Oecologia
DOI 10.1007/s00442-015-3339-x

ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Changing gears during succession: shifting functional strategies in young tropical secondary forests

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Received: 14 July 2014 / Accepted: 1 May 2015

Abstract Adaptations to resource availability strongly shape patterns of community composition along successional gradients in environmental conditions. In the present study, we examined the extent to which variation in functional composition explains shifts in trait-based functional strategies in young tropical secondary forests during the most dynamic stage of succession (0–20 years). Functional composition of two size classes in 51 secondary forest plots was determined using community-weighted means of seven functional traits, which were intensively measured on 55 woody plant species ($n = 875$–1,761 individuals). Along the successional gradient in forest structure, there was a significant and consistent shift in functional strategies from resource acquisition to resource conservation. Leaf toughness and adult plant size increased significantly, while net photosynthetic capacity (A_{mass}) decreased significantly during succession. Shifts in functional strategies within size classes for A_{mass} and wood density also support the hypothesis that changes in functional composition are shaped by environmental conditions along successional gradients. In general, 'hard' functional traits, e.g., A_{mass} and leaf toughness, linked to different facets of plant performance exhibited greater sensitivity to successional changes in forest structure than 'soft' traits, such as leaf mass area and leaf dry matter content. Our results also suggested that stochastic processes related to previous land-use history, dispersal limitation, and abiotic factors explained variation in functional composition beyond that attributed to deterministic shifts in functional strategies. Further data on seed dispersal vectors and distance and landscape configuration are needed to improve current mechanistic models of succession in tropical secondary forests.

Keywords Secondary succession · Resource acquisition · Resource conservation · Hard traits · Soft traits

Introduction

Tropical forests contain a remarkable array of ecological strategies whose diversity can be reduced elegantly to a continuous axis representing the trade-off between growth and mortality (Fortunel et al. 2012; Welden et al. 1991; Wright et al. 2010). Where species occur along this axis is strongly governed by the partitioning of resource gradients, principally light (Poorter et al. 2010; Sterck et al. 2006, 2011; Wright et al. 2010), as well as soil nutrients (Russo et al. 2008). Consequently, species-specific adaptations to

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Communicated by Walt Carson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3339-x) contains supplementary material, which is available to authorized users.

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environmental conditions underlie variation in spatial and temporal patterns of abundance that shape forest composition (Poorter 1999). Successional gradients are characterized by clear shifts in resources and environmental conditions, i.e., from high to low light availability, air temperature and soil moisture, and species composition, i.e., from shade-intolerant to shade-tolerant species (Breugel et al. 2007; Dent et al. 2013; Lebrija-Trejos et al. 2010; Norden et al. 2009, 2011a), which lend support to the idea that adaptations to resource availability shape successional patterns of community composition (Rees et al. 2001; Tilman 1985). To date, the mechanisms driving these patterns in tropical secondary forests have been tested explicitly in regions that vary markedly in terms of climate, soil, land-use history, and landscape configuration (e.g., Becknell and Powers 2014; Dent et al. 2013; Lohbeck et al. 2013; Whitfeld et al. 2014).

In forgoing a priori classification of species into functional groups or types, a trait-based approach provides a direct, mechanistic link between ecological strategies, e.g., plant response to environmental stress and disturbance (Grime 1977; Reich 2014), and patterns of abundance (Shipley 2010; Westoby et al. 2002). Variation in functional traits illustrates how species acquire and utilize resources to grow, reproduce, and tolerate herbivores, pathogens, and mechanical damage (Adler et al. 2013; Chave et al. 2009; Onoda et al. 2011; Reich et al. 1997; Wright et al. 2004). In general, species with low leaf mass area (LMA), high foliar N content, short leaf lifespans, and low wood density rapidly convert light energy to carbon, and thus growth, at the cost of greater susceptibility to herbivore and pathogen attacks and reduced shade and drought tolerance (Adler et al. 2013; Reich 2014; Reich et al. 1997). Conversely, species with trait values associated with resource conservation, e.g., high LMA, low foliar N content, long leaf lifespans, and high wood density, utilize resources to conserve carbon or water by investing in structures that decrease susceptibility to abiotic and biotic stressors, which results in slower growth but greater shade and drought tolerance (Adler et al. 2013; Reich 2014; Reich et al. 1997).

Coordinated shifts in functional trait values along resource gradients are thought to reflect species- and community-level responses to changes in resource availability within tropical forests (e.g., Kraft et al. 2008; Lebrija-Trejos et al. 2010; Rees et al. 2001; Sterck et al. 2011; Uriarte et al. 2010). When and where resources are more available, species with trait values associated with resource acquisition are expected to perform better, while those with trait values associated with resource conservation exhibit better performance where resources are limiting (Rees et al. 2001; Reich 2014). For example, Sterck et al. (2006) found that high specific leaf area (SLA), photosynthesis rates, and leaf N content facilitated faster growth in forest gaps and that species with long-lived leaves and low SLA had higher survival rates under a closed canopy. However, not all functional traits or trait syndromes explain variation in ecological processes equally well (Lasky et al. 2013, 2014; Wright et al. 2010). Moreover, other important ecological processes, such plant-soil feedbacks, might not be captured by commonly measured functional traits.

