



Functional convergence and phylogenetic divergence during secondary succession of subtropical wet forests in Puerto Rico

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Keywords

Acquisitive–conservative spectrum;
Community-weighted mean traits;
Competition-colonization trade-off; Functional diversity; LMA; Maximum height; Seed size; Successional niche hypothesis; Tropical secondary forests; Wood density

Abbreviations

WD = Wood density; LMA = leaf mass per area;
 $H_{\max}$ = maximum height; $\text{SES.MPD}_{\text{FUN}}$ = standardized effect size of mean pair-wise functional distance; $\text{SES.MPD}_{\text{PHY}}$ = standardized effect size of mean pair-wise phylogenetic distance.

Nomenclature

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Abstract

Question: Understanding how the relative importance of different community assembly processes changes during secondary succession of diverse systems remains elusive. Functional and phylogenetic approaches that place species along continuous axes of niche differentiation and evolutionary relatedness, however, are deepening our understanding of the mechanisms that drive successional dynamics. We ask whether successional shifts in the functional and phylogenetic composition of post-agricultural tropical forests provide evidence for niche partitioning or competitive dominance hierarchies as drivers of successional change.

Location: Subtropical wet forests, Puerto Rico.

Methods: We combined data on four functional traits [leaf dry mass per area (LMA), wood density (WD), maximum height ($H_{\max}$), seed dry mass] and a well-resolved molecular phylogeny to characterize taxonomic, functional and phylogenetic composition of sapling and adult tree communities along a regionally replicated chronosequence. We used a null model approach to assess how functional and phylogenetic diversity change with forest age.

Results: Corresponding increases of community-weighted mean LMA, $H_{\max}$ and seed mass with forest age reflected a shift in dominance of species with acquisitive resource-use strategies and small seeds towards species with more conservative resource use and larger seeds. A negative relationship between forest age and local diversity of $H_{\max}$ and seed mass suggested increased importance of competitive hierarchies for light capture and shade-tolerant regeneration in older forests. In contrast, the colonization of palms in older forest plots led to a positive relationship between forest age and local phylogenetic diversity, suggesting functional convergence of distantly related lineages on traits that confer competitive dominance under low resource conditions.

Conclusions: We linked both functional and phylogenetic dimensions of community diversity with successional trajectories of post-agricultural tropical forests. Contrasting patterns of these dimensions of diversity shed light on the underlying community assembly processes. We argue that integrating traits and phylogeny with specific hypotheses about physiological and historical mechanisms is essential for advancing our understanding of the drivers of community change during succession.

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Introduction

Today, the majority of the Earth's forests are undergoing secondary succession (FAO 2015). Understanding the dynamics of these forests is essential to clarify the long-term implications of land-use change on biodiversity and ecosystem services (Chazdon 2014). For instance, Pan et al. (2011) estimated that at a global scale, regrowing tropical forests account for 43% of the total forest carbon sink. Additionally, the highly dynamic nature of secondary forests provides valuable opportunities for gaining general insight into drivers of community assembly (Lasky et al. 2014a).

In diverse tropical forests, existing research has been more successful at predicting structural aspects of change (e.g. biomass accumulation, stem density) than in characterizing the dynamics of species composition during succession (Guariguata & Ostertag 2001). Trait-based approaches that place species along quantitative axes of niche differentiation, however, are helping to deepen our understanding of the mechanisms that drive community assembly and successional dynamics (Chazdon et al. 2003; Lebrija-Trejos et al. 2010; Lasky et al. 2014a; Lohbeck et al. 2014, 2015; Craven et al. 2015). For example, declining light availability in the understorey (i.e. increased leaf area index) is a fundamental feature of forest succession (Bazzaz & Pickett 1980; Nicotra et al. 1999; Lebrija-Trejos et al. 2011). Two non-mutually exclusive

mechanisms that anticipate shifts in the functional composition of communities from this change in light conditions are the competition–colonization trade-off and the successional niche hypothesis (Fig. 1).

Under the competition–colonization trade-off, species with traits associated with strong colonization ability (e.g. small seeds and high fecundity) occupy available sites in early succession because of the relative dispersal limitation of competitively dominant species (Fig. 1a; Levins & Culver 1971). As succession proceeds, the relative importance of non-local seed input declines, resource availability declines and competitively dominant species exclude initial colonists (Fig. 1b; Chazdon 2008). It is important to note that 'competitive dominance' can encompass traits that confer both hierarchical advantages (e.g. tall adult stature; Givnish 1995) or tolerance to limited light availability and the ability to regenerate in low resource conditions of the understorey (e.g. large seeds; Foster 1986).

According to the successional niche hypothesis, species that rapidly exploit abundant resources can temporarily dominate early successional or high resource sites (e.g. gaps) regardless of a colonization advantage, because species with more conservative resource-use strategies have slower growth rates (Fig. 1c; Pacala & Rees 1998). For example, species with traits associated with acquisitive resource strategies [e.g. low wood density (WD; $\text{g}\cdot\text{cm}^{-3}$), leaf dry mass per area (LMA; $\text{g}\cdot\text{cm}^{-1}$) and seed mass (g)] are predicted to flourish in early succession when light

