

additional fixed categorical predictor variable in the model. The interaction effects between trait groups and island area represent the log-odds that the relative frequencies of trait groups vary with area (which is exactly equivalent to the main effects in a multinomial logistic model).

3 | RESULTS

3.1 | Total species richness and functional diversity relationships with island area

Species richness and three of the four functional diversity indices, FRic, FEve and FDiv, all showed significant 'threshold' nonlinearity with declining island area (Figure 1a–d), with the segmented models having substantially lower AIC scores ($\Delta\text{AIC} > 6.92$ in all cases) compared to simple GLM (or LM) models (Table S4). For FDis (Figure 1e), the observed relationship was similar to FDiv, but the segmented model was only marginally better than the simple GLM model ($\Delta\text{AIC} = 0.85$; Table S4), and the difference in slopes across the breakpoint was not significant (Figure 1e; slope difference $p = 0.151$; Table S5).

For species richness, the rate of increase in species richness with island area was significantly higher below the threshold (breakpoint estimate = 1.16 ha, CI = 0.65–2.07 ha), than above the threshold (Figure 1a; slope difference $p < 0.001$; Table S5). The null random draw from the reference community indicated that species richness would also be expected to increase more strongly with area below the threshold (grey triangles in Figure 1a), but observed richness was significantly lower (up to three-fold less) than null expectation below the threshold (Figure 1a).

FRic was highly correlated with species richness across islands (Pearson $r = 0.937$, $p < 0.001$), and FRic responses to island area were correspondingly similar to those observed for species richness (Figure 1b). A greater increase in FRic with area was observed below the threshold (Figure 1b, breakpoint estimate = 6.88 ha, CI = 2.29–20.67 ha; slope difference $p < 0.001$, Table S5), with values significantly lower than could be predicted by stochastic small sample biases on small islands (grey triangles in Figure 1b).

For FEve, there was a significant threshold nonlinearity in response to island area, with a statistically similar breakpoint estimate to that observed for species richness and FRic (breakpoint estimate = 1.31 ha, CI = 0.44–3.93 ha; slope difference $p = 0.002$; Figure 1c; Table S5). In this case, though, FEve showed opposing trends (shifting from negative to positive) on either side of the threshold. Below the threshold, FEve increased significantly with decreasing area, whereas above the threshold FEve increased significantly with increasing island area (Figure 1c). For most islands, standardized effect sizes for FEve differed significantly from null random draws of the reference community (solid circles in Figure 1c), but caution is needed in interpreting results as there was high heterogeneity across islands below the threshold (Figure 1c).

