Community re-assembly and divergence of woody plant traits in an island–mainland system after more than 50 years of regeneration

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Abstract

Aim: Understanding long-term community assembly trajectories following habitat fragmentation remains a major challenge. Varying time since disturbance and heterogeneous initial starting conditions confound real-world comparisons of re-assembly trajectories in fragmented versus intact systems. Here, we overcome these issues in a novel manner using a system of islands and adjacent mainland habitats with common initial starting conditions following clear-felling of forests during hydroelectric dam construction in 1959. Fifty years after resetting 'future-islands' and 'future-mainland sites' to common initial starting conditions, we determine the outcome of re-assembly trajectories in plant taxonomic, phylogenetic and functional trait composition, and how these have diverged between islands versus continuous mainland habitats.

Location: Thousand Island Lake, China.

Methods: We surveyed woody plant communities on 26 islands and 26 adjacent mainland plots, and characterized 12 functional traits for 91 woody plant species (>46,000 total stems with DBH ≥1 cm). We used variance partitioning analysis to discriminate major environmental and spatial drivers of compositional differences, and generalised linear models to test trait and phylogenetic responses to underlying environmental gradients in island versus mainland plots.

Results: We found striking differences in species composition between island and mainland plots. Variance partitioning showed that species composition on islands was governed by local environmental variables, suggesting an important role for environmental filtering, while compositional variation across mainland plots was determined by spatial variables. Ten of 12 functional traits showed significant divergence in community-weighted mean values between island and mainland plots. Moreover, most traits exhibited significant interaction effects between isolation (island versus mainland) and underlying environmental gradients in soil fertility and stress tolerance.

Main conclusion: These findings strongly suggest divergence in trait–environment relationships following isolation in fragmented habitats, with important implications for understanding future re-assembly trajectories in fragmented systems that now dominate the planet.
1 | INTRODUCTION

One of the fundamental aims of ecology is to understand the factors that determine variation in community assembly through space and time. Recent advances in community assembly theory provide a solid framework for the spatial determinants of local assembly from the regional species pool, due to stochastic drift, dispersal limitation and selection processes such as environmental filtering and biotic interactions (Götzenberger et al., 2012; Hillerislambers et al., 2012; Kraft & Ackerly, 2014; Ovaskainen et al., 2017; Vellend, 2016). However, despite decades of research our understanding of the longer-term temporal trajectories of community response and recovery from large-scale disturbance events is still limited (Jin et al., 2020; Liu et al., 2016; Myers et al., 2015; Rozendaal et al., 2019). Tackling this limitation has never been more urgent, as large-scale habitat destruction and land use change continue to transform the planet (Foley et al., 2005; Tilman et al., 1994).

Globally, at least half of all natural habitats have already been lost (Secretariat of the Convention on Biological Diversity, 2020), and in most regions of the world, the remaining habitat fragments are small (Liu, Coomes, Gibson, et al., 2019) and dominated by edge effects (Haddad et al., 2015), exacerbating the effects of ecosystem decay on biodiversity (Chase et al., 2020). Increasingly, prospects for effective biodiversity conservation hinge on successional re-assembly processes in secondary forests that now dominate most landscapes (Feng et al., 2014; Norden et al., 2009). While we might have a clear idea of the dominant assembly processes at work in these systems (at least in very general terms; Bhaskar et al., 2014; Pinho et al., 2018), all of the key drivers of assembly are fundamentally altered in highly fragmented landscapes. For instance, key assembly processes such as environmental filtering and competitive exclusion covary along environmental gradients of changing soil fertility, light or water availability (Döbert et al., 2017; Kraft & Ackerly, 2010) and all of these environmental gradients are strongly affected by fragmentation (Laurance et al., 2018). Furthermore, in plant communities, functional traits related to regeneration have been found to display more divergent patterns with shifting environmental conditions, while traits related to the use of limited resources and increased environmental tolerance may display more convergent patterns of functional trait assembly (Bernard-Verdier et al., 2012; Grime, 2006; Kraft & Ackerly, 2010; Swenson & Enquist, 2009). The consequences of altered early-successional processes for long-term community re-assembly are less certain (Mason et al., 2012; Schamp et al., 2008), particularly in the context of altered spatial configuration and increasing isolation of remnant habitats.