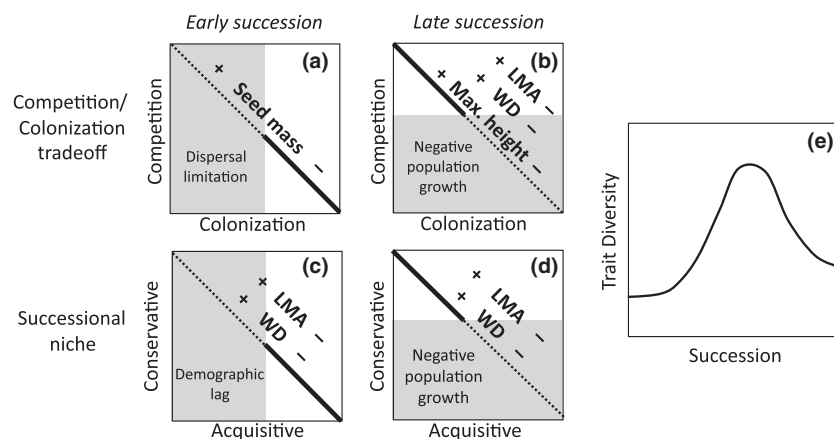


Fig. 1. Two potential mechanisms that underlie successional dynamics are a trade-off in competition–colonization ability (a, b) and successional niches (c, d). Under the competition–colonization trade-off, a colonization advantage (e.g. low seed mass) enables weak competitors to occupy early successional habitats where competitive dominants are absent because of dispersal limitation (shaded area of a). As the relative importance of non-local seed input declines in later stages of succession, the benefits of early colonization are diminished and weak competitors (shaded area of b) are excluded by species with traits that convey competitive dominance (e.g. conservative resource-use strategies, tall $H_{\max}$). Under the successional niche hypothesis (c, d), competitive ability depends on local resource levels (e.g. successional stage). Early in succession, when resource levels are high, species with acquisitive resource traits (e.g. low LMA and WD) dominate because they achieve more rapid rates of growth and reproduction (c). As resource levels become depleted, species with conservative resource-use strategies (e.g. high LMA and WD) increase in abundance and draw resources down to levels where acquisitive species cannot persist (d). Based on the functional turnover during succession predicted by the competition–colonization trade-off and successional niche mechanisms, functional diversity is expected to peak at intermediate stages of succession because species associated with early and late succession co-occur (e).

levels in the mid- and understorey are high. Over time, however, species with conservative traits associated with shade-tolerant regeneration (e.g. high WD, LMA, seed mass) are predicted to increase in abundance and dominate later stages of succession (i.e., during the stand thinning stage; Fig. 1d; Chazdon 2008). Thus, species sorting with respect to shifting abiotic conditions within a site acts as a primary driver of vegetation change.

Besides predicting directional shifts in locally dominant trait values (i.e. community-weighted mean traits), the competition–colonization trade-off and successional niche models also anticipate shifts in functional diversity during succession (Fig. 1e). Specifically, functional diversity should initially be low when sites are dominated by early successional species with either high colonization or acquisitive resource-use strategies (Kinzig & Pacala 2001; Grime 2006; Lasky et al. 2014b). During intermediate stages of succession, a mixture of species associated with early and late succession is predicted to co-occur, resulting in an increase of functional diversity (Réjou-Méchain et al. 2014). Eventually, low resource conditions associated with late succession should constrain the diversity of traits that convey competitive dominance (e.g. tall maximum height; $H_{\max}$) or the ability to tolerate low resource conditions (e.g. large seeds; Mason et al. 2012). Alternative scenarios may arise, however, if local environmental heterogeneity drives community composition, promoting high functional diversity (Questad & Foster 2008). For example, canopy gaps that occur from mortality of large trees in the later stages of succession increase heterogeneity of the light environment, potentially favouring a high diversity of life-history strategies at the stand scale (Bazzaz & Pickett 1980; Nicotra et al. 1999; Loehle 2000).

The few existing studies that have examined changes in plant functional diversity during tropical succession have reported mixed results that appear to depend, in part, on the abiotic context (e.g. wet vs dry forests; Lohbeck et al. 2013; soil types; Réjou-Méchain et al. 2014), the range of successional ages studied (e.g. Swenson et al. 2012) or the particular traits considered (Lasky et al. 2014a; Lohbeck et al. 2014). A number of other studies have used metrics of phylogenetic diversity to infer community assembly processes during tropical succession (e.g. Letcher 2010; Ding et al. 2012; Letcher et al. 2012; Norden et al. 2012). These studies have generally emphasized the idea that increasing phylogenetic diversity over succession (which has been the most commonly reported result; Meiners et al. 2015) reflects strong abiotic filtering during early succession and an increased importance of negative biotic interactions later in succession. However, contrasting assembly mechanisms (e.g. competitive dominance, abiotic filtering) can generate similar phylogenetic patterns depending, in part, on the degree to which relevant traits

are phylogenetically conserved (Grime 2006; Mayfield & Levine 2010; Bernard-Verdier et al. 2013; Gerhold et al. 2013; Mason & Pavoine 2013). Currently, we have limited understanding about the degree to which traits related to successional strategies are phylogenetically conserved, and more generally, the links between phylogenetic and functional diversity patterns during forest succession (Letcher et al. 2015). For instance, Norden et al. (2012) presented evidence supporting shared ancestry of early successional specialists in the Costa Rican lowlands. In contrast, Chazdon et al. (2003) argued that phylogenetically conserved reproductive traits appeared to be more important determinants of tree composition in late successional forests. Ultimately, achieving a synthesis of existing results requires (1) explicit hypotheses about how particular traits should respond to successional change, and (2) a better understanding of the links between functional and phylogenetic diversity patterns during succession.

To date, we are aware of only two studies that have simultaneously examined temporal turnover in functional and phylogenetic diversity as tropical forests recover from disturbance events (Ding et al. 2012; Swenson et al. 2012), and only one (Ding et al. 2012) focused on post-agricultural systems. Additional work is required to understand the relationships between various dimensions of biodiversity as forests recover from human land use. Here, we used an integrative approach to examine functional and phylogenetic shifts in sapling and adult tree communities along a regionally replicated chronosequence of wet forests regrowing on abandoned pastures in Puerto Rico. We combined data on four functional traits related to colonization ability, competitive dominance, resource use and acquisition strategies, and a well-resolved molecular phylogeny to address the following questions:

1. How does the community-level functional composition of forest plots vary with respect to forest age? We predicted that species with high colonization ability and acquisitive life-history traits (e.g. small seed size, low LMA and WD) would dominate early in succession, whereas later stages of succession would be marked by increasing abundance of species with traits associated with conservative resource-use strategies (e.g. high LMA and WD), shade-tolerant regeneration (e.g. large seed size) and dominance for light competition (e.g. tall $H_{\max}$). We expected these changes to be more pronounced among saplings than adult trees due to their relatively rapid turnover.
2. How do local functional and phylogenetic diversity vary with respect to forest age? If a competition–colonization trade-off and successional niches explain community dynamics during succession, we expected functional diversity to peak during intermediate stages of succession. On the other hand, if an increase in light hetero-

geneity drives patterns of trait diversity during succession, we expected the diversity of traits related to light use and shade-tolerant regeneration to increase with stand age. Alternatively, lower overall resource availability may lead to functional convergence on traits that convey competitive dominance (e.g. tall $H_{\max}$) and the ability to persist in low resource conditions (e.g. large seed size). If the traits underlying these functional shifts are strongly conserved on the phylogeny, we expected corresponding patterns of phylogenetic diversity during succession. If traits are convergent with respect to phylogeny, however, we expected independence between functional and phylogenetic patterns. As above, we expected changes in diversity during succession to be more pronounced among saplings than adults.

