RESEARCH ARTICLE

Functional groups, determinism and the dynamics of a tropical forest

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Abstract

1. Unravelling the drivers of forests dynamics is one of the main challenges in tree community ecology. These drivers include niche differentiation, dispersal limitation and stochasticity. Previous work has demonstrated that these mechanisms likely interact such that no one process is responsible for forest dynamics.

2. One possibility is that the functional composition in a forest changes in a deterministic fashion, but the abundances of individual species that are functionally similar and have similar life-history strategies drift in a neutral fashion. This framework aligns with the *functional group*-based version of the neutral theory proposed more than 30 years ago, but it has remained poorly understood and is not well-integrated in tree community ecology.

3. To investigate the possibility that determinism and neutrality may operate on the functional and species levels, respectively, we studied the long-term dynamics of trees on Barro Colorado Island, Panama. Specifically, we sorted tree species into functional groups. We defined them as groups of species that cluster together based upon continuous functional trait measurements that are believed to reflect key life-history trade-offs. This information was then used to quantify the observed species and functional group dynamics in the forest and to compare them to that expected from neutral simulations.

4. We found that forest dynamics are likely governed by deterministic processes at the between-functional group level where species relative abundances change or drift through time within group. Species rank distributions for each functional group remained relatively stable suggesting that these groups may act as broad adaptive zones for both common and rare species that may promote species coexistence. Moreover, we found that these functional groups associate with different habitats in the forest.

5. *Synthesis*. The results indicate that deterministic processes control the relative proportion of each functional group in the tropical forest studied and that individual species within groups may have apparently neutral dynamics. Furthermore, the results demonstrate that observed stable functional group relative proportions can be produced by deterministic or neutral dynamics, which underscores the importance of comparing the observed functional dynamics to that expected under neutral dynamics.

1 | INTRODUCTION

Understanding the mechanisms that maintain species richness and abundance is a central focus in ecology (Brown, 1995; Ricklefs & Schluter, 1993). Tropical forests occupy about 7% of Earth's surface, but contain more than 50% of the Earth's biodiversity (Wilson, 1988). Disentangling the mechanisms that explain the diversity and dynamics of tropical forests is, therefore, important for our ability to predict future changes in ecosystems in response to ongoing global climate change (Grime, 1998). However, due to the high levels of tree diversity in tropical forests, distinguishing between these mechanisms and their dynamics in space and time is challenging (Hubbell, 2001, 2005; Wright, 2002). Hypothesized mechanisms range from neutrality to determinism. A neutral model or dispersal-assembly perspective allows for demographic stochasticity and ecological equivalence among different species (Hubbell, 2001, 2005, 2006) without considering habitat structure, while deterministic models or niche-assembly perspective generally revolve around performance and niche differences (e.g. Chase & Leibold, 2003; Chesson, 2000; Gleason, 1926; MacArthur, 1970) with habitat preferences as one of the mechanisms promoting species coexistence (e.g. Clark et al., 1999; Harms et al., 2001; Hubbell & Foster, 1986; Webb & Peart, 2000). Despite the stark differences between these two types of models, it is important to underscore that there is a spectrum between them, and it is unlikely that community structure and dynamics are explained by one of the extreme ends of this spectrum. It is more likely that multiple processes interact to produce the patterns we observed in communities (e.g. Adler et al., 2007; Chase & Leibold, 2003; Gaston & Chown, 2005; Gravel et al., 2006; Hurtt & Pacala, 1995; Purves & Pacala, 2005; Tilman, 2004).

Quantifying the degree to which species are ecologically similar is important for inferring the mechanisms underlying community structure and dynamics, and functional traits have been widely used for this purpose (e.g. McGill et al., 2006; Swenson, 2013; Swenson et al., 2011; Swenson, Erickson, et al., 2012). Functional traits, such as those from the leaf and wood economics spectra, represent morphological, physiological or phenological features which impact fitness indirectly via its effects on growth, reproduction and survival (Pérez Harguindeguy et al., 2013; Reich et al., 2003). Importantly, work of the last several years has demonstrated that analyses of communities that use functional trait information often come to opposing and more refined inferences regarding the drivers of community structure and dynamics than what can be achieved from analyses based upon only species names and abundances (e.g. Fukami et al., 2005; McGill, 2003; Messier et al., 2010; Purves & Pacala, 2005; Swenson et al., 2011; Swenson, Erickson, et al., 2012; Swenson, Stegen, et al., 2012; Swenson, 2013; Webb et al., 2002).

Therefore, the inclusion of analyses of the functional composition of communities should give us insights into the fundamental mechanisms driving the community structure and dynamics that are not elucidated by analyses only focused on species names and abundances.

Research has found that functional composition of plant communities appears to shift or converge in a predictable manner due to the abiotic environment filtering structuring plant communities. For example, Messier et al. (2010) found trait-based abiotic filtering in three old-growth lowland tropical forests in Panama. Similarly, Swenson, Stegen, et al. (2012) found that the functional composition of a tropical forest turned over less than expected given the amount of species turnover, with abiotic filtering playing an important role governing the spatial turnover in community composition (Swenson, Erickson, et al., 2012). Non-random functional turnover (i.e. non-random replacement of individuals with respect to species function) involving several axes of plant functional differentiation (i.e. functional trait axes) has been found along an elevation gradient indicating the major role of deterministic processes in tropical tree communities (Swenson et al., 2011). In these plant communities, the changes in the taxonomic composition of the community was less predictable and it was attributed to filtering acting solely on traits (Messier et al., 2010), random phylogenetic turnover (Swenson, Stegen, et al., 2012) and priority effects (Fukami et al., 2005). These findings together suggest that deterministic functional composition and random species turnover resulting from abiotic filtering may act as a mechanism allowing multiple species to coexist by shifting species names and abundances while maintaining the functionality and species richness of the forest.