Several previous studies provide insight into how assembly processes might change in fragmented habitats. For example, Negoita et al. (2016) found that increasing habitat isolation can drive alteration of functional trait assembly trajectories in plant communities on islands. In the Kansas long-term habitat fragmentation experiment, several small-scale studies have been instrumental in disentangling the impacts of declining habitat area and spatial habitat configuration on community assembly (Collins et al., 2017; Robinson et al., 1992). However, there is a disparity between the small scale at which it is feasible to conduct direct experimental manipulation, versus the larger real-world scales at which natural landscapes are fragmented and conservation priorities are set. We still know little about how ecological processes such as environmental filtering, dispersal and biotic interactions affect community assembly in fragmented landscapes (Patiño et al., 2017; Wilson et al., 2016).

A key part of the challenge in understanding long-term assembly trajectories in fragmented landscapes lies in the heterogeneous initial starting conditions that exist in most real-world comparisons of fragmented versus intact systems, which confound any simple comparison of temporal re-assembly trajectories. Here, we describe a study system that overcomes this confounding issue in a novel manner. In 1959, during construction of a hydroelectric dam in eastern China, all surrounding forests were clear-felled at the same time, effectively resetting “future-islands” and “future-mainland sites” to a common initial starting point of plant community re-assembly. Now, 50 years later, we determine the outcome of re-assembly trajectories in plant taxonomic, phylogenetic and functional trait composition, and how these have diverged between fragmented island versus continuous mainland habitats. Notionally, this is analogous to E.O. Wilson’s original island defaunation studies that created a common starting point to re-assembly as an effective means of assessing the underlying processes of community assembly in fragmented systems (Simberloff & Wilson, 1969; Wilson & Simberloff, 1969).

At the taxonomic assemblage level, we characterized changes in species composition and the relative importance of environmental filtering and dispersal limitation in the Thousand Island Lake (TIL) system after more than 50 years of regeneration. Species turnover (β-diversity) not only links species diversity at local (α-diversity) and regional (γ-diversity) scales (Whittaker, 1960, 1972), but can also provide insight into the processes driving community assembly (Anderson et al., 2011; Tuomisto et al., 2003). We test the hypothesis that species turnover will be lower among island plots, than among mainland plots, due to greater dispersal limitation among islands and the likelihood that only a small subset of species have high colonization potential. However, focusing solely on β-diversity measures might overlook important ecological changes in species selection during community assembly (i.e. similar amounts of turnover, but divergence into different parts of functional trait or phylogenetic space). We use measures of functional and phylogenetic dispersion to further disentangle potential mechanisms underlying community assembly processes (Cadotte et al., 2017; Kraft et al., 2008;
Swenson, 2014; Tucker et al., 2017). We test the hypothesis that islands will have increased abiotic edge exposure and disturbance, leading to a greater importance of environmental filtering processes and greater functional and phylogenetic convergence within island assemblages compared with mainland assemblages (in which greater divergence might suggest strong competitive exclusion processes are operating; Mayfield & Levine, 2010; Shipley, 2009). Lastly, for community-wide shifts in assembly trajectories, we determine the key trait–environment relationships that are altered in fragmented island system versus continuous mainland system. We test the hypothesis that altered environmental conditions in island versus mainland plots will result in a divergence in trait–environment relationships, with trait–mean shifts in island assemblage composition favouring species with high dispersal and traits associated with disturbance tolerance and fast growth. We discuss the importance of these findings for understanding future re-assembly trajectories in fragmented systems that now dominate the planet.

2 | METHODS

2.1 | Study system

Our study was conducted at TIL in Zhejiang Province, eastern China (29°22′−29°50′N, 118°34′−119°15′E) (Figure 1). The lake is an artificial hydroelectric reservoir formed in 1959 by the construction of the Xin'anjiang Dam. According to our latest remote sensing data, the total area of the lake is 581 km² (water area is 540 km², and island area is 41 km²) and the lake has more than 1,000 land bridge islands larger than 0.25 ha. During dam construction, forests around TIL were cleared through organized logging during the “Great Leap Forward,” and near-complete deforestation by local people before the lake’s inundation (Liu, Coomes, Hu, et al., 2019). Currently, most land area on the islands and adjacent lowland mainland at TIL is covered by unmanaged secondary forests dominated by Masson pine, Pinus massoniana, which is an important pioneer tree species of subtropical lowland forest communities in China. Climatic conditions at the study sites are typical of the middle subtropical climatic zone, with an average annual temperature of 17.0°C (range: −7.6°C in January to 41.8°C in July) and mean annual precipitation of 1,430 mm (Wang et al., 2010).