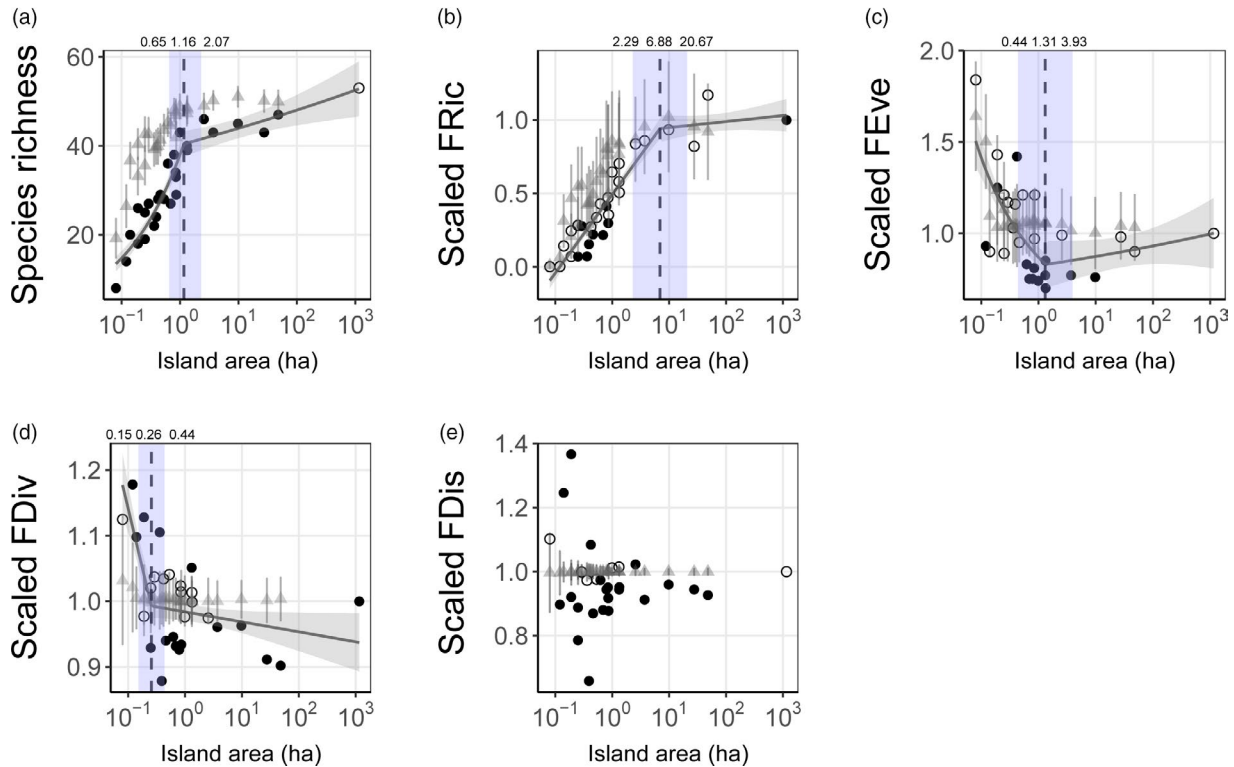


FIGURE 1 Nonlinear effects of island area on species richness (a) and functional diversity indices ([b] functional richness, [c] functional evenness, [d] functional divergence, [e] functional dispersion). The estimated significant breakpoint ($p < 0.05$) in each relationship is represented by the dotted vertical black line, and the light purple shaded area represents the 95% confidence interval (CI) around the breakpoint. Light grey triangles and error bars represent the mean and 95% CI of values from randomly generated null communities, respectively ($n = 1,000$). Black circles represent observed values, in which solid circles represent values that fall outside the 95% CI of null values (i.e. standardized effect sizes that are <-1.96 or >1.96) and open circles represent values that fall within the 95% CI of null values. The light grey shaded area is the 95% CI predicted from the segmented regression. The ISAR in (a) was fitted with log area and a log-link function, but back-transformed to a linear scaling of species richness for ease of interpretation. Functional diversity indices were scaled relative to the values of the largest island

FDiv showed a similar segmented model trend to FEve (Figure 1d), but with a breakpoint that was significantly lower than the estimated breakpoint intervals for richness, FRic or FEve (Figure 1d, breakpoint estimate = 0.26 ha, CI = 0.15–0.44 ha; slope difference $p = 0.005$, Table S5). Some caution is needed in interpreting the relationship as the lower confidence limit for the breakpoint is close to zero, and a few small islands had high leverage on the relationship (Figure 1d). Nevertheless, below the threshold, observed FDiv was significantly higher than expected from null random draws of the reference community, whereas above the threshold observed FDiv was significantly lower than expected by chance alone (Figure 1d).

3.2 | Varying trait group–area relationships

To test whether thresholds in functional diversity were associated with shifts in trait group composition, we used K-means partitioning to cluster trait composition of the 76 woody plant species. This procedure delineated two trait groups (Figure 2; Table S6): the ‘fast’ group (which we refer to as species at the ‘fast’ end of the trait spectrum with high resource-acquisition traits), comprising 36 species

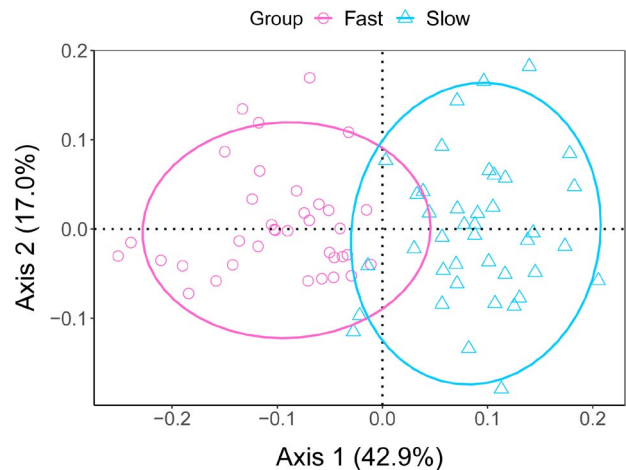


FIGURE 2 Relative trait differences among the 76 species, visualized using a principal coordinates analysis (PCoA) ordination biplot, calculated using the Gower distance metric. Symbols with different shapes represent species in different leaf trait groups clustered by K-means partitioning. Here, ‘Fast’ refers to species with traits at the fast end of the leaf economic spectrum (species with ‘high resource-acquisition traits’) and ‘Slow’ refers to species with traits at the slow end of the leaf economic spectrum (species with ‘high resource-conservation traits’)