A possible way in which functional determinism could occur is that functionally similar trees replace one another through time (e.g. Swenson, Erickson, et al., 2012), but the species identity of those trees can be simply represented as a random sampling of a pool of functionally similar species weighted by their relative abundance (Figure 1). The backbone of such a model is that pools of functionally similar species are generated by species clustering naturally into functional groups and species within functional groups replace one another as trees die and recruit. The dynamics of this model could lead to neutrality occurring within functional groups, but habitat partitioning and habitat associations, in a deterministic manner, between functional groups with the environmental conditions determining the availability of resources and the functional groups that can fill them based on their resource requirements (Lavorel & Garnier, 2002; Watkins & Wilson, 2003; Weiher et al., 1998). Thus, habitat partitioning contributes to the maintenance of local diversity by allowing multiple species to coexist if they use resources based on their functional trade-offs (Clark et al., 1999; Hubbell &
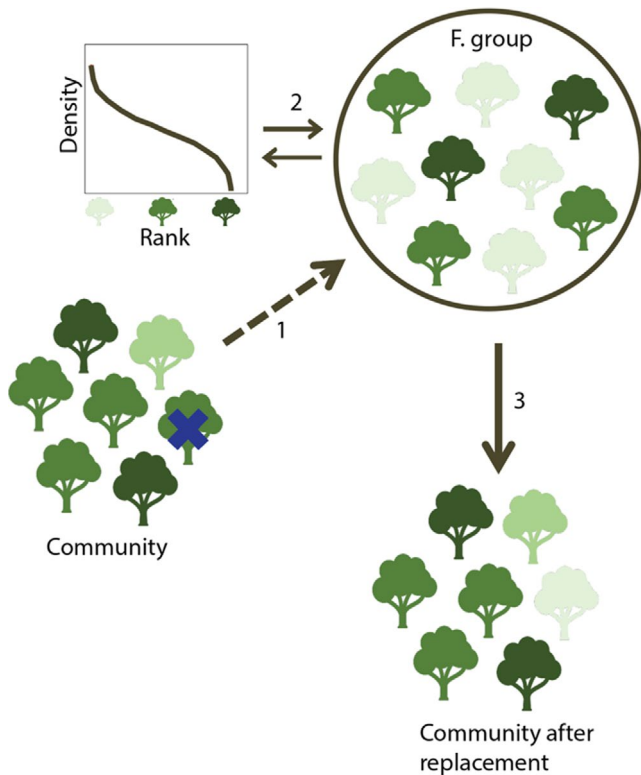
FIGURE 1 A cartoon depicting the functional group version of Hubbell's neutral theory. The trees represent different individuals, and the different colours represent different species. When one individual dies in the community (blue cross on a tree) a new individual is selected (arrow 1) from the species that comprise a functional group (species circled in the F. group) based on the within-group abundance distribution (arrow 2) resulting in a replacement in the community (arrow 3)

Foster, 1986; Webb & Peart, 2000). This is, effectively, a *functional* group-based version of Hubbell's neutral theory initially proposed by Stephen Hubbell and Robin Foster over three decades ago (Hubbell & Foster, 1986).

If determinism occurs at the functional group level (Fukami et al., 2005; Hubbell, 2005; Hubbell & Foster, 1986), then one would expect that the functional group composition in the forest would remain relatively stable or converge through time in an undisturbed forest where common and rare species are found in each functional group despite high species turnover. For this to occur, species with equivalent or near-equivalent functional traits, which reflect ecological similarities and responses to local environmental factors (e.g. light, water, soil nutrients), should naturally cluster together into functional groups and spatially co-occur (Hubbell, 2005; Hubbell & Foster, 1986). The total number of species that can be packed together within a functional group is then defined by an upper limit of similarity of coexisting species (Abrams, 1983). Thus, one would expect that several species, despite their different taxonomic identities, comprise a functional group and within each group species dynamics may be governed by stochastic forces (Hubbell, 2005; Hubbell & Foster, 1986). In other words, a species from a functional

group may die, but a species from the same functional group may replace it via a weighted lottery processes due to shared ecological requirements aligning with previous findings of functional determinism and unpredictable species turnover (e.g. Fukami et al., 2005; Messier et al., 2010; Swenson, Stegen, et al., 2012).

Here, we test these expectations using functional trait data and long-term forest dynamics data from a forest plot in Panama. We then analyse the empirical dynamics of the tree community through the lens of functional groups, compare these results to that expected under a purely neutral model of community dynamics and examine whether these functional groups demonstrate habitat partitioning in the forest. The specific questions we ask are: (a) Does the relative proportion of functional groups change in the forest through time?; (b) Does the rank abundance distribution within functional groups change through time?; (c) Do the empirical functional group relative proportions and rank abundance distributions differ from that expected under a neutral model?; and (d) Are functional groups associated with habitats?

2 | MATERIALS AND METHODS

2.1 | Census data and functional traits

We used existing census data from Barro Colorado Island (BCI) in Panama in this study. Specifically, we used data from the 50-ha lowland tropical forest dynamics plot that was established in 1981–1982 (Condit, 1998; Hubbell et al., 2010). This area of forest has remained undisturbed in the past 1,000 years aside from 2-ha that were disturbed during the building of the Panama Canal (Piperno, 1990). In the plot, all free-standing woody stems ≥1 cm in DBH (1.3 m above the ground) were measured, mapped and identified every 5 years for a total of seven censuses (Condit, 1998). Over the past 35 years, the individual turnover has been high with more than 50% of the initial individuals dying and being replaced (Feeley et al., 2011).