2.1.1 | Vegetation sampling on islands

In 2014–2015, we selected 26 study islands (island area >0.185 ha; Figure 1) covered by unmanaged secondary Masson pine forests and with minimum human disturbance. Within each island, one permanently marked 0.09-ha plot was established at a randomly chosen location (out of a larger set of permanent plots established in 2009; Hu et al., 2016; Liu et al., 2020). For the 17 relatively large islands, it was possible to have a square plot with sides of 30 m (made up of a contiguous square array of 5 × 5 m quadrats). For the nine smaller islands, the plot was made up of several connected 5 × 5 m quadrats with total area of 0.09 ha, constrained by the irregular shape and small size of the islands. Using the protocols of the Center for Tropical Forest Sciences (Condit, 1998), all free-standing woody plants with diameter at breast height (DBH) ≥1 cm were identified, measured, tagged and mapped in 5 × 5 m quadrats. Species accumulation curves for the 26 island plots approached an asymptote in all cases (Figure S1), suggesting that field surveys of 30 × 30 m adequately reflect variation in species richness across islands.

2.1.2 | Vegetation sampling on the adjacent mainland

In 2016, we established 26 permanent 30 × 30 m plots on the adjacent mainland within protected areas of secondary forest
regeneration that were not subject to planted reforestation and were not in close proximity to agricultural land (Figure 1). We sampled the mainland plots using the same census method used in island plots. Sites were selected so that plots were similar in habitat type to the island plots (i.e., dominated by Masson pine), had a minimal amount of human disturbance and were predominantly on upper slope and hilltop sites at relatively low elevation. Because of the nature of the topography in the region, it was not possible to exactly match elevational distributions between island and mainland sites. The mean elevation of the 26 island plots and 26 mainland plots was 117 m (range = 101 m–152 m) and 206 m (range = 118 m–276 m), respectively. It was also not possible to locate sufficient mainland sites within the same narrow geographic dispersion as the island plots. The geographical distances (the distance between geographical coordinates) among island plots varied from 0.08 km to 12.14 km and among mainland plots (around TIL) varied from 0.07 km to 48.11 km. This wider distribution of mainland plots may increase the effects of dispersal limitation.

2.1.3 Validating the time course of deforestation and vegetation re-assembly

Masson pine is an evergreen coniferous species of tree that grows to mature DBH up to 150 cm. We conducted a tree-core survey of 231 trees (range: 5.4–39.3 cm DBH) across 24 study islands in TIL in 2010, and we found a significant linear relationship between DBH and age (linear mixed-effects models with DBH as a fixed effect and island identity as a random effect, $df = 206, F = 466.8, p < .001, R^2 = .73$). Based on this evidence, we assumed that the largest DBH trees in each island and mainland plot surveyed in the current study were the oldest trees. We cored two trees with maximum DBH per plot in the 26 island and 26 mainland sites in 2016 and found that the maximum age at all sites was consistently around 50 years (mean = 47.7 and 51.4 years per plot, respectively; Wilcoxon rank-sum test: $p > .05$). This strongly suggests that all sites were clear-felled harvested prior to 1959, as the historical records suggest, and that regeneration of canopy trees started to occur after a lag of approximately 6–9 years.

2.2 Environmental gradients

We quantified environmental conditions in each of the 52 plots using 4 topographic variables and 10 soil variables (Table S1). Topographic variables included aspect (°), elevation (m) and slope (°) obtained from field measurements. Aspect is a circular variable, so we standardized it using the formula of $\cos((2\pi \times \text{aspect})/360)$ (COSA) reflecting northerly facing slopes (range = -1 to +1) and $\sin((2\pi \times \text{aspect})/360)$ (SINA) reflecting easterly facing slopes (range = -1 to +1). These two fractions increase as the aspect faces more northerly and easterly directions, respectively. Soil properties were measured in each island and mainland plot in October 2015 and 2016, respectively. Soil depth (SDEP, cm) and rock coverage (RCOV, %) were measured during soil sampling. Soil variables were measured from three to five composite samples collected using 50.46 (diameter) × 50 (depth) mm soil cutting rings and 4.5 (diameter) × 20 (depth) cm soil augers in 10 × 10 m subplots (at all mainland locations and on 15 small islands: island area <1 ha) or in 20 × 20 m areas (on 11 large islands: island area ≥1 ha). The top organic horizon was removed before sampling. Soil maximum water holding capacity (MAXWH, g/kg) was measured using cutting ring method (LY/T 1215-1999) (Forestry Industry Standards of China, 1999). Samples were also analysed for available phosphorus (available P, mg/kg), total phosphorus (P, mg/kg), carbon (C, %), carbon-to-nitrogen ratio (CN, %), total nitrogen (N, %), ammonium nitrogen (NH$_4^+$, mg/kg) and nitrate nitrogen (NO$_3^-$, mg/kg) at Chengdu Institute of Biology, Chinese Academy of Sciences. Visible plant and root residues were removed, and soil samples were air-dried and then passed through 2.0- and 0.15-mm sieves. Available P was extracted with 0.03 mol/L NH$_4$F-0.1 mol/L HCl solution and then determined using ICP-OES (Optima 8300; Perkin Elmer). NH$_4^+$ and NO$_3^-$ were extracted with 2 mol/L KCl solution and then determined using the Continuous Flow Analytical System (San+++, Skalar, Holland). Environmental variables (soil only and topography only) were not correlated with geographic distance among plots in either island or adjacent mainland habitats (Figure S2).