with higher LA, higher SLA, higher Chloro, higher LNC, higher LPC, lower LT, lower LDMC, lower LCC and lower MH (one-way ANOVA, all $p < 0.05$; Figure S2), such as *Albizia kalkora*, *Quercus fabri* and *Liquidambar formosana*; and the 'slow' group (which we refer to as species at the 'slow' end of the trait spectrum with high resource-conservation traits), comprising 40 species with the opposite trait characteristics of lower LA, lower SLA, lower Chloro, lower LNC, lower LPC, higher LT, higher LDMC, higher LCC and higher MH (Figure S2), such as *Castanopsis jucunda*, *Quercus acutissima* and *Ternstroemia gymnanthera*.

In the multinomial models, we found evidence of significant threshold nonlinearities along the island area gradient (i.e. model goodness of fit for segmented models was substantially lower than for non-segmented GLM models; Table S7), for both species richness per trait group (Figure 3a,c) and abundance per trait group (Figure 3b,d). Richness per trait group increased more rapidly with

island area below the threshold than above the threshold (breakpoint estimate = 1.17 ha, CI = 0.68–2.04 ha; Figure 3a), and area effects varied significantly between trait groups (Figure 3a), but there was no evidence to support a model with separate breakpoint estimates for each trait group over one with a single common breakpoint for both trait groups (Table S5). The richness model (Figure 3a) can be re-expressed as relative frequencies (i.e. proportion of total richness, Figure 3c), and in this re-plotted graph the contrasting slopes of area effects for the two trait groups resulted in the relative species richness of 'fast' species group increasing with island area, whereas the relative richness of 'slow' species group decreased with increasing island area (Figure 3c). The rate of change in relative frequencies above and below the threshold was small (Figure 3c).

In contrast, abundance per trait group was best explained by an interaction model containing separate breakpoint estimates for