We defined a functional group as a group of functionally similar species, with their delimitation based on discontinuities in functional space, and within which adaptive convergence and generalization could occur (Hubbell & Foster, 1986). We estimated the functional group of 241 species in this study using four functional traits that reflect where species land on key trade-off axes (Cornelissen et al., 2003; Swenson, Erickson, et al., 2012; Wright et al., 2004). These species comprise about 97% of the total stems in the 50-ha plot per census. Specifically, we used measurements of wood specific gravity (wsg; g/cm^3), maximum height ($hmax$; m), leaf area (la; cm^2) and leaf mass per area (lma; g/m^2). These data were previously collected using standardized protocols and published by Wright et al. (2010). Wood specific gravity (i.e. wood density) has been associated with resistance to mechanical rupture and hydraulic cavitation (Chave et al., 2009); plant maximum height is related to light competition, reflecting carbon acquisition strategies and significant individual growth variation (Westoby et al., 2002); leaf area may be linked with ecological strategies and

allometric plant factors as well as response to air temperatures (Pérez Harguindeguy et al., 2013); and leaf mass per area is one of the key functional traits of the leaf economics spectrum and measures the leaf-dry mass investment per unit of light-intercepting leaf area deployed (Wright et al., 2004).

2.2 | Functional group assignment

Because functional traits might covary, we performed a principal component analysis (PCA) where we log-transformed leaf area, maximum height and leaf mass per area (after failing a Shapiro test of normality) and Z-scaled all the traits. Using the broken-stick model, we retained two PC axes that accounted for 41.12% and 30.94% of the total variance respectively. These values were used to estimate the best number of partitions of functional groups using the *Nbclust* function in the NBCLUST package (Charrad et al., 2014) in R statistical software version 4.0.3 (R Development Core Team, 2010). Briefly, this function calculates the best partitioning of the functional trait space into clusters (i.e. functional groups) using 30 different indices. The Euclidean distance in PCA space between species is used to minimize the within-cluster variances using the Ward method. This analysis showed that the best partitioning of the functional trait space that reduces the within-cluster variances (i.e. distances) was the three functional groups (Table S2; Figure S1). Next, one of the three functional groups was assigned to each individual tree in each census based on the species identity (Table S1).

2.3 | Analysis

The functional group relative proportion in each census was calculated using the total number of standing trees in each of the seven censuses as follows:

$$\text{Functional group relative proportion}_{ij} = \frac{\text{individuals}_{ij}}{\text{total individuals}_j}, \quad (1)$$

where individuals$_{ij}$ is the number of individual trees in the functional group i for the census j, and total individuals$_j$ is the total number of standing trees in the census j. Census j goes from census 1 to census 7 which correspond to the vegetation census taken in 1981/1983, 1985, 1990, 1995, 2000, 2005 and 2010 respectively.

Next, we calculated the species rank distribution inside each of the three functional groups in each of the seven censuses. To determine whether the observed patterns in the species distribution inside each functional group were the result of deterministic forces, in which the functional groups have consistent species evenness, we calculated the temporal Shannon diversity index using the VEGAN package (Oksanen et al., 2017) in R statistical software version 4.0.3 (R Development Core Team, 2010). This index calculates the evenness by considering species abundances.

To gain further insight into the mechanisms shaping the patterns observed in the functional group relative proportions and the species rank distributions, for each census j we calculated the patterns expected under neutrality by performing parametrized simulations with the empirical data using all the seven census available. More precisely, we modelled a random lottery process, similar to Hubbell's neutral theory (Hubbell, 2001), in which all individuals had the same chance of dying and the new recruits were selected randomly from the species abundance distribution of the survivors (species higher abundances lead to a higher probability of dispersal and establishment). The number of trees dying and recruiting was equal to the exact number of individuals that died and recruited in each empirical census. We ran the simulation 500 times. Finally, for the simulated results, we calculate the functional group relative proportion and the Shannon index with confidence intervals at 95% for the median.

2.4 | Torus-translation test of habitat association

To gain further insight into the distribution and possible habitat associations of functional groups in the BCI forest plot, we performed a torus-translation (TT) analysis through time (i.e. seven census). This method allows us to remove the lack of independent tree distributions within species that are known to occur in this forest (Condit et al., 2000) and caused by seed dispersal limitation and recruitment (Condit et al., 1992). We compared the observed habitat relative densities of functional groups with the expected habitat relative densities resulting from a null distribution (i.e. by chance). Each 20×20 m quadrat was assigned a topographic type (Figure 6a) based on the habitat categories defined by Harms et al. (2001). These categories consist of old forest low plateau (slope <7 degrees and elevation <152 m), old forest high plateau (slope <7 degrees and elevation ≥152m), old forest slope (slope ≥7 degrees and all elevations), old forest swamp, old forest streamside, young forest and mixed (mixed habitats). Consequently, we followed the methodology described in Harms et al. (2001). Briefly, this method moves the true habitat map about a two-dimensional torus by 20-m increments in four cardinal directions for a total of 1,250 unique habitat translated-maps. In addition, a translation of 180° rotation, a mirror image and a 180° rotation of the mirror image were generated for a total of 4,999 unique translated maps. A functional group is significantly positively or negatively associated with a habitat if the observed relative density is more extreme than at least 97.5% ($\alpha = 0.05$) of the expected (i.e. simulated) relative density.