Changes in species abundance during secondary succession in tropical forests are generally presumed to reflect transitions in ecological strategies, from fast growth and shade intolerance to slow growth and shade tolerance (e.g., Bazzaz 1979; Chazdon et al. 2007; Ewel 1980; Finegan 1996). Frequently operating in parallel, two mechanisms—the competition–colonization trade-off and the successional niche—drive this transition (Rees et al. 2001); over time, 'late-successional' species outcompete the initially abundant, fast-growing 'early-successional' species by reducing resource availability below levels at which the latter can establish. Particularly in moist tropical forests, light availability strongly influences competition and species replacement (Galia Selaya et al. 2008; Lohbeck et al. 2013; van Breugel et al. 2012). Comparative studies of plant adaptations to contrasting environmental conditions have further substantiated the importance of light and the ability to endure shade in distinguishing species from different successional stages (Ellsworth and Reich 1993, 1996; Reich et al. 1995). Recent chronosequence studies in Mexico, Costa Rica, Panama, and New Guinea have corroborated that successional changes in environmental conditions, principally light availability, but also air and soil temperatures and soil pH, occur in parallel with changes in species and functional composition (Becknell and Powers 2014; Dent et al. 2013; Lebrija-Trejos et al. 2010; Lohbeck et al. 2013; Whitfeld et al. 2014).

The objective of this study was to examine shifts in functional strategies during the first 20 years of secondary succession. This is the most dynamic phase of succession, during which quick shifts in species composition occur in parallel with rapid changes in forest structure and micro-climate (Lebrija-Trejos et al. 2008; van Breugel et al. 2013). 'Hard' traits (e.g., photosynthesis) have direct, mechanistic links with multiple aspects of plant performance, yet 'soft' functional traits (e.g., specific leaf area and leaf dry matter content) are easier to obtain and have been used more frequently to assess plant performance (Cornelissen et al. 2003; Lavorel and Garnier 2002). Using a highly replicated chronosequence and a combination of 'hard' and 'soft' functional traits, we examined variation in the functional composition of secondary forests during succession in central Panama. We hypothesized that dominant ecological strategies would shift during secondary succession from resource acquisition to resource conservation. Second, we expected that contrasting environmental conditions in the canopy and understory of secondary forests would lead to differences in functional composition between two size classes.

Materials and methods

Site description

The study was performed in the Agua Salud Project (ASP), Panama (9°13′N, 79°47′W, 330 masl), which is located within the Panama Canal Watershed and abuts Soberania National Park. The landscape is a mosaic of active and abandoned cattle pastures and agricultural fields and secondary forests with undulating topography. Soils are mostly silt clay to clay (van Breugel et al. 2013) and mean annual precipitation for the site is 2,700 mm year^{-1}, with a dry season lasting from mid-December until early May (Ogden et al. 2013).

We used a chronosequence approach to infer temporal trends from static vegetation plot data. While chronosequences have well-known limitations (Chazdon 2008; Chazdon et al. 2007; Johnson and Miyanishi 2008), our focus in the present study is on long-term trends and not short-term dynamics. We have attempted to mitigate possible limitations of this approach by using a high number of replicates concentrated over a short time span. In 2008 and 2009, 108 plots, each measuring 20 × 50 m (0.1 ha), were established at 52 sites within secondary forests across the study site as part of ASP's Secondary Forest Dynamics study. Sites were selected at random within the forested area of Agua Salud and represent an unbiased, representative sample of landscape-wide variation in stand age, structure, and composition (van Breugel et al. 2013). At each site, plots were located at upper and lower slope positions and were oriented parallel to the slope. Time since abandonment of these secondary forests ranged from 0 to 30 years for most plots, with some older plots of unknown age and prior land use ($n = 10$ plots >50 years but none old growth). Information on time since abandonment was determined in interviews with former landowners and local residents. In each plot, all stems with a diameter at breast height (DBH) $\geq$5 cm were identified to species and labeled, and DBH was measured. In one half of each plot, all stems $\geq$1 cm DBH were treated similarly. Across all study plots, 403 species of trees, palms, and hemi-epiphytes $\geq$1 cm DBH were found in all inventories (2008–2011). Within each plot, 11 hemispherical photographs were taken during the wet season in 2009 using a Canon Rebel XSi Digital SLR camera with a 180° lens attached to a self-leveling mount; canopy openness was estimated from these photographs with WinSCANOPY V2008 (Regents Instruments, QC, Canada).