Methods

Study area and tree community surveys

We combined data from 48 secondary forest plots located in three regions of subtropical wet forests in Puerto Rico (Appendix S1). Most plots ($n = 45$) were sampled in 1995 (Aide et al. 1996) and two were newly established in 2012. We also included a subset of data from 2010 from a portion of the Luquillo Forest Dynamics Plot (LFDP) that had experienced high land-use intensity during the 1930s (i.e. cover class 1 in Thompson et al. 2002). We subsampled the LFDP data to match the sample design of the other plots (see below). Sites were selected with as similar abiotic conditions as possible in order to help meet the assumptions of the chronosequence approach. The age of each plot was determined with aerial photographs taken between 1936–1994 and/or interviews with local landowners. Together, the plots ranged in age from 4–91 yr of natural forest growth at the time of census. Here, we focus on analyses using forest age as a metric of succession, however, hurricane disturbance can alter some aspects of forest structure (e.g. basal area) that are commonly associated with successional stage. In our plots, forest age and basal area are strongly correlated (Appendix S2). We present results of analyses using stand basal area as the predictor variable in the Supporting information.

In each plot, we counted, identified and measured the freestanding woody individuals (excluding lianas and tree ferns) that were 1–10 cm DBH ('saplings') in four parallel 1 m $\times$ 50 m transects, each separated by 10 m (200 m²). We also measured larger individuals (≥ 10 cm DBH; 'adults') in two parallel transects measuring 10 m $\times$ 50 m and separated by 10 m (1000 m²). For each plot, we calculated rarefied species richness based on the minimum number of stems (of both size classes) recorded from a single plot ($n = 47$). We accounted for potential spatial autocorrelation among

plots in the same region using a mixed effects model (see Statistical analyses below).

Functional traits

We collected data on four functional traits from one to 61 individuals (mean = 13.5) of each species using methods outlined in Cornelissen et al. (2003), with some exceptions noted below. *Leaf dry mass per area* (LMA; g·cm⁻²) is a key component of the leaf economics spectrum and positively related to leaf longevity; species with low LMA tend to grow fast and achieve rapid return on carbon investment, whereas species with high LMA have slow growth and retain nutrients for longer periods (Wright et al. 2004). We measured LMA on entire leaves (including petiole) of fully expanded foliage from the outer crown (sun-exposed, when possible) of mature trees. *Wood density* (WD; g·cm⁻³) is related to a trade-off between relative growth rate and mortality; species with low WD tend to grow relatively rapidly because of low investment in structural material, while species with high WD have higher resistance to structural damage and drought-induced mortality (Chave et al. 2009). For trees 10–20 cm in diameter, we measured WD using an increment borer. For species that do not reach this size, we included branch WD measurements and used regressions of branch and core samples from the same individuals to correct for this difference (Appendix S2). *Maximum height* ($H_{\max}$; m) is positively associated with competitive dominance in light-limited environments and time to reproduction (Givnish 1995). We calculated $H_{\max}$ for each species as the maximum between (1) the tallest individual observed in our study and (2) the maximum height reported by local experts (e.g. Little & Wadsworth 1964). *Dry seed mass* (SS; g) corresponds to a seed size–fecundity trade-off (Smith & Fretwell 1974); empirical evidence suggests that smaller seeds have a dispersal advantage and can persist for long periods in the soil (Dalling & Brown 2009), whereas large, recalcitrant seeds tend to have higher probability of initial establishment, particularly in shady conditions (Foster 1986). We log-transformed species estimates for all traits except WD prior to analyses, and we excluded palms from analyses involving WD. Across traits, we obtained data for an average of 93% of the observed species (range = 90–99%), representing >97% of the individuals per plot.

Community phylogeny

We constructed a community phylogeny for the majority of species recorded in our study by pruning a DNA barcode phylogeny of the native and naturalized trees of Puerto Rico (Muscarella et al. 2014). This phylogeny contains 95% of the species (>99% of the individuals) in our data

set. To aid in interpretation of functional and phylogenetic patterns, we used maximum likelihood methods in the R package ‘caper’ (Orme et al. 2011) to estimate Pagel’s λ (Pagel 1999), which quantifies the phylogenetic signal of each trait (i.e. the degree to which phylogenetic relatedness predicts functional similarity). Pagel’s λ normally ranges from 0 to 1: $\lambda = 0$ if trait values have no phylogenetic signal (i.e. they are random with respect to phylogeny) and $\lambda = 1$ if trait values correspond to a Brownian motion model of trait evolution.

Statistical analyses

To evaluate how the average functional composition of forest plots varies during succession (*Question 1*), we quantified community-weighted mean trait values separately for saplings and adults in each plot based on species’ relative abundance and mean trait values. Weighing trait values by relative basal area gave qualitatively similar results (Appendix S2). To help understand how traits may act in a coordinated manner to drive community patterns, we measured pair-wise correlations between species mean trait values using Pearson’s correlation coefficient. To account for shared evolutionary history of species, we also quantified trait correlations using phylogenetic independent contrasts (PICs). We note that species with incomplete data for a particular trait comparison (e.g. palms for comparisons involving WD) were necessarily excluded. To determine how functional and phylogenetic diversity change during succession (*Question 2*), we calculated the abundance-weighted mean pair-wise distance in functional trait space (MPD_{FUN}; calculated separately for each trait) and phylogenetic branch length (MPD_{PHY}) among co-occurring individuals (for saplings and trees separately) in each plot. We used a null model to control for the variation in species richness, species occupancy rates and stem density among plots. Specifically, we calculated the standard effect size of the MPD metrics (SES.MPD) as: $(r_{\text{obs}} - \text{mean}(r_{\text{rand}}))/\text{sd}(r_{\text{rand}})$, where r is the distance in trait space (for SES.MPD_{FUN}) or phylogenetic branch length (for SES.MPD_{PHY}) among all co-occurring individuals in a plot. The observed value is r_{obs} , and r_{rand} is a vector of values based on a null model. For the null model, we generated 9999 random assemblages from the list of species in our data set by randomizing species names across the trait matrix (or phylogeny tips) and calculating a value of r_{rand} for each iteration. This procedure maintains the observed species occupancy rates and plot-level species richness while randomizing traits (or position on the phylogeny) and is appropriate when species abundances do not exhibit phylogenetic signal (Hardy 2008), as was the case in our data set (95% CIs for λ of abundance = 0.00–0.13 for saplings; 0.00–0.75 for adults). Positive values of SES.MPD

indicate over-dispersion (i.e. co-occurring individuals are less similar than expected by chance); negative values indicate clustering (i.e. co-occurring individuals are more similar than expected by chance).