3 | RESULTS

3.1 | Functional group composition

Previous work on BCI has indicated the presence of three functional groups (Condit et al., 1996; pioneer, building phase and shade-tolerant species). Additional work focusing on demographic data has

suggested that there are five clusters of species (Rüger et al., 2020). Our results showed that the forest studied was composed of three functional groups (Figure 2; Table S1). The first group in our study represents short-statured species with intermediate wood density, low leaf mass per area and low leaf area values (*n* = 47). The second group represents tall species with high wood density, high leaf mass per area and low leaf area values (*n* = 117); and the third group represents tall species with low wood density, high leaf mass per area and high leaf area (*n* = 77; Figure 3). The first goal of this study was to determine how the functional group relative proportion in the community changed through time. The functional composition of the plot, represented by three functional groups, appeared to remain relatively steady. Specifically, there is an apparent stability of the relative proportion of each functional group in the community through time (Figure 4a). In addition, apparent stochasticity at the species level was observed when plotting the species inside each functional group through time (Figure S6).

3.2 | Species abundance distributions and evenness inside each functional group

A second goal of this study was to examine whether functional groups have stable rank abundance distributions and patterns of evenness in the species rank distribution through time inside each functional group. The BCI forest plot showed little to no change in within-functional group species rank distributions through time (Figure 5). The patterns of within-functional group species evenness showed relatively stable patterns, with functional groups being less even than neutral (Figure 4b).
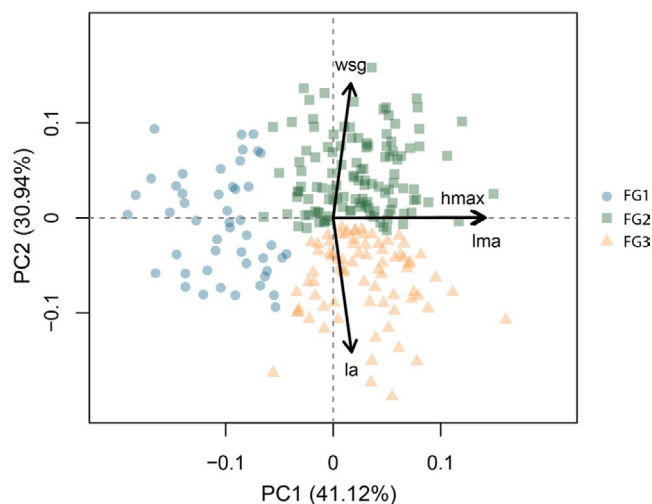
FIGURE 2 Principal component analysis plot for the first and second components (PC1 and PC2) with their corresponded variance explained (%) for 242 tree species classified into functional groups (FG). Wood density (wsg), maximum height (hmax), leaf mass per area (lma) and leaf area (la) loadings are displayed

3.3 | Neutral model

The third goal was to test if the empirical patterns observed in the functional group composition and evenness were different from that expected via neutral processes. The results from the neutral model for BCI showed that the patterns observed in the empirical data are not a result of a purely neutral process shaping the functional group relative proportion in the forest (Figure 4a; Figure S4). Similarly, the Shannon index values calculated from the neutral simulations did not overlap with the empirical data rejecting the possibility of neutral processes shaping the evenness inside the functional groups (Figure 4b; Figure S5). For both functional group relative proportions and within-functional group evenness, the patterns generated by the neutral simulations were more stable than the patterns shown in the empirical data.

3.4 | Functional group habitat association

Lastly, the TT analysis found habitat associations for some functional groups with different habitats through time (Table 1; Table S3). More specifically, functional group 1 was positively associated (i.e. aggregated) with swamps and young forests and negatively associated (i.e. repelled) with slopes (Figure 6b). Functional group 2 did not show any positive associations but was negatively associated with streams and young forests. Likewise, from visual inspection, this group distribution was relatively uniform in the forest (Figure 6c). Finally, functional group 3 was positively associated with slopes and negatively associated with mixed and young forests (Figure 6d).

4 | DISCUSSION

Here we aimed to test whether an undisturbed forest showed functional determinism between functional groups. We found that deterministic processes dominated the functional group level, while within-functional group species relative abundances changed in a less predictable manner. In addition, each functional group maintained apparently stable rank abundance distributions and patterns of evenness through time suggesting the maintenance of the functionality of the community. We compared these empirical results to neutral simulations and found that the empirical dynamics were actually less stable than expected by a neutral model. Lastly, functional groups showed habitat associations with particular habitat types. In the following, we discuss the results in detail.