To simplify the environment variables available for further analysis, a principal component analysis (PCA) was used to reduce the number of dimensions of less important variables. Together, the first two PCA axes explained 40.0% of the variance of the 14 environmental variables. PCA1 was negatively associated with SDEP, elevation, NO$_3^-$ and COSA and positively associated with C, N, CN, P and NH$_4^+$, which we refer to as a “soil fertility gradient” (soil fertility decreases as PCA1 increases). PCA2 was strongly positively associated with slope, elevation, SDEP, N, AP, P and C, which we refer to as a “topography” gradient (Figure S3).

2.3 Phylogeny and functional traits

Nomenclature was standardized according to The Plant List (version 1.1; http://www.thep plantlist.org/). For the molecular phylogeny of our study species, we used a pruned version of the phylogeny produced by Zanne et al. (Qian & Jin, 2016; Zanne et al., 2014), which included more than 30,000 species of global seed plants. All the species in our study plots were included in PhytoPhylo (Figure S4). Gymnosperms can have a large effect on average relatedness values even though gymnosperms accounted for only 4.4% of the species in our data set. Therefore, we also tested the results after the exclusion of gymnosperms.

We collected five continuous traits (maximum plant height, leaf area, wood density, specific leaf area and leaf dry matter content) and seven categorical traits (seed dispersal mode, fruit type, growth form, leaf texture, shade tolerance, leaf margin and leaf phenology) in this study (Table S2). The five continuous traits were not highly correlated (Pearson's $r < .70$). Within the categorical traits, seed
dispersal mode was coded with four levels (birds, mammals, wind and gravity; each species assigned to just one main dispersal mode), fruit type with ten levels (achene, berry, capsule, cones, drupe, follicle, legume, nut, pome, samara), growth form with three levels (shrub = 1, small tree = 2, tree = 3), leaf texture with three levels (papery = 1, leathery = 2, thick leathery = 3), shade tolerance with two levels (true and false), leaf margin with two levels (entire and non-entire) and leaf phenology with two levels (evergreen or deciduous). These traits were chosen to represent multidimensional attributes of plants associated with resource use, dispersal ability, competitive ability and species tolerance. Data on maximum height and all seven categorical traits were determined from the literature (Du et al., 2012; Editorial Committee of Flora of Zhejiang, 1993). Leaf area, specific leaf area, leaf dry matter content and wood density of each species were obtained from measurements of 5–10 individuals from the TIL area following standard protocols (Yu et al., 2017).

To quantify the degree to which variation in species functional traits is predicted by the relatedness of species, we quantified the phylogenetic signal for both continuous and discrete traits. For continuous traits, the phylogenetic signal was quantified using Blomberg's K statistic (Blomberg et al., 2003). This analysis was performed using the "picante" package (Kembel et al., 2010) and "phytools" package (Revell, 2012) in R. For discrete traits, the phylogenetic signal was quantified with Pagel’s λ statistic (Pagel, 1999) using the fitDiscrete function in the "geiger" package (Harmon et al., 2008) in R. The significance of Blomberg’s K and Pagel’s λ was estimated using 999 randomizations. There was strong phylogenetic signal in contrasting trait-mean shifts between island and mainland plots. Pagel’s λ values indicated that all seven discrete traits exhibited significant phylogenetic structuring in species responses (p < .05, Table S3), while Blomberg’s K values indicated that two of the five continuous functional traits (SLA and LDMC) exhibited significant phylogenetic signal (p < .05, Table S3). More closely related species were significantly more similar in trait responses than would be expected by chance alone.