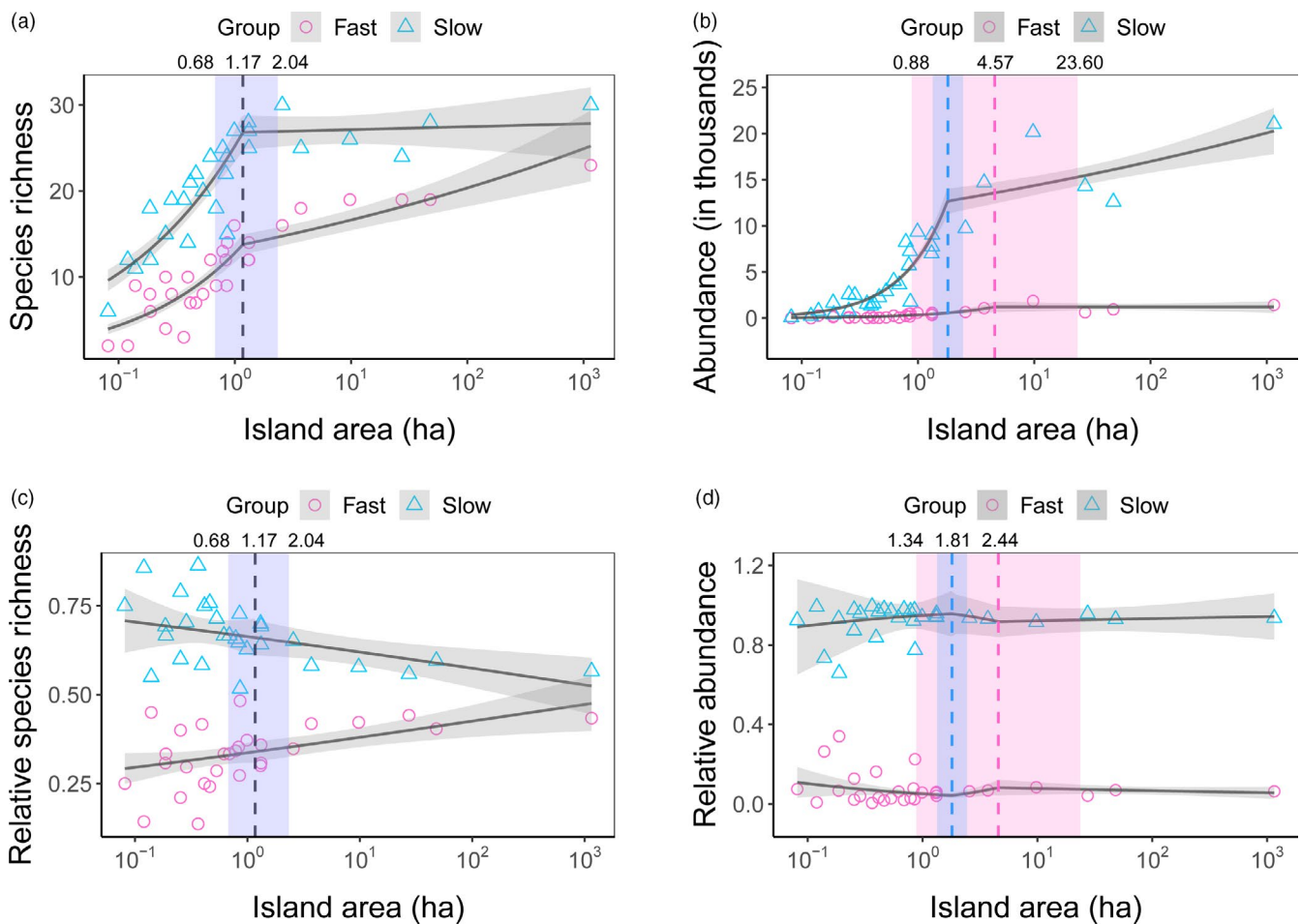


FIGURE 3 Plant trait group composition (fast vs. slow species groups; see Figure 2) along the island area gradient, shown as absolute species richness (a) and abundance (b) per trait group, as well as re-plotted representations of the same data (i.e. from the same analyses as in (a) and (b)), this time shown as relative (i.e. proportional) species richness (c) and relative abundance (d) per trait group. Fitted lines (with light grey shaded area representing predicted 95% CI) are the predicted model estimates from a multinomial generalized linear model. Models were fitted with log area and log-link function, but back-transformed to a linear scaling of richness or abundance response, for ease of interpretation. The dotted vertical black lines represent the predicted breakpoints ($p < 0.001$) calculated from species richness and abundance, with light pink shaded areas (for fast species group), light blue shaded areas (for slow species group) and light purple shaded areas (for both groups combined) representing the 95% CI. Breakpoint and CI values for the abundance of 'fast' species group are given in (b), whereas the breakpoint and CI values for 'slow' species group are given in (d)

each trait group (Table S5), leading to significant changes in relative frequencies of trait groups below the thresholds (Figure 3b,d). Abundance of species in the 'slow' group showed a more rapid increase in abundance with island area below the threshold than above the threshold (breakpoint estimate = 1.81 ha, CI = 1.34–2.44 ha, slope difference $p < 0.001$; Figure 3b; Table S5), whereas the 'fast' species group did not show a significant difference in slope at the breakpoint (breakpoint estimate = 4.57 ha, CI = 0.88–23.60 ha; slope difference $p = 0.326$; Figure 3b; Table S5). Some caution is needed in interpreting the different area thresholds between trait groupings, as the confidence interval for breakpoint estimates is high (Figure 3c). Expressed as relative frequencies (i.e. proportion of total abundance, Figure 3d), trait group composition changed in the opposite direction to that observed for relative richness, with the relative abundance of 'fast' species decreasing with island area below the threshold, whereas the relative abundance of 'slow' species increased with island area below the threshold (Figure 3d).

4 | DISCUSSION

Plant communities in small habitat fragments are very different than might be expected from a null random draw of intact communities observed in an equivalent area of continuous habitat (Harrison, 1999; Liu et al., 2020). Habitat heterogeneity tends to be lower on small islands (Collinge, 1996; Yu et al., 2012), the probability of population persistence is reduced (particularly for rare species with low dispersal capacity; Liu, Slik, et al., 2019), and the alteration of biotic and abiotic conditions at habitat edges favours some species over others (Harper et al., 2005). Here we have shown that habitat reduction leads not just to a gradual attrition of species richness on smaller habitat islands (over and above what might be expected from null sampling) but also to a striking threshold nonlinearity in the 'collapse' of plant species richness on islands of less than c. 1–2 ha. This has been noted before (see e.g. Matthews et al., 2014; Wang et al., 2018) but for the first time, we also provide evidence that these nonlinear thresholds in the ISAR are accompanied by nonlinear thresholds in how functional trait diversity changes with decreasing island area. We discuss the patterns and potential drivers of these functional diversity effects, and how they might influence ecological processes and conservation management strategies in fragmented landscapes.