The results of our analysis suggest that tree community assembly in this undisturbed tropical forest is governed principally by deterministic processes at the functional group level. Specifically, we found that the functional group composition showed little empirical change through time suggesting that functionally similar roles are maintained in this forest through time both at the plot level (Figure 4a), quadrat level (Figure S2) and different size class of trees (Figure S3). It is likely that individual dead trees are replaced
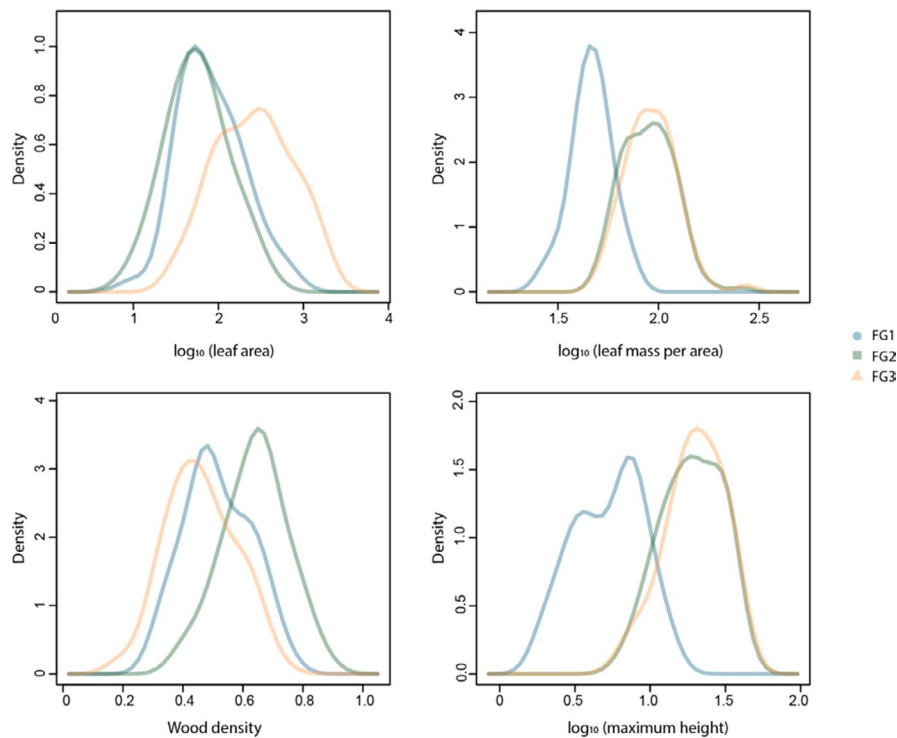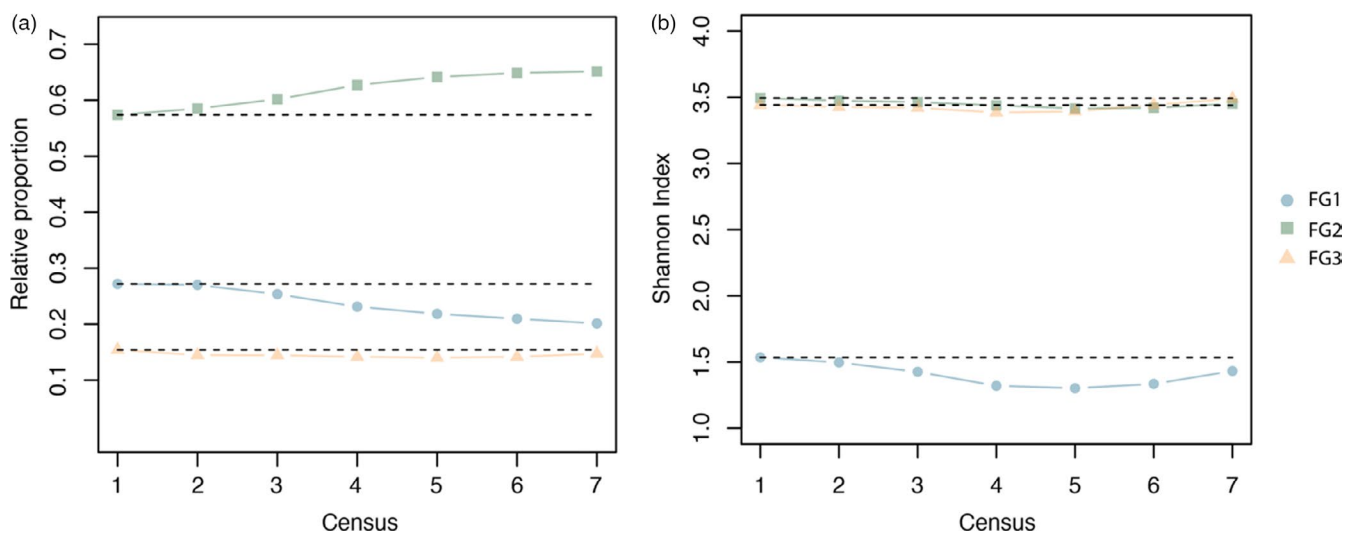
FIGURE 4 (a) Empirical relative proportion of functional groups in BCI calculated as the relative proportion of the total number of stems represented by each functional group in each census. Dotted lines represent the values resulting from the neutral simulations. Confidence intervals for the simulations are so small that they cannot be seen on this scale; however, they are represented in Figure S4. (b) A measure of evenness (Shannon Index) through time on each functional group on BCI. Dotted lines represent the values resulting from the neutral simulations. Confidence intervals for the simulations are so small that they cannot be seen on this scale; however, they are represented in Figure S5

by functionally similar tree species in BCI (Swenson, Erickson, et al., 2012; Swenson, Stegen, et al., 2012), where the identity of the species that exploits the resources available is determined by chance, dispersal or subtle environmental differences (Watkins & Wilson, 2003). The replacement of trees by functionally similar species allows for the relatively maintenance of the number of individuals inside each functional group relative to the total number