Mean pairwise phylogenetic distance (MPD) and functional dispersion (FDIs) were calculated using the Gower dissimilarity coefficient to evaluate the phylogenetic and functional trait structure, respectively, for plant communities in each island or mainland plot. The standardized effect sizes (SES) of MPD (called the Net Relatedness Index, NRI) and FDis (called SES.FDis) were calculated as follows:

\[
\text{Standardized effect size} = -1 \times (\bar{y}_{\text{obs}} - \bar{y}_{\text{null}})/\text{SD}_{\text{null}};
\]

where \(y_{\text{obs}}\) is the observed MPD or FDis value; \(y_{\text{null}}\) is the mean value of the random draw; and \(\text{SD}_{\text{null}}\) is the standard deviation of the expected values. The null communities were generated by randomly shuffling the species names at the tips of the phylogenetic or functional tree (with 999 repeats). Negative NRI or SES.FDis indicate greater overdispersion of community phylogenetic and functional structure (respectively) than expected by chance alone, whereas positive NRI or SES.FDis values indicate greater clustering of community phylogenetic and functional structure than expected by chance (Webb et al., 2002). These analyses were performed using the "picante" package (Kembel et al., 2010) and "FD" package (Laliberté et al., 2014) in R.

### 2.4 Data analysis

We measured β-diversity as the dissimilarity between each pair of plots within island versus mainland sites using both an incidence-based (Jaccard's) metric and abundance-based (Hellinger) metric. The Hellinger metric was selected because it deals effectively with the double-zero problem in numerical ecology, where joint absences do not convey the same information as joint presences when using ordination by principal coordinate analysis (PCoA) (Legendre & De Caceres, 2013).

We conducted PCoA based on the Hellinger and Jaccard's dissimilarity to investigate the differences in species composition between island and adjacent mainland plots, and permutational multivariate ANOVA (PERMANOVA) was used to test for significant differences (Anderson, 2001). We tested for a difference in the degree of community turnover among plots on islands versus among plots on the mainland using permutational analysis of multivariate dispersion (PERMDISP) (Anderson, 2006).

We used distance-based redundancy analysis (dbRDA) to partition variation in β-diversity into relative proportions explained by environmental and spatial variables (e.g. dispersal limitation) (Legendre & Anderson, 1999; Myers et al., 2013, 2015). Spatial variables included plot geographical coordinates (latitude and longitude) and spatial eigenfunctions obtained from principal components of neighbour matrices (PCNM), which represent an orthogonal series of vectors describing spatial autocorrelation of plot locations from broad to fine scales (Borcard et al., 2004; Legendre et al., 2009). PCNM eigenfunctions with significant positive eigenvalues were used as explanatory variables. As a result, three spatial eigenfunctions were obtained for island plots and seven spatial eigenfunctions were obtained for mainland plots. To account for collinearity among environmental and spatial variables, we removed one environmental variable (C) and three spatial variables (i.e. longitude and PCNM1 for island plots and latitude for mainland plots) that were highly correlated with other variables (Pearson’s r ≥ .70) (Table S4). To avoid overestimation of explained variance, we used forward selection ("ordiR2step" function in the R vegan package) to identify significant explanatory variables (Blanchet et al., 2008). For Jaccard's dissimilarity, forward selection resulted in three and six variables for island and mainland plots, respectively. For the Hellinger dissimilarity, forward selection resulted in four and eight variables for island and mainland plots, respectively (Table S4). These variables were then used to partition variation in β-diversity into individual fractions explained by environmental, spatial and spatially structured environmental variables in the dbRDAs. For all models, we report results based on adjusted R² values (Peres-Neto et al., 2006).
To investigate the relationships between plant traits and the environment at the community level in island and mainland plots, we computed the community-weighted mean (CWM) of five continuous traits, which represents the mean of a trait for a whole plant community, weighted by the abundance of each species that occurs in the community (Garnier et al., 2004). We fit multiple linear models to estimate how CWM of the five traits respond to PCA1 (soil fertility) and habitat (island vs. mainland). We developed a set of 6 candidate models that included all subsets of predictors and their interaction. Variable selection and model estimation were based on the Akaike information criterion (AIC). For each of the seven discrete traits, we used a multinomial generalized linear model (GLM) with a quasi-Poisson link function to test how the relative frequency of the different levels of that trait varied with PCA1 (soil fertility) and habitat (island vs. mainland). The GLMs take the log-linear Poisson approach to multinomial analysis, with the response variable being the number of individuals per trait level, and the “trait level” identities being entered as an additional fixed categorical predictor variable in the model. The interaction effects between trait level, soil fertility and habitat (island vs. mainland) represent the log-odds that the relative frequencies of trait groups vary across the other predictors in the model (which is exactly equivalent to the main predictor effects in a multinomial logistic model). Model simplification was performed using a multimodel inference method (Anderson & Burnham, 2002) in the “MuMIn” package (Bartoń, 2013) in R. All analyses were performed using R (R Core Team, 2020).