4.1 | An area threshold in plant species richness

Despite more than 150 years of interest in the ISAR (Watson, 1835, 1859) and widespread recognition of scale dependence in the form of the relationship (Rosenzweig, 1995; Triantis et al., 2012), explicit evidence for threshold nonlinearities is still comparatively rare (Matthews et al., 2014; Wang et al., 2018). In a meta-analysis of 76 of the habitat island datasets available, Matthews et al. (2014) found that 69% of ISAR models were linear or non-significant (in log–log

space). Only 16% had the 'steep-shallow' form of nonlinear threshold identified in the current study (i.e. steeply increasing with area below a threshold, then flattening to a shallower slope above it), despite this traditionally being widely sought as a prescriptive tool for nature reserve design in conservation planning (Huggett, 2005). For example, Drinnan (2005) suggested that a minimum area of 2 ha was required to conserve plant species richness and 4 ha to conserve bird and frog species richness in a fragmented urban environment of southern Sydney, Australia. Such recommendations implicitly assume 'break-points' in species–area relationships.

Putting these analytical issues to one side, we would point out that we are not interested principally in the nature reserve planning implications of a rapid decline in richness below a defined area threshold. Moreover, we make no value judgement on what this observation might imply about the potential contribution of small fragments to conservation. Even tiny habitat remnants (as small as single trees) can provide stepping stones enhancing connectivity in fragmented landscapes (Tscharntke et al., 2002) and can contribute high complementarity of assemblage composition in networks of small remnants (aka the 'SLOSS' debate; Ovaskainen, 2002). Instead, we are most interested in the ecological implications of threshold nonlinearities for the trait structure of communities and, potentially, altered ecosystem functioning in small fragments below the threshold.

4.2 | Area thresholds in functional diversity

Even though species richness declined more below the area threshold than might have been expected, it is still plausible that species present in small remnants could have been random with respect to the functional trait attributes of species. We tested this using functional diversity indices that reflect trait diversity and differentiation among species, and found evidence that species assemblages were not random. There was a clear trait dependence in response, with striking evidence for nonlinear thresholds in some measures of plant functional diversity.

Functional richness (FRic), measured as the convex hull volume of trait space (Villéger et al., 2008), declined significantly below a threshold island area of c. 7 ha, and was significantly lower than expected. The evidence shows that threshold declines in functional richness might occur first, prior to threshold declines in species richness, suggesting species with the most dissimilar traits might be missing. However, FRic is not a sensitive measure of divergence in traits, and it is known to be strongly dependent on underlying richness trends (Mouchet et al., 2010). As such, it would be difficult to separate the effects of random versus non-random absences of species as drivers of area thresholds in FRic. By contrast, the evenness (FEve), divergence (FDiv) and dispersion (FDis) components of functional diversity are not spuriously correlated with species richness (Laliberté & Legendre, 2010). All three functional diversity indices showed significant deviations from null expectations on one or more islands, but evidence for nonlinear thresholds in trait differentiation with declining island area was only strongly evident for FDiv and