We used linear mixed models to regress community mean trait values, SES.MPD_{FUN} and SES.MPD_{PHY} against stand age, including a random effect to account for potential correlations among plots in the same region (Appendix S1). We used AIC to select between models with and without a quadratic term for stand age to account for the possibility of non-linear responses. Posterior distributions of model parameters were obtained using the R package ‘arm’ (Gelman et al. 2006). We calculated marginal and conditional R^2_{GLMM} (R^2_m , variance explained by fixed factors alone; and R^2_c , variance explained by fixed and random factors combined) using the R package ‘MuMIn’ (Nakagawa & Schielzeth 2012). Analyses were conducted in R 3.1.1 (R Foundation for Statistical Computing, Vienna, AT) using ‘picante’ (Kembel et al. 2010), ‘lme4’ (Bates et al. 2015) and Phylocom 4.2 (Webb et al. 2008).

Results

In total, we recorded 8804 individuals of 135 species (Appendix S3). Rarefied species richness ranged from 5.8 to 20.5, and increased with stand age (Appendix S1). Stands in relatively early stages of succession tended to be dominated by *Alchornea latifolia* Sw., *Tabebuia heterophylla* (DC.) Britton and two common exotic species, *Spathodea campanulata* P. Beauv. and *Syzygium jambos* (L.) Alston. Species with high abundance in medium-aged stands included *Guarea guidonia* (L.) Sleumer and *Ocotea leucoxylon* (Sw.) Laness. In the oldest stands, the most abundant species included several that are often associated with late successional forests in Puerto Rico (e.g. *Dacryodes excelsa* Vahl and *Manilkara bidentata* (A. DC.) A. Chev.), as well as a long-lived pioneer (*Cecropia schreberiana* Miq.) and the palm, *Prestoea montana* (R. Graham) G. Nicholson.

Traits varied widely across species (range for LMA = 15.9–388.6 g·m⁻²; WD = 0.17–0.98 g·cm⁻³, H_{max} = 2.5–35.0 m, dry seed mass = 2×10^{-5} –35.2 g). Based on species mean values, we found significant correlations for three of six pair-wise comparisons (Table 1). Specifically, LMA was positively correlated with WD and H_{max} , and H_{max} was positively correlated with seed mass. In contrast, correlations of species mean trait values were not significant between seed mass and LMA, WD and H_{max} , and WD and seed mass. Correlation analyses based on phylogenetic independent contrasts (PICs) showed some differences from the analysis of species mean values (Table 1). Specifically, there was no significant correlation between PICs of WD and LMA or between PICs of seed mass and

Table 1. Pair-wise correlation coefficients (Pearson's r) for species mean trait values (above diagonal) and phylogenetic independent contrasts (below diagonal). Statistically significant correlations are indicated in bold and with asterisks.

	LMA	Wood Density	$H_{\max}$	Seed Mass
LMA		0.39*	0.26*	0.14
Wood Density	0.03		0.02	0.13
$H_{\max}$	0.43*	−0.13		0.38*
Seed Mass	0.02	−0.55*	0.13	

$H_{\max}$, indicating that the correlations of species mean values for these traits are explained by shared evolutionary history. In contrast, the correlation between PICs of seed mass and WD was significantly negative (as opposed to uncorrelated species mean values). All four traits showed some degree of phylogenetic signal (i.e. $\lambda > 0$), although none strongly enough to match a Brownian motion model of trait evolution (i.e. $\lambda < 1$). Phylogenetic signal was strongest for seed mass (λ [95% CI] = 0.84 [0.59–0.96]), followed by WD (0.69 [0.43–0.85]), $H_{\max}$ (0.57 [0.29–0.78]) and LMA (0.47 [0.09–0.74]).

Question 1: Shifts in community-weighted mean traits during succession

For saplings (stems 1–10 cm DBH), directional shifts of community mean trait values were generally consistent

with our hypothesized transition from species with acquisitive resource strategies and high colonization abilities in early succession, to species with more conservative resource strategies and competitive dominance for light capture in later stages of succession. Specifically, the community mean value for LMA, $H_{\max}$ and seed mass increased with forest age, and linear models provided better fits than quadratic models (Appendix S4). As predicted, these patterns were similar but less marked for adults (stems >10 cm DBH): adult community-weighted mean LMA and seed mass both increased with forest age (Fig. 2). Contrary to our predictions, however, community-weighted mean WD was not significantly associated with forest age for either saplings or adults.

Question 2: Functional and phylogenetic diversity during succession

We detected two significant shifts in functional diversity during succession, and linear models provided better fits than quadratic models in all cases (Fig. 3, Appendix S4). Among saplings, functional diversity (SES.MPD_{FUN}) of seed size declined with forest age (Fig. 3d), indicating a convergence towards species with large seeds. Among adults, functional diversity of $H_{\max}$ declined with forest age, suggesting convergence towards species of relatively tall stature as forests age (Fig. 3i).