3 | RESULTS

Across the 52 plots, we identified 91 woody plant species belonging to 70 genera and 34 families. Island plots contained higher densities of woody plant individuals than mainland plots, at both local scales (mean = 987.6 vs. 782.1 stems per plot, respectively; GLM with the Poisson error structure: $z$ value = −24.85, $p < .001$; Figure 2a) and a regional scale (25,678 vs. 20,335 total stems, respectively; Table S5). However, island plots had significantly lower species richness than mainland plots (mean = 21.8 vs. 25.9 species per plot, respectively; $z$ value = 3.06, $p < .001$; Figure 2b). Island plots and mainland plots shared the most abundant understorey species Loropetalum chinense (11,090 vs. 7,033 total stems, respectively) and canopy species Pinus massoniana (2,836 vs. 1,714 total stems, respectively). However, island plots contained fewer rare species (e.g. 9 vs. 22 species with ≤2 total stems, respectively). Moreover, there were just six species (e.g. Ilex cornuta, Quercus acutissima) that were only present in island plots, whereas there were 35 species (e.g. Schoepfia jasminodora, Ormosia henryi, Cleyera japonica) that were only present in mainland plots and not in island plots (Figure 2c and Table S5).

3.1 | Environmental and spatial effects on beta diversity

Ordination (PCoA) showed similar compositional patterns based on abundance-weighted (Hellinger) and incidence-based (Jaccard)
dissimilarity (Figure 3a and Figure S5, respectively), with strong clustering and discrimination of plot-level species composition between island versus mainland habitats (PERMANOVA $F = 5.97, p < .001$, $R^2 = .11$ for the Hellinger dissimilarity; and $F = 5.22, p < .001$, $R^2 = .09$ for Jaccard dissimilarity). The ordination plot (Figure 3a) indicated a greater heterogeneity of composition among plots on islands, compared with plots on the mainland, but the plot-level dispersion was not significantly different between islands versus mainland for the abundance-weighted dissimilarity (PERMDISP test: $F = 3.76, p > .05$; Figure S6a). For incidence-based dissimilarity, there was a small but significant difference in plot-level dispersion between island and mainland habitats (PERMDISP test: $F = 5.72, p < .05$; Figure S6b), indicating that mainland plots were more similar to each other in their species incidence than island plots, whereas island plots were significantly more divergent in species incidence (Figure S6b).

In the dbRDA variation partitioning, the relative importance of environmental and spatial drivers of β-diversity differed between island and mainland plots (Figure 3 and Figure S7), with environmental variation explaining a larger fraction of β-diversity in island plots (Figure 3b, Figure S7a), whereas pure spatial effects and spatially structured environmental variation explained a larger fraction of β-diversity in mainland plots (Figure 3c, Figure S7b). The key variables contributing to environmental drivers of β-diversity also differed between island and mainland plots (Table S4). On islands, key environmental drivers were slope, NO$_3^-$, north aspect and carbon-to-nitrogen ratio (Table S4), whereas in mainland plots the key environmental drivers were soil depth, NH$_4^+$, nitrogen, water holding capacity and elevation (Table S4).

### 3.2 | Functional and phylogenetic dispersion

The degree of functional dispersion of traits (SES.FDis) varied from small negative values (weak trait over-dispersion) to small positive values (weak trait clustering) across plots (Figure 4a), and this trend was significantly related to PCA1 (soil fertility) values (Table S6), but none of the dispersion values for any of the island or mainland plots deviated significantly from random expectations (Figure 4a).

Similarly, for phylogenetic dispersion (NRI) there was a weak trend from (largely) negative values (phylogenetic over-dispersion) to weak positive values (phylogenetic clustering) across plots (Figure 4b, Table S6), but dispersion was not significantly different from random expectation at any of the island or mainland plots (Figure 4b). In sensitivity tests, excluding the potentially high leverage effect of gymnosperms on patterns of dispersion, both functional and phylogenetic dispersion values were higher (greater clustering; Figure S8) and stronger relationships to environmental gradients were found (Table S6), but again few of the plot-level dispersion values were significantly different from random expectation (Figure S8).