FEve. Moreover, FDis deviated markedly from the null expectation on almost all islands, but variability among islands was high and no statistically significant area threshold was detected. For FDiv (divergence of the most abundant species in functional space, which can indicate the degree of niche differentiation among species in the community; Mason et al., 2005), the trend was comparable with that observed for FDis, but with lower random scatter, and a significant area threshold was detected at c. 0.26 ha. On larger islands above the area threshold, the degree of trait divergence among species was lower than expected, whereas on very small islands below the area threshold, trait divergence was significantly higher than the null expectation. This is the opposite of our initial expectation that functional divergence would decline with decreasing island area, a hypothesis based on the rationale that extreme environmental conditions on smaller islands might favour species with a narrow range of similar traits that promote persistence (Mayfield & Levine, 2010). For instance, Enrique et al. (2018) found a decrease in FDiv within woody plant communities in response to increasing aridity. However, the response of FDiv to deforestation and habitat fragmentation is inconsistent across taxa, with no clear trend found in studies of birds (Ding et al., 2013), insects (Tu et al., 2019) or woody plant fruit traits (Pessoa et al., 2017) while other studies have even found higher FDiv of woody plant reproductive traits in smaller fragments (Magnago et al., 2014) or under low forest cover (Rocha-Santos et al., 2020). Few studies have assessed FDiv of woody plant traits in fragmented landscapes, but Apaza-Quevedo et al. (2015) did find a slight decrease in FDiv at the forest edge in a tropical montane forest. In the TIL system, high FDiv on islands below the threshold suggests that in this region the most abundant co-occurring species on very small islands were quite dissimilar in functional traits, leading to a high level of niche differentiation in resource use. MacArthur (1972) suggested that even modest competitive overlap could lead to extinctions or prevent colonizations on small islands, so for species to coexist, they need to be even more different on small islands than on large islands.

The disparity in the area threshold between FRic and FDiv is notable. Area threshold values as low as that observed for FDiv are not unheard of, but ours are at the lower end of the range of recorded values (0.3–50 ha; Matthews et al., 2014). Given the limited number of islands in that size range within our study system, such patterns could conceivably arise by chance (even though the statistical evidence for a breakpoint appears strong). Nevertheless, we tentatively interpret these findings to mean that small islands below c. 1–2 ha might have increased constraints on the colonization or persistence of species with particular traits, as well as a lower total range or diversity of functional traits in the community. When island area is extremely small, communities might diverge dramatically onto different trait assembly trajectories (see Miedema et al., 2019). Habitat fragments can show dramatically different trajectories in their community composition, depending, for instance, on whether or not successional dynamics are occurring (Collins et al., 2017). It would be valuable to examine the relationship between trait diversity and fragment area across a broad range of experimental and non-experimental fragmented landscapes.

4.3 | Threshold shifts in trait group composition

If thresholds in functional diversity are associated with non-random shifts in trait group composition, reflecting, for instance, environmental harshness or increased disturbance effects on smaller islands, we might expect that species with resource-conservation attributes (such as higher LDMC and lower SLA) would increase disproportionately on small islands below the threshold (Grime, 2006; Pérez-Harguindeguy et al., 2013), while species with resource-acquisition traits (such as lower LDMC and higher SLA) would decrease (Liancourt et al., 2015; Wright et al., 2004). We used a K-means clustering approach as a statistically objective method to delineate species groupings directly relevant to the above-ground functional trait measures used in the functional diversity analyses. As expected, this separated species groupings that spanned different sectors of the resource-use spectrum (Wright et al., 2004). Of the two groups identified, species in the 'fast' group had 'high resource-acquisition traits' with relatively high SLA, high leaf nutrient concentration and low LDMC values, adapted to a strategy of rapid biomass production (Garnier et al., 2001), typical of species at the 'fast' end of the leaf economic spectrum (Wright et al., 2004). Meanwhile, species in the 'slow' group had 'high resource-conservation traits' with low SLA, low leaf nutrient concentration and high LDMC values, typical of species adapted to resource conservation (Garnier et al., 2001) at the 'slow' end of the leaf economic spectrum (Wright et al., 2004).

As observed for total plant species richness, there were significant nonlinear thresholds in the richness of both functional trait groupings as well. What is more, richness per trait group showed almost identical breakpoint and change-in-slope statistics as observed in the ISAR, regardless of trait group identity. As predicted, the relative richness of species with resource-conservation traits increased disproportionately on small islands below the threshold while the relative richness of species with resource-acquisition traits decreased. Without time-series data, one cannot evaluate whether or not the patterns we have documented reflect impacts of traits on colonization, or extinction following colonization. Extinction debts should be paid out faster on small islands than large islands (Gonzalez, 2000), and more slowly for species with resource-conservation traits than with resource-acquisition traits (as might be predicted if they are typically also longer-lived species; Jackson & Sax, 2010). An alternative explanation might be an immigration credit (*sensu* Jackson & Sax, 2010) for species with resource-acquisition traits, although this seems less plausible as light-demanding species typically living in 'edgy' habitat tend to have good dispersal capacity.