of individuals in the local community and therefore maintaining the functionality of the forest. Previous studies suggested that a stable functional turnover could be the result of the abiotic environment constraining the functional composition of plant communities (Fukami et al., 2005; Kraft & Ackerly, 2010; Messier et al., 2010; Swenson, Erickson, et al., 2012). Specifically, it could be that the local abiotic environment on BCI has remained relatively constant
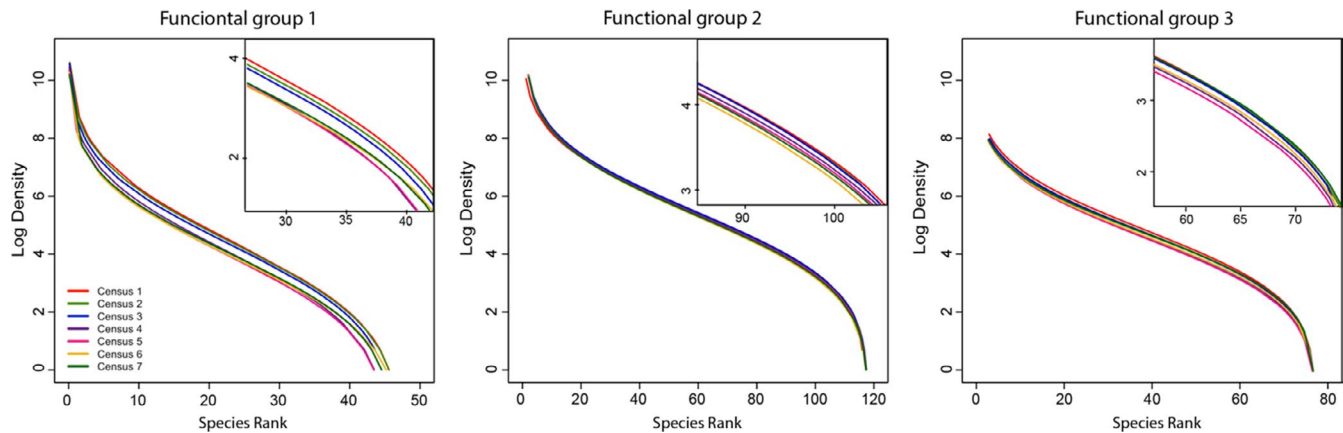
FIGURE 5 The empirical species rank distribution inside each functional group for Barro Colorado Island. Different colour lines represent different censuses. Most censuses have similar rank distribution for a group: see inset

TABLE 1 Functional group habitat associations. Torus-translation habitat associations for each functional group (FG) through time. Topographic habitats: Low plateau, Mixed, Slope, Stream, Swamp and Young forest (Young F). (+) and (−) reflect positive (i.e. aggregated) and negative (i.e. repelled) associations respectively

	FG 1 (+)	FG 1 (−)	FG 2 (+)	FG 2 (−)	FG 3 (+)	FG 3 (−)
Census 1	Young F	Swamp	Mixed	—	Slope	Mixed, Young F
Census 2	Young F	Swamp	Mixed	—	Slope	Mixed, Young F
Census 3	Young F	Swamp	Mixed	—	Slope	Mixed, Young F
Census 4	—	Swamp	Mixed	—	Slope	Mixed, Young F
Census 5	—	Swamp	Mixed	—	Slope	Mixed, Young F
Census 6	—	Swamp	Mixed	Stream	Slope	Mixed
Census 7	Low plateau	Swamp	Mixed	—	Slope	Mixed

through time (Chisholm et al., 2014; Condit et al., 2017; Swenson, Erickson, et al., 2012) allowing different species to locally adapt to the environmental conditions (Hubbell, 2005) and that the relative proportion of functional group could reflect the relative proportion of habitats available. This functional group determinism can be analysed further by looking at the within-group dynamics. The species rank distribution of each functional group, composed of ecologically similar common and rare species, showed little change through time (Figure 5) with the species evenness remaining relatively stable through time (Figure 4b) despite changes in species composition (Figure S6). These trends suggest that despite the high species turnover in BCI (Feeley et al., 2011; Swenson, Erickson, et al., 2012), there is little to no effect on the forest functional composition and the species diversity of BCI (Swenson, Erickson, et al., 2012). Recent analyses by Katabuchi et al. (2017) that have focused on population changes in the BCI plot as it relates to traits have found that a handful of species have experienced large population crashes. A few of those species have light wood, but overall, there is no relationship between population change and functional trait values in this forest. In other words, species have experienced population changes through time in the BCI plot, but the overall functional composition of the plot has been stable. We suggest this is caused by a population of one species declining within a functional group being offset by the growth in population of one or a few species within that functional group in the plot. What causes individual species to experience

population crashes in the BCI forest plot is an open question, but Katabuchi et al. (2017) have hypothesized that these crashes are more likely linked to pathogen outbreaks, which would not be easily predicted by the traits typically measured by forest ecologists.