### 3.3 | Shifts in functional trait distributions

Although there were no significant changes in trait clustering (SES.FDis) between communities, we found highly significant trait–mean shifts in 11 of the 12 functional traits along environmental gradients in both island and mainland habitats (Figures 5 and 6, Tables S7–S9). Only maximum plant height showed no significant variation in community-weighted mean values along the soil fertility PCA1 gradient, or between island versus mainland plots (Figure 5a). For community-weighted mean LA, there was a significant decrease with increasing soil fertility PCA1 values (i.e. higher LA values at higher soil fertility), but no difference in the LA response to soil fertility between island versus mainland plots (Figure 5b). In contrast, trait–mean values for wood density remained comparatively invariant across the soil fertility PCA1 gradient, but differed significantly between island versus mainland (Figure 5c). For all other traits,
FIGURE 4  The relationship between plot-level environmental variation and (a) functional dispersion and (b) phylogenetic dispersion. Graphs show a principal component analysis (PCA) ordination of environmental conditions in 52 plots (N = 26 island plots, N = 26 mainland plots), and different symbols show standardized measures of phylogenetic and functional trait dispersion in the island and mainland plots. The size of the symbols is proportional to the total number of woody plants in the plot.

FIGURE 5  Variation in the community-weighted mean of five continuous traits (a) maximum plant height, (b) leaf area (LA), (c) wood density, (d) specific leaf area (SLA) and (e) leaf dry matter content (LDMC) along an environmental gradient (PCA1 soil fertility gradient) for N = 26 island plots (light grey symbols and dotted lines) and N = 26 mainland plots (black symbols and dashed lines). The size of the symbols is proportional to the total number of woody plant individuals in the plot.

FIGURE 6  Variation in categorical traits of (a) dispersal mode, (b) fruit type, (c) growth form and (d) leaf texture along an environmental gradient (PCA1 soil fertility gradient) for N = 26 island plots (light grey symbols and dotted lines) and N = 26 mainland plots (black symbols and dashed lines). The size of the symbols is proportional to the total number of woody plant individuals in the plot.
(a) Dispersal mode

(b) Fruit type

(c) Growth form

(d) Leaf texture

Abundance: 500 750 1000 1250 1500

Group: Iseland Mainland
there was a significant interaction effect between variables, indicating varying trait responses to environmental gradients between island and mainland plots. For example, for plant communities on islands, community-weighted mean SLA decreased from high to low soil fertility (along the PCA1 soil fertility gradient), whereas the opposite was observed in mainland plots, with SLA increasing from high to low soil fertility (Figure 5d). Meanwhile, the reverse trends were observed for LDMC, with opposing trait–mean responses of island versus mainland plant communities to the same environmental gradient (Figure 5e). Among the discrete traits measured, there were significant differences in proportional representation of different types of dispersal mode, fruit type, growth form and leaf texture (Figure 6a–d), as well as shade tolerance, leaf shape and leaf phenology (Figure S9), with decreasing soil fertility, and these trait shifts depended on island versus mainland habitat. For example, dispersal mode shifted proportionately more towards bird dispersal and wind dispersal of seeds with decreasing soil fertility on islands, rather than towards proportionately more gravity dispersal of seeds on the mainland (Figure 6a).

4 | DISCUSSION

After 50 years of regeneration following the “re-setting” of plant community assembly trajectories in island versus adjacent mainland plots at TIL, we found striking differences in species composition and functional trait assembly due to isolation and fragmentation. At the plot scale, island plots had approximately 1.3 times greater stem density than mainland plots (larger community size) but lower species richness. At the regional scale, island plots had more common species but fewer rare species than mainland plots. Islands also lacked important late-successional species such as Cleyera japonica and Castanopsis eyrei, and species that were predominantly mammal-dispersed or with high woody density, but were instead dominated by species that were predominantly wind- and bird-dispersed.

In our study system, island and mainland plots did not have equivalent spatial dispersion in the landscape, but this was unlikely to confound comparisons as environmental heterogeneity did not vary significantly with geographic distance among sites. Surprisingly, although island plots had lower spatial dispersion in the landscape, they actually had greater variability in plant community composition from island to island, which was the opposite of the prediction from our hypothesis. Island plots also appeared to show greater environmental variation after 50 years of isolation. Specifically, soil erosion appeared to be higher (e.g. lower soil depths) and nutrient retention lower (e.g. higher C/N and lower available P) on islands, even though mainland plots were typically on steeper slopes. Plots on small islands were also closer to habitat edges, on average, than mainland plots, which is likely to alter abiotic edge effects (Liu et al., 2020; Morgan & Farmilo, 2012). All these factors may lead to the alteration of environmental filtering effects in island versus adjacent mainland plots.