Unexpectedly, we also found discordant patterns in the relative abundance versus relative richness of trait-group composition. In direct contrast to the findings for relative richness, the relative abundance of species with resource-acquisition traits increased disproportionately on small islands below the threshold while the relative abundance of species with resource-conservation traits decreased. We offer the following tentative explanation. These contrasting trait group effects might be explained by differing scales at which niche differentiation might operate, one between major

functional groups, and the other, within such groups. At a coarse scale, strong environmental filtering (Girão et al., 2007; Sonnier et al., 2014), such as in early- versus late-successional habitats might favour species with differing trade-off strategies in their ability to exploit versus conserve resources (Díaz et al., 2004), or tolerate disturbance. In the flooded valley system of the TIL, forests were clear-cut before lake formation, giving a common starting point to secondary succession across all islands (Liu, Coomes, et al., 2019), but smaller islands intrinsically have a higher proportion of near-edge habitat and higher degree of edge penetration into the forest interior, which is thought to favour fast-growing pioneer species (e.g. Benchimol & Peres, 2015). At a coarse scale, then, niche differentiation might well favour a higher relative abundance of early-successional species on small islands compared with large islands. At a finer scale, however, the determinants of species richness within trait groups might be different, and involve different and perhaps more subtle niche axes than measured in the current study. Some of these niche axes could potentially lead to emergent priority effects. For instance, given the lower carrying capacity of small habitat patches, we might expect stronger priority effects for early-arriving species (Fukami, 2015), which are typically fast-growing species with resource-acquisitive traits (Boukili & Chazdon, 2017). Biotic interactions, including such effects as facilitation by ectomycorrhizal mutualists in the soil, might then favour dominance of early colonists over later colonists with similar functional traits. It is possible, then, that priority effects could underlie the lower relative richness of species with resource-acquisition traits on small versus large islands, and the observed discordant patterns between relative richness and relative abundance. Although the mechanisms remain to be elucidated, our results suggests there might be strong context dependence in relative richness and abundance responses, even within the same system, which will require even more careful consideration of comparative findings when comparing across different study systems with varying trait group composition and varying selective pressures. Moreover, successional dynamics are likely still underway, playing out at different rates and trajectories on islands differing in size, so it is possible that some of the patterns we have reported here will shift over time.

Taken together, the stronger effect of area on relative trait group representation (and the complexity we found in such effects) below the threshold might explain why functional divergence (FDiv), in particular, had a significant nonlinear relationship with island area. However, there is not a clear match in the location of the area threshold (being markedly lower for FDiv than for trait group representation). Further work is clearly needed to tease apart the drivers of changing functional diversity on small islands, but our results suggest that it may be driven not only by the gains and losses of species with differing trait complexes but also by shifting selection pressures acting on relative abundances within trait groups. Determining the functional basis for these effects would be a crucial step forward, which would require direct ecophysiological measurements to understand the trait-environment relationships driving community re-assembly.

ACKNOWLEDGEMENTS

We thank students in the Community Ecology and Conservation laboratory of Zhejiang University for assistance with field surveys and trait measurements, especially Guang Hu, Jinfeng Yuan and Jingjing Yu. This research was supported by the National Natural Science Foundation of China (grant no. 31930073, 31870401, 31901211, 31361123001, 31570524), International Collaborative Project of National Key R & D Plan (2018YFE0112800), the Zhejiang Provincial Natural Science Foundation (LY21C030006) and the Fundamental Research Funds for the Central Universities (2019QNA6002). R.D.H. and S.Z. thank the University of Florida Foundation for support. The authors declare they have no conflicts of interest.

AUTHORS' CONTRIBUTIONS

M.Y. conceived and coordinated the study; R.K.D. developed the nonlinear threshold approach and R.K.D., S.Z. and A.Z. analysed the data; A.Z., S.Z. and R.K.D. wrote the initial manuscript, and R.D.H. and M.Y. contributed conceptual insights and writing to later iterations of the manuscript. All authors contributed critically to the final manuscript and gave approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13632>.

DATA AVAILABILITY STATEMENT

The data of island attributes and species diversity are provided in the Supporting Information. Functional diversity data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2z34ttmpm0> (Zhang et al., 2021).

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SUPPORTING INFORMATION

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

How to cite this article: Zhang A, Zheng S, Didham RK, Holt RD, Yu M. Nonlinear thresholds in the effects of island area on functional diversity in woody plant communities. *J Ecol*. 2021;109:2177–2189. <https://doi.org/10.1111/1365-2745.13632>