The observed patterns of within-functional group species composition could be the result of functional groups acting as broad adaptive zones in which species, regardless of their commonness or rarity, converge on similar life-history strategies over evolutionary time (Hubbell, 2005; Hubbell & Foster, 1986). This trait convergence (e.g. similar life-history strategies) likely result from strong abiotic filtering (Fukami et al., 2005; Swenson, Erickson, et al., 2012). These life-history strategies are presumably adaptations to the most frequently encountered environments in which species can co-occur with no competitive exclusion occurring, and species naturally clustering into functional groups (Hubbell, 2005, 2006; Hubbell & Foster, 1986). Likewise, the emergence of self-organized clusters of similar species, which likely reflect different favoured combinations of traits that are favoured, has been suggested as an intrinsic property of communities resulting from competitive interactions between species (Barabás et al., 2013; Sakavara et al., 2018; Scheffer & van Ness, 2006). Species can escape the limits to similarity by coexisting within the functional group via superior performance within a given environment (D'Andrea et al., 2019; Sakavara et al., 2018; Scheffer & van Ness, 2006). This clustering reflects the importance of differing from others (i.e. niche partitioning) while sharing similarities
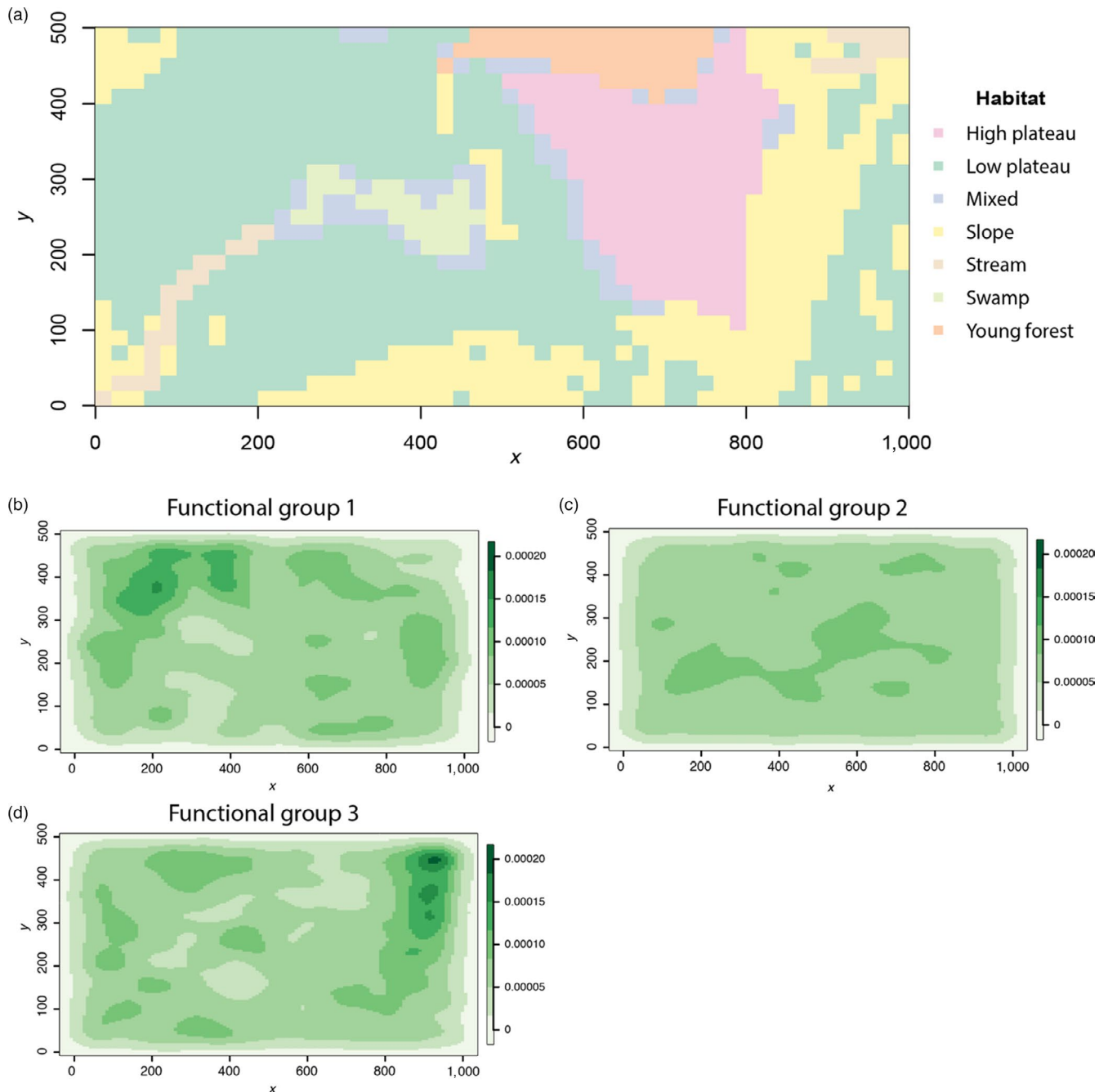
FIGURE 6 Functional group distribution in the Barro Colorado Island map. (a) Habitat topographic types, the *x*-axis increases from west to east in metres and *y*-axis increases from south to north in metres. (b) Two-dimensional kernel density estimates for the stems in functional group 1; (c) Two-dimensional kernel density estimates for the stems in functional group 2; and (d) Two-dimensional kernel density estimates for the stems in functional group 3. Refer to (a) for habitat map. Two-dimensional kernel density estimates are normalized by mean and represent stem distribution in census 7

with the favoured life-history strategies in a given environment (D'Andrea et al., 2020; Hubbell & Foster, 1986; Hubbell, 2005) that ultimately maintains high diversity. Previous work in BCI has suggested the presence of demographic functional groups (Condit et al., 1996; Rüger et al., 2020) that capture successional patterns of forest composition and carbon dynamics by capturing the relevant dimensions of variation among species, suggesting that community responses to environmental changes can be predicted with a limited

number of functional groups. Thus, here we are not arguing that competition for resources does not occur in tropical forests. Quite the contrary, we are arguing that functional groups partition habitats within this forest and there are functional group-level performance differences between habitats (Hubbell, 2005). Lastly, we believe it is important to note that the functional groups used in this study were constructed using functional traits that are known to convey information about species distributions and life-history trade-offs. Thus,

while they were quantitatively supported and constructed from key plant functional traits, we think future work focusing on functional group dynamics in this forest and others is essential as is work that includes a wider array of traits when defining functional groups.

Our neutral simulation supports the hypothesis that the dynamics in this forest are likely governed by a non-random process at the functional group level. Specifically, the neutral model estimates of functional group relative proportions and the within-functional group evenness were more stable and did not overlap with the empirical results reported here (Figure 4a; Figure S4). This is important for two reasons. First, the relative proportion of functional groups in the BCI forest has changed non-randomly through time, but these changes have been subtle. Second, a purely neutral model parameterized from the plot data produces a stable functional structure. This stable functional structure is due to the presence of common and rare species within each functional group and the relatively stable habitat availability of resources in the plot. In other words, the observation that functional group relative proportions appear stable through time is not evidence of determinism as both a neutral model and a deterministic model can produce patterns of functional stability.