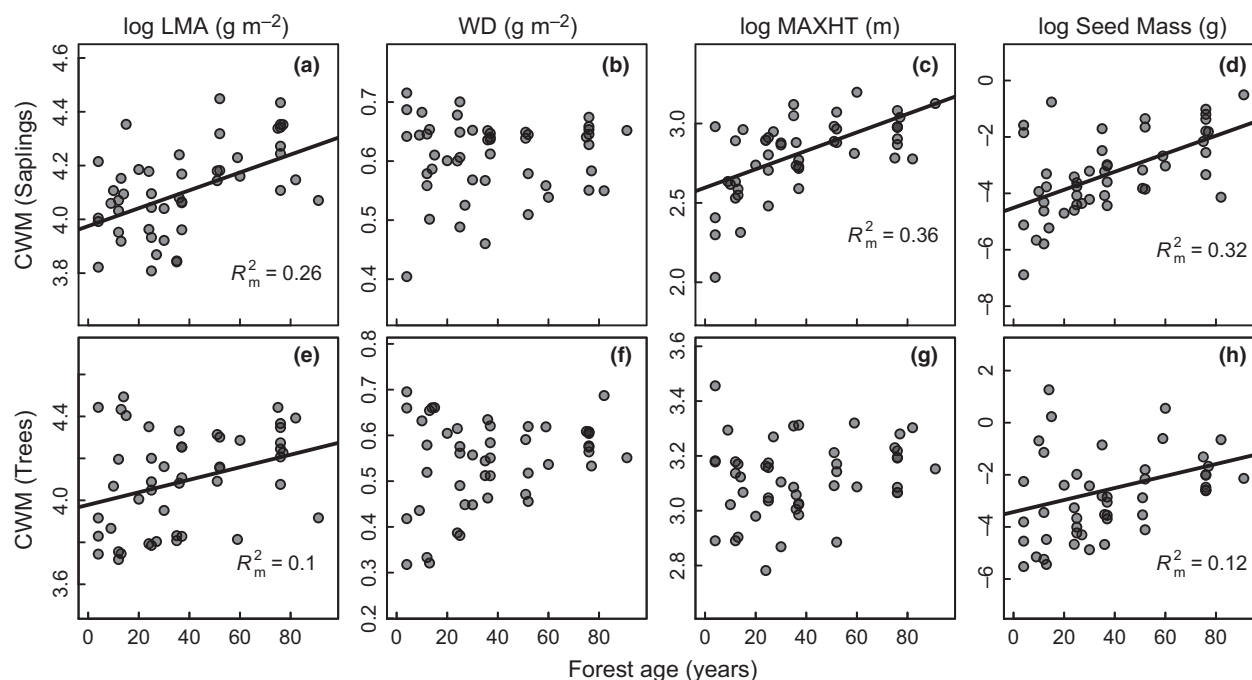


Fig. 2. Community mean trait values (weighted by relative abundance) for saplings (1–10 cm DBH; **a–d**) and adults (>10 cm DBH; **e–h**) in wet forest plots of Puerto Rico. Regression lines are shown with marginal R^2_{GLMM} (Nakagawa & Schielzeth 2012) when 95% confidence intervals of the slope did not overlap with zero. See Appendix S4 for full regression results.

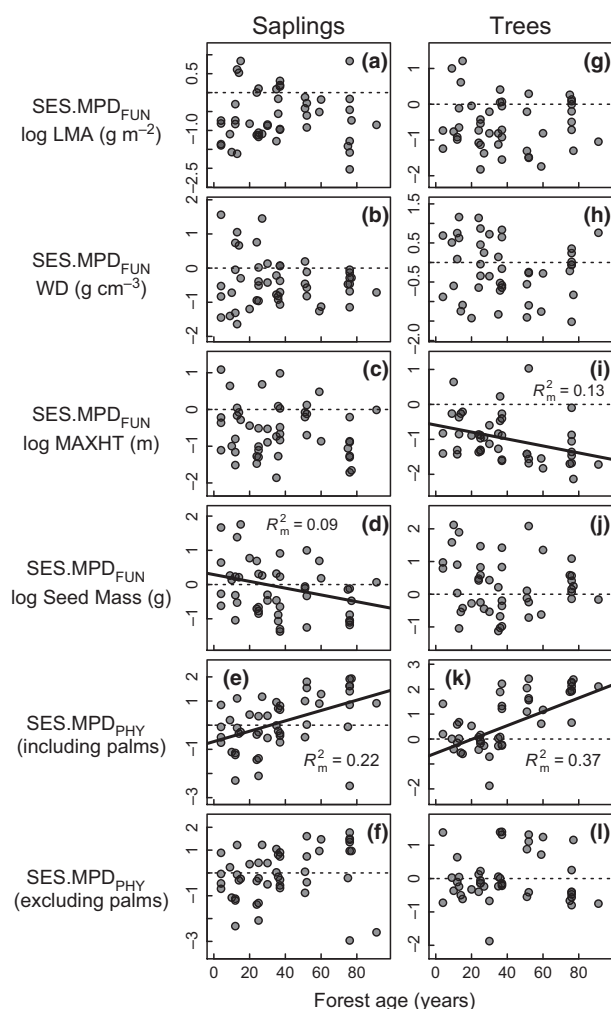


Fig. 3. Mean pair-wise distance in trait space ($\text{SES.MPD}_{\text{FUN}}$) and phylogenetic branch length ($\text{SES.MPD}_{\text{PHY}}$) for saplings (1–10 cm DBH; **a–f**) and adults (>10 cm DBH; **g–l**) in wet forest plots of Puerto Rico. Negative values indicate functional (or phylogenetic) clustering; positive values indicate functional (or phylogenetic) evenness. Regression lines are shown with marginal R^2_{GLMM} (Nakagawa & Schielzeth 2012) when 95% confidence intervals of the slope did not overlap with zero. See Appendix S4 for full regression results.

Phylogenetic diversity also shifted during succession, but the patterns contrasted with those reported for functional diversity. Among both saplings and adults, phylogenetic diversity ($\text{SES.MPD}_{\text{PHY}}$) increased with forest age (Fig. 3). Relatively low phylogenetic diversity of early successional plots was due to particularly high abundances of several species of *Miconia* (Melastomataceae) as well as two species from the Bignoniaceae, *T. heterophylla* and *S. campanulata*. The increase of phylogenetic diversity in older plots was driven by the colonization of palms (especially *P. montana*), and the trend was not statistically significant when palms were excluded from the analysis (Fig. 3).

Removal of palms from the functional trait analyses, however, did not qualitatively change the results (data not shown).

Discussion

We recorded shifts of community mean trait values and functional diversity that support a shift in the relative importance of colonization ability in early stages of succession towards dominance for light capture and shade-tolerant regeneration during later stages of succession. We also recorded an increase of phylogenetic diversity with forest age that was primarily driven by the colonization of some older forest plots by palms. We did not find evidence that niche partitioning becomes a relatively stronger driver of community composition as forests age. Instead, our results support both a competition–colonization trade-off and successional niches as important drivers of post-agricultural successional dynamics in Puerto Rican wet forests.

Question 1: Shifts in community mean traits

The observed increase in community mean LMA during succession reflects a shift of communities dominated by species with acquisitive light capture strategies that capitalize on rapid exploitation of high light conditions, towards communities dominated by species with more conservative strategies that make higher initial investments in leaf construction with long-term pay-offs (Wright et al. 2004). This finding is consistent with other studies of forest succession in wet tropical forests (e.g. Reich et al. 1995; Craven et al. 2015; Lohbeck et al. 2015), highlighting the link between high LMA and shade-tolerant life-history strategies.