In TIL, as in the majority of fragmented systems, we did not have a complete time series of vegetation change since isolation. However, the consistent age and known time course of re-assembly allow a plausible comparison of the determinants of species turnover between island and mainland plots using variation partitioning. As expected from our hypotheses, environmental filtering has a stronger effect on woody plant communities in fragmented habitats (islands), whereas purely spatial effects, such as seed dispersal limitation or priority effects, were more important in mainland plots. A feasible explanation is that increases in soil erosion and abiotic edge exposure, and reduction in nutrient retention, resulted in greater effects of environmental filtering in island plots compared with adjacent mainland plots. Even though most previous studies have not been able to directly compare the relative importance of environmental versus spatial controls on community composition between land bridge islands and adjacent mainland, some of the results showed in previous studies in this system are in accordance with our findings (Liu et al., 2020; Liu, Vellend, et al., 2018). Nevertheless, we still would have expected dispersal limitation to be more important for isolated islands than for mainland plots in our system, but this was not the case. Interestingly, Carvajal-Endara et al. (2017) also found that environmental filtering was more important than dispersal limitation in determining species composition on the Galapagos archipelago.

As predicted, the role of environmental filtering in community re-assembly on islands was further supported by dramatic shifts in the functional trait distribution of woody plants. Generally, increases in soil fertility (NO$_3^-$, soil depth), soil moisture (depth of soil above bedrock) and light (edge aspect) resulted in shifts towards more acquisitive and less conservative resource-use strategies, including greater leaf area, increased specific leaf area and lower leaf dry matter content on our study islands. In Cypress Hills Interprovincial Park in Canada, Shovon et al. (2020) found similar results for understorey plant communities. In addition, we also found directly contrasting patterns of SLA and LDMC shifts along environmental gradients in island versus mainland plots. A plausible explanation for this is that mainland plots are not predominantly constrained by soil resource quality, and therefore, it is not as important a limiting factor for woody plant colonization, growth and reproduction as it is on islands. This explanation parallels our variation partitioning results. With acquisitive traits (low wood density, high SLA and small seeds), pioneer species tend to occupy small islands and edge niches (Slik et al., 2008; Tabarelli et al., 2010). Plots on islands also have lower wood density and fewer mammal-dispersed plants, but more wind- and bird-dispersed species.

Despite the striking differences in species composition and contrasting community-weighted mean shifts in functional traits along soil fertility gradients in island versus mainland plots, we found no evidence for non-random patterns of phylogenetic and functional dispersion among plots. This means that the degree of complementarity (in traits and phylogenetic distance) among species remains essentially the same across assembling plant communities, even
though the traits needed to survive can be quite different from site to site. This implies strong trait-based rules to assembly, but some sort of upper limit to the ecological dimensionality of the system. To some extent, it might also suggest a net balance between environmental filtering and competitive exclusion (neither dominating), or potentially that other assembly processes overwhelmed these two (Kraft & Ackerly, 2014; Mayfield & Levine, 2010; Parmentier et al., 2014). Lastly, it may also be that 50 years of succession is not long enough to determine the full trajectory of change in function trait and phylogenetic dispersion. Liu, Chen, et al. (2018) found that understorey communities in boreal forests showed contrasting trends in phylogenetic and functional patterns through time, with dispersion shifting from random to clustered with increasing stand age.

In conclusion, with the advantage of a common starting point to re-assembly after forest clearance, our study showed that island and adjacent mainland plots have striking differences in species composition, very different trait-environment relationships and differing assembly mechanisms after 50 years of regeneration. Remarkably, island plots were mostly governed by local environmental variables, suggesting an important role for environmental filtering processes. The environmental drivers were strong enough to cause significant trait-mean shifts, yet the degree of complementarity among traits was similar at all sites, implying some sort of ecological limit to the range of trait combinations that can be packed in. These findings will provide a better understanding of community re-assembly processes in fragmented systems and deliver important insights into trait assembly processes under varying environmental conditions.

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Some data are acquired from other collaborators, which are not allowed for the public repository.

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**BIOSKETCH**

Our research involves a broad range of topics related to habitat fragmentation effects and subtropical forest community dynamics.

Author contributions: M.Y. led conceptualization of the project. L.Z., J.L., Y.J. and M.Y. collected the data. L.Z. and R.K.D. analysed the data. L.Z., R.K.D. and M.Y. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**SUPPORTING INFORMATION**

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

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