The within-functional group species relative abundances also seemed to change in a manner that could not be predicted by a neutral model (Figure S6). Feeley et al. (2011) found that species composition in BCI shifted to more drought-tolerant species that cannot be explained by stochastic processes alone. Our results show a slight increment in the relative proportion of functional group 3 (Figure 4a) which corresponds to tall and heavy-wooded species (Figure 3). However, Swenson, Stegen, et al. (2012) found no significant changes in wood density composition through time supported by the finding that this apparent shift towards more drought-tolerant species was a result of population crashes of light wood species (Katabuchi et al., 2017). In diverse communities, in theory, the distribution of species abundances may be determined by ecological drift (Hubbell, 2001; Purves & Pacala, 2005; Hubbell, 2006; but see Chisholm et al., 2014). However, the maintenance of the functioning of the community should be governed by processes that deviate from complete neutrality (e.g. Purves & Pacala, 2005). In accordance with Hubbell's ideas (Hubbell, 1979, 2001, 2005, 2006; Hubbell & Foster, 1986), if ecological equivalence occurs at the functional group level, a species that is locally present and possesses a given set of traits, as a result of evolutionary history, will colonize the empty space left by a dead individual of its same functional group maintaining the functionality of the community.

This replacement of functionally similar individuals, suggested to result from adaptations to a discrete set of environmental factors (Hubbell, 2005, 2006; Hubbell & Foster, 1986), could manifest in patterns of functional group habitat preferences given the differences in environmental conditions of different habitats. Previous work on BCI showed that habitat variation (the same topographic types used in this study) was not enough to explain the maintenance of alpha diversity (Harms et al., 2001). While some of the associations at the species level found by Harms et al. (2001) were not maintained when

the species were clustered into functional group, the habitat associations found at the functional group level suggest that topographic characteristics might play an important role in the distribution of functional groups in the forest and in the maintenance of diversity (Hubbell & Foster, 1986). For example, in the last census, functional group 1 was associated positively with low plateau and negatively with the swamp (Table 1; Figure 6b). The species in this functional group have short-intermediate statures with low values of leaf area and intermediate values of wood density (Figure 3). Functional group 2 was positively associated with mixed habitats (Table 1; Figure 6c) with slow-growing and long-lived species (Figure 3). Both functional groups were associated with areas in BCI that have lower soil water potentials (Daws et al., 2002) and usually stay dried during dry seasons (Becker et al., 1988; Condit et al., 1996). Lastly, functional group 3 was positively associated with slope and negatively associated with mixed forest (Table 1; Figure 6d). These species show high turnover and fast growth (Figure 3) and are associated with areas with high soil water potentials (Daws et al., 2002) and therefore are wetter during the dry season (Becker et al., 1988; Condit et al., 1996). It is important to highlight that functional groups 2 and 3 have associations with less abundant habitats in BCI that might be playing a relevant role in promoting coexistence (e.g. better performance of these functional groups in spatially rare habitat types). However, the current data are not suitable to test this possibility as it would require information about the spatial rarity of habitats and species distributions on regional scales.

Additionally, phylogenetic analyses conducted in this forest found that species tend to be phylogenetically overdispersed in swamp and slope habitats, while phylogenetically clustered in young forests and plateau (Kembel & Hubbell, 2006; Kress et al., 2009). Phylogenetic overdispersion suggests that biotic interactions interact to give rise to the species co-occurring (Webb et al., 2002) in the swamps and slope habitats. However, if environmental conditions in those specific habitats are selecting for species with certain traits, phylogenetic overdispersion could be expected as a result of trait evolutionary convergence (e.g. Cavender-Bares et al., 2004). Thus, functional group habitat associations reflect the interplay between the convergent life-history strategies, regardless species commonness, and the environmental conditions of each specific habitat (Hubbell, 2005, 2006; Hubbell & Foster, 1986).

5 | CONCLUSIONS

Our results suggest that plant community assembly mechanisms in this forest may be acting at different levels of community organization aligning with the *functional group*-based version of Hubbell's neutral (Hubbell, 2005, 2006; Hubbell & Foster, 1986). On the one hand, there is determinism at the functional group level, in which the relative proportion of functional groups changes through time in a way that cannot be predicted by neutrality. Although neutrality generated stable patterns through time, the functional group dynamics deviate from that neutrality. On the other hand, apparent ecological

drift allows within-functional group species relative abundances to drift randomly. These patterns might be attributed to environmental filtering in which abiotic interactions promote similarity in species functioning, regarding their commonness, reflected in clusters (i.e. functional groups) of species sharing life-history strategies. Likewise, habitat associations may occur at the functional group level highlighting the importance of abiotic interactions in selecting species with certain traits based on different resource availability. These processes ultimately maintain the functionality of the community and may promote species coexistence.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

V.E.R. and N.G.S. developed and framed the research idea; V.E.R. analysed the data; N.G.S. oversaw data analyses; and V.E.R. and N.G.S. wrote the manuscript.

DATA AVAILABILITY STATEMENT

BCI survey data are publicly available here: https://datadryad.org/stash/dataset/doi:10.15146/5xcp-0d46. Code for this study is available in a public GitHub repository: https://github.com/VanessaRubio/Fgroups-functional-determinism

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