Because WD is generally negatively correlated with mortality rate (Chave et al. 2009; Lasky et al. 2014a), we expected that long-lived species with high WD would increase in abundance and basal area during succession, and lead to an increase in community-level WD. We did not, however, find a significant shift in community mean WD of trees with stand age. We suspect that at least two separate factors contribute to our results. First, *C. schreberiana*, a long-lived pioneer and gap-specialist with low WD, had a high basal area in some of the older successional plots, driving down community mean WD. The relatively high abundance of *C. schreberiana* in these plots is likely related to repeated disturbance by hurricanes, which result in the creation of large gaps and tree tip-ups, which are required for *C. schreberiana* recruitment (Brokaw 1998; Flynn et al. 2010). Second, early successional plots exhibited a high amount of variation in their community mean WD. High dispersal limitation or stochastic colonization of early successional plots, followed by subsequent biotic and

abiotic filtering processes could lead to such a pattern, particularly if species WD values are unrelated to their dispersal abilities. In fact, the lack of correlation between species mean values of seed mass and WD in our data set lends some support to this explanation. To date, few studies have examined community mean shifts of stem traits during succession, and have found inconsistent patterns that partly depend on the abiotic context. For instance, Lohbeck et al. (2013) found that community mean WD declined with forest age among tropical dry forest plots, but was unrelated to age among wet forest plots. Examining how abiotic conditions and disturbance regimes influence functional trajectories of forests during succession will be an important area for future research. Additionally, further information on the relationship between stand age and metrics of forest structure (e.g. basal area) in disturbance-prone systems would be a valuable contribution that may shed additional light on the links between disturbance and functional diversity.

Consistent with the hypothesized link between seed size and colonization ability (Foster 1986), we observed an increase in community mean seed mass during succession. Trade-offs mediated by seed size ultimately involve an energetic trade-off between seed size and fecundity (Smith & Fretwell 1974). Small-seeded species tend to have a colonization advantage through high fecundity and low dispersal limitation, whereas large-seeded species are associated with a higher probability of establishment, particularly under low resource conditions (Foster 1986). Our results underscore the role of seed size in mediating a competition–colonization trade-off, and as an important dimension of the successional niche.

We observed an increase in community mean $H_{\max}$ among saplings but not among adults. As discussed with WD above, one likely explanation for this difference is the long-term and repeated effect of hurricane damage on Puerto Rican forests (Boose et al. 2004; Uriarte et al. 2009; Flynn et al. 2010). Interspecific variation in adult stature can best be understood in terms of the benefits gained in light competition vs the construction and maintenance costs of achieving tall heights (Givnish 1995). In Puerto Rico, an island with a high incidence of hurricanes, the competitive advantages of achieving tall heights may be outweighed by greater susceptibility to hurricane damage (Canham et al. 2010). As a result, the different in maximum height strategies exhibited by early vs late successional canopy species may be less pronounced than in forests that are not exposed to regular wind disturbance (Gouvenain & Silander 2003). In summary, we argue that the strength of the relationship between tree stature and forest age may depend, in part, on the importance of wind disturbance in mediating community dynamics.

One limitation of our study is that we relied on species mean trait values because of the difficulty of adequately characterizing intraspecific trait variation in highly diversity systems. Intraspecific trait variation can be a substantial component of overall functional variation (Bolnick et al. 2011), and future work will benefit by incorporating these data whenever possible. Nonetheless, we suspect that considering intraspecific variation would not change our overall conclusions because the high degree of species turnover during succession can lead to a relatively low contribution of intraspecific variation to total functional variation in successional forests (Craven et al. 2015).

Question 2: Functional and phylogenetic diversity during succession

We did not find evidence that functional diversity was hump-shaped along the successional gradient, as expected from a mixture of early and late successional species co-occurring in intermediate-aged stands. Additionally, for none of the four traits examined here did functional diversity increase with stand age, as expected from stronger niche partitioning during later states of succession (Lasky et al. 2014a). Instead, we observed functional convergence towards large seeds among saplings, and towards tall stature (high $H_{\max}$) among adults. These results provide additional support for a shift in the relative importance of colonization ability in early stages of succession towards dominance for light capture and shade-tolerant regeneration during later stages of succession.

We are aware of only two studies that have quantified changes in light conditions during tropical forest succession (Nicotra et al. 1999; Lebrija-Trejos et al. 2011). Both of these studies found a decline in overall light availability during succession, which is consistent with our observation of increased $H_{\max}$ and shade-tolerant regeneration as major components of successional change. However, Nicotra et al. (1999) and Lebrija-Trejos et al. (2011) also reported increased light heterogeneity during succession, which we expected would lead to higher diversity of traits reflecting resource-use strategies. The few existing studies that have examined changes in functional diversity during tropical forest succession have reported mixed results. In Mexican wet tropical forests, Lohbeck et al. (2014) reported an increase in diversity of leaf traits, suggesting an increasingly important role of niche partitioning for light resources during succession. Their study focused on the first 25 yr of succession, however, which represents a particularly dynamic period of environmental change (Chazdon 2008; Lebrija-Trejos et al. 2011). In seasonally dry tropical forests of Mexico, Bhaskar et al. (2014) also reported an increase in LMA diversity with succession, but diversity of WD and leaf N did not change. Lasky et al.

(2014a) found an increase of LMA diversity at neighbourhood scales during succession in wet forests of Costa Rica, however, diversity of WD decreased with succession. As mentioned above, a fruitful area for future research will be to investigate how variation in site conditions (e.g. wet vs dry forests, disturbance regimes) influences changes in functional diversity during succession (Lohbeck et al. 2013; Meiners et al. 2015).

Given the moderate to high level of phylogenetic signal in the traits we studied, we expected patterns of phylogenetic diversity to mirror those of functional diversity. In contrast, we found an increase in phylogenetic diversity along the successional gradient – a finding consistent with a number of existing studies that have examined phylogenetic diversity during tropical forest succession (Letcher 2010; Ding et al. 2012; Letcher et al. 2012; Norden et al. 2012). In our study, several closely related species commonly co-occurred in early successional plots (e.g. several bird-dispersed *Miconia* species and two wind-dispersed species belonging to the Bignoniaceae). Previous work in Puerto Rico has shown these species to often be associated with early successional secondary forests (e.g. Zimmerman et al. 2000). The increase of phylogenetic diversity with forest age was driven, however, by the colonization of some late successional plots by palms, particularly *P. montana*. In Puerto Rico, *P. montana* is a prominent member of wet forest communities (Thompson et al. 2002) that appears to have a positive response of fecundity to hurricane disturbance (Gregory & Sabat 1996). *P. montana* is rarely found in early secondary forests, however, which appears to be a result of dispersal limitation, given its relatively large seeds (0.73 g dry mass; Uriarte et al. 2005) and previous work demonstrating that it is capable of establishing in early successional plots when planted (Zimmerman et al. 2000). Thus, the observed contrast between functional and phylogenetic diversity patterns was driven by functional convergence among distantly related lineages (i.e. palms) on traits that confer competitive dominance in low resource conditions.

Some previous studies that lacked data on functional traits have argued that relatively low phylogenetic diversity in early successional forests may stem from phylogenetic conservatism of traits associated with early successional strategies (e.g. Letcher 2010; Norden et al. 2012). Later in succession, an increase in habitat heterogeneity, continued colonization or increased importance of negative biotic interactions could then lead to more phylogenetically (and functionally) diverse assemblages. In contrast, Chazdon et al. (2003) reported that 'overly' abundant species in old growth forests were phylogenetically clustered, whereas 'overly' abundant species in secondary (12–25 yr old) forests represented a phylogenetically random subset of the species pool. Although we did

find an increase of phylogenetic diversity in older forest stands (driven by palms), we found no indication that early successional plots comprised functionally convergent strategies relative to late successional plots.

Some previous studies that have examined phylogenetic diversity during tropical forest succession have also found palms to be of key importance in generating phylogenetic patterns. For instance, Letcher (2010) reported an increase in phylogenetic diversity during tropical forest succession that was due, in part, to the recruitment of palms in late successional forests. Letcher (2010) did not, however, report a separate analysis with palms excluded in order to determine the extent to which the pattern was driven by palms. Norden et al. (2012) also reported an increase in phylogenetic diversity during tropical forest succession. The authors mentioned that some of the significant increases disappeared if palms were excluded from the study but did not provide detailed results. In summary, it appears the relationship between palms and phylogenetic diversity is not unique to our system because palms are very often dominant members of tropical forests (e.g. Chazdon et al. 2003; Couvreur & Baker 2013). In fact, palms account for a disproportionate number of hyperdominant tree species in the Amazon (including seven of the 20 most dominant species; ter Steege et al. 2013). We recommend that future work investigating phylogenetic patterns in tropical forest communities should pay close attention to the influence of palms in driving the observed patterns.

Overall, our results underscore the challenges of using phylogenetic patterns to infer community assembly processes in the absence of information on species functional characteristics (Mayfield & Levine 2010; Bernard-Verdier et al. 2013; Gerhold et al. 2013; Mason & Pavoine 2013). Although limited evidence supports the idea that successional status of tropical trees is phylogenetically conserved (e.g. Chazdon et al. 2003; Norden et al. 2012), the relationships between particular functional traits and successional habitat specialization remains an open question (Letcher et al. 2015). Our results contribute to the limited existing information linking functional and phylogenetic dimensions of diversity during tropical forest succession.

Conclusions

By relating information about species functional traits and evolutionary history directly to hypotheses about the drivers of community change, our study helps to synthesize existing theory of community assembly in the context of secondary forests. Better understanding of how diversity is constrained and maintained in these systems will be critical for understanding links between biodiversity and

ecosystem function in the face of environmental change (Lasky et al. 2014b). Importantly, we showed an unexpected divergence between functional and phylogenetic patterns that refined our inferences about underlying processes. Specifically, species occupying young secondary forests appear to be a relatively random functional and phylogenetic subset of the regional pool. As succession proceeds, competitive dominance for light capture and the ability to regenerate in shade then appear to drive community change in this system. We strongly advocate such an integrated approach in future studies to help establish a more general understanding of the processes that drive post-agricultural tropical forest succession.

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References

- Acevedo-Rodríguez, P. & Strong, M.T. 2011. *Flora of the West Indies: Catalogue of the Seed Plants of the West Indies*. Smithsonian Institution, National Museum of Natural History, Washington, DC, US.
- Aide, T.M., Zimmerman, J.K., Rosario, M. & Marciano, H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28: 537–548.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48.
- Bazzaz, F.A. & Pickett, S.T.A. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11: 287–310.
- Bernard-Verdier, M., Flores, O., Navas, M.-L. & Garnier, E. 2013. Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *Journal of Vegetation Science* 24: 877–889.
- Bhaskar, R., Dawson, T.E. & Balvanera, P. 2014. Community assembly and functional diversity along succession post-management. *Functional Ecology* 28: 1256–1265.
- Bolnick, D.I., Amarasekare, P., Araújo, M.B., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26: 183–192.
- Boose, E.R., Serrano, M.I. & Foster, D.R. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs* 74: 335–352.
- Brokaw, N.V.L. 1998. *Cecropia schreberiana* in the Luquillo mountains of Puerto Rico. *Botanical Review* 64: 91–120.
- Canham, C.D., Thompson, J., Zimmerman, J.K. & Uriarte, M. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42: 87–94.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.
- Chazdon, R.L. 2008. Chance and determinism in tropical forest succession. In: Carson, W.P. & Schnitzer, S.A. (eds.) *Tropical forest community ecology*, pp. 384–408. Blackwell Scientific, Oxford, UK.
- Chazdon, R.L. 2014. *Second growth: the promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press, Chicago, IL, US.
- Chazdon, R.L., Careaga, S., Webb, C. & Vargas, O. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecological Monographs* 73: 331–348.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., (...) & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Couvreur, T. & Baker, W. 2013. Tropical rain forest evolution: palms as a model group. *BMC Biology* 11: 1–4.
- Craven, D., Hall, J., Berlyn, G., Ashton, M. & van Breugel, M. 2015. Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia* 179: 1–13.
- Dalling, J.W. & Brown, T.A. 2009. Long-term persistence of pioneer species in tropical rain forest soil seed banks. *American Naturalist* 173: 531–535.
- Ding, Y., Zang, R., Letcher, S.G., Liu, S. & He, F. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos* 121: 1263–1270.
- FAO. 2015. *Global Forest Resources Assessment 2015: how are the world's forests changing?* Food and Agriculture Organization of the United Nations, Rome, IT.
- Flynn, D.F.B., Uriarte, M., Crk, T., Pascarella, J.B., Zimmerman, J.K., Aide, T.M. & Caraballo Ortiz, M.A. 2010. Hurricane disturbance alters secondary forest recovery in Puerto Rico. *Biotropica* 42: 149–157.
- Foster, S. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52: 260–299.
- Gerhold, P., Price, J.N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A. & Pärtel, M. 2013. Functional and phylogenetic commu-

- nity assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science* 24: 843–852.
- Gelman, A., Su, Y.-S., Hill, J., Grazia Pittau, M., Kerman, J. & Zheng, T. 2006. Package 'arm', version: 1.0–1. Data Analysis Using Regression and Multilevel/Hierarchical Models.
- Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner, B.L. (ed.) *Plant stems: physiology and functional morphology*, pp. 3–49. Academic Press, San Diego, CA, US.
- Gouvenain, R.C.d. & Silander, J.A. 2003. Do tropical storm regimes influence the structure of tropical lowland rain forests? *Biotropica* 35: 166–180.
- Gregory, F.A. & Sabat, A.M. 1996. The effect of hurricane disturbance on the fecundity of Sierra palms (*Prestoea montana*). *Bios* 67: 135–139.
- Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.
- Guariguata, M.R. & Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206.
- Hardy, O.J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96: 914–926.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Kinzig, A.P. & Pacala, S.W. 2001. Successional biodiversity and ecosystem functioning. In: Kinzig, A.P., Pacala, S. & Tilman, G.D. (eds.) *The functional consequences of biodiversity: empirical progress and theoretical extensions*, pp. 175–212. Princeton University Press, Princeton, NJ, US.
- Lasky, J.R., Uriarte, M., Boukili, V. & Chazdon, R.L. 2014a. Multiple effects of functional trait variation on successional forest dynamics. *Proceedings of the National Academy of Sciences of the United States of America* 111: 5616–5621.
- Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W. & Chazdon, R.L. 2014b. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters* 17: 1158–1167.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F. & Poorter, L. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91: 386–398.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L. & Bongers, F. 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* 27: 477–489.
- Letcher, S.G. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences* 277: 97–104.
- Letcher, S.G., Chazdon, R.L., Andrade, A.C.S., Bongers, F., van Breugel, M., Finegan, B., Laurance, S.G., Mequita, R.C.G., Martínez-Ramos, M. & Williamson, G.B. 2012. Phylogenetic community structure during succession: evidence from three neotropical forest sites. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 79–87.
- Letcher, S.G., Lasky, J.R., Chazdon, R.L., Norden, N., Wright, S.J., Meave, J.A., Pérez-García, E.A., Muñoz, R., Romero-Pérez, E., (...) & Williamson, G.B. 2015. Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites. *Journal of Ecology* 103: 1276–1290.
- Levins, R. & Culver, D. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the United States of America* 68: 1246–1248.
- Little, E.L. & Wadsworth, F.H. 1964. *Common trees of Puerto Rico and the Virgin Islands*, vol 1. USDA Forest Service, Washington, DC, US.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist* 156: 14–33.
- Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-García, E.A., Romero-Pérez, I.E., Tauro, A. & Bongers, F. 2013. Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* 94: 1211–1216.
- Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., van Breugel, M. & Bongers, F. 2014. Changing drivers of species dominance during tropical forest succession. *Functional Ecology* 28: 1052–1058.
- Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Poorter, L. & Bongers, F. 2015. Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS ONE* 10: e0123741.
- Mason, N.W.H. & Pavoine, S. 2013. Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? *Journal of Vegetation Science* 24: 820–833.
- Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A. & Allen, R.B. 2012. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology* 100: 678–689.
- Mayfield, M.M. & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- Meiners, S.J., Cadotte, M.W., Fridley, J.D., Pickett, S.T.A. & Walker, L.R. 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. *Functional Ecology* 29: 154–164.
- Muscarella, R., Uriarte, M., Erickson, D.L., Swenson, N.G., Zimmerman, J.K. & Kress, W.J. 2014. A well-resolved phylogeny of the trees of Puerto Rico based on DNA barcode sequence data. *PLoS ONE* 9: e112843.

- Nakagawa, S. & Schielzeth, H. 2012. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.
- Nicotra, A.B., Chazdon, R.L. & Iriarte, S.V.B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80: 1908–1926.
- Norden, N., Letcher, S.G., Boukili, V., Swenson, N.G. & Chazdon, R. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. *Ecology* 93: S70–S82.
- Pacala, S.W. & Rees, M. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist* 152: 729–737.
- Orme, D., Freckleton, R.P., Thomas, G., Petzoldt, T., Fritz, S. & Issac, N. 2011. *Caper: Comparative Analysis of Phylogenetics and Evolution in R*. Version 0.4, Imperial College, London, UK.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., (...) & Hayes, D. 2011. A large and persistent carbon sink in the world's forests. *Science* 333: 988–993.
- Questad, E.J. & Foster, B.L. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* 11: 717–726.
- Reich, P.B., Ellsworth, D.S. & Uhl, C. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. *Functional Ecology* 9: 65–76.
- Réjou-Méchain, M., Flores, O., Pélissier, R., Fayolle, A., Fauvet, N. & Gourlet-Fleury, S. 2014. Tropical tree assembly depends on the interactions between successional and soil filtering processes. *Global Ecology and Biogeography* 23: 1440–1449.
- Smith, C.C. & Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *The American Naturalist* 108: 499–506.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C.V., Magnusson, W.E., (...) & Sillman, M.R. 2013. Hyperdominance in the Amazonian Tree Flora. *Science* 342: 325.
- Swenson, N.G., Stegen, J.C., Davies, S.J., Erickson, D., Forero-Montaña, J., Hurlbert, A.H., Kress, W.J., Thompson, J., Uriarte, M., (...) & Zimmerman, J.K. 2012. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology* 93: 490–499.
- Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham, E.M., Lodge, D.J., Taylor, C.M., García-Montiel, D. & Fluet, M. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12: 1344–1363.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K. & Brokaw, N. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *Journal of Ecology* 93: 291–304.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., Fetcher, N. & Haines, B.L. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecological Monographs* 79: 423–443.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098–2100.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., (...) & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Zimmerman, J.K., Pascarella, J.B. & Aide, T.M. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8: 350–360.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed information on study plots.

Appendix S2. Additional details on wood density methods and supplementary figures.

Appendix S3. Table of total abundance for each species in each plot.

Appendix S4. Detailed results of regression analyses.