We selected 55 of the most abundant tree and shrub species for functional trait measurement (Online Resource 1). The analysis was restricted to 51 plots where the selected species represent at least 80 % of plot basal area (Lohbeck et al. 2013; Pakeman and Quested 2007) and where there had not been agricultural activity or cattle ranching within the past 20 years. Across the selected plots, the sampled species represent 88.81 ± 0.75 (mean ± standard error) % of basal area and 87.11 ± 1.2 % of individuals.

Functional traits

We selected seven functional traits for their capacity to differentiate ecological strategies using standardized measurement protocols (Cornelissen et al. 2003): leaf mass area (LMA, m^2 g^{-1}), leaf dry matter content (LDMC, g g^{-1}), net photosynthetic capacity per unit leaf mass (A_{mass}, nmol g^{-1} s^{-1}), leaf toughness (mN m^{-1}), foliar N content (leaf N, %), maximum DBH (D_{max}, cm), and wood density (WD, g cm^{-3}). We sampled using an intensive species-based approach to capture intraspecific variation across plots and precisely estimate species' means (Baraloto et al. 2010; Lavorel et al. 2008). Samples were collected from at least four plots per species during the wet season (June–November 2010).

For each species, LMA and LDMC were measured on 32 trees per species from at least four plots (Table 1; range 32–33 trees). To account for light-related variation, we recorded the crown exposure (1–5, ranging from no direct light to full direct light) of each sampled tree as a proxy for canopy openness (Poorter and Rozendaal 2008). From each tree, two branches located at similar crown positions were selected, placed in sealed plastic bags, and stored in a cooler. Leaves were not detached from branches until processed in the laboratory to minimize dehydration and were processed within 12–16 h of collection. Fresh mass, including the petiole or rachis, was determined using an electronic balance with ±0.01 g precision. Fresh leaves, including petioles or rachii, were scanned using a digital flatbed scanner at 300 dots per inch, and leaf area and size were determined using ImageJ (ImageJ 1.45a, National Institutes of Health, USA). For species with compound leaves, leaflets were considered to be functionally equivalent to simple leaves and were treated similarly. Leaves were oven-dried at 70 °C for at least 4 days and weighed.

We measured net photosynthetic capacity (A_{area}, μmol CO$_2$ m^{-2} s^{-1}) on two sun-exposed leaves for 16 individuals per species between 0700 and 1200 h using a Li-6400 Portable Photosynthesis System (Li-6400, LI-COR Biosciences Inc., Lincoln, NB, USA). Photon flux density was set to 1,800 μmol m^{-2} s^{-1}, reference CO$_2$ concentrations were maintained at 400 μmol mol^{-1}, average vapor deficit pressure was 1.76 ± 0.01 kPa, and average relative

Table 1 Functional traits of 55 woody species sampled within young secondary forests in central Panama

Functional trait	Abbreviations	Units	Mean (95 % CIs)	Individuals (*n*)
Leaf mass area	LMA	g m^{-2}	76.91 (75.96, 77.78)	1,761
Leaf dry matter content	LDMC	g g^{-1}	0.327 (0.324, 0.33)	1,761
Leaf toughness	Leaf toughness	mN m^{-1}	0.00081 (0.00078, 0.00083)	875
Foliar N content	Leaf N	%	2.02 (1.96, 2.08)	–
Net photosynthetic capacity (per unit dry mass)	A_{mass}	nmol g^{-1} s^{-1}	144.9 (141.0, 149.02)	880
Maximum DBH	D_{max}	cm	211.0 (167.1, 261.0)	–
Wood density	WD	g cm^{-3}	0.499 (0.467, 0.533)	–

Values are means (95 % confidence intervals) and number of individuals sampled. Confidence intervals were calculated from 1,000 bootstrap replicates using the percentile method. Foliar N content was measured using pooled samples, and WD and D_{max} were obtained from regional databases

humidity was 55.92 ± 0.15 %. A_{area} was later converted to A_{mass} by dividing it by SLA (LMA^{-1}, excluding petiole mass).

Leaf toughness, the maximum force to puncture per fracture length, was measured using a digital force gauge on a modular stand (Chatillon DFX-100 with MT-150, Ametek Inc., USA) with a flat-end aluminum piston attachment on approximately 16 individuals per species (range 8–20 trees). Using the same fresh leaves measured for leaf structural traits, three measurements spaced evenly along the lamina while avoiding primary veins were taken per leaf. Thick veins were excised prior to being positioned firmly between two plates to minimize plastic deformation (Sanson et al. 2001). Leaf toughness was normalized by dividing force (N) by the circumference of the piston (Onoda et al. 2011).

For leaf N, we analyzed leaves using pooled samples from four individuals per species per plot in four plots. Petioles were removed, leaves were oven-dried at 70 °C for at least 4 days, and the dried material was then ground and homogenized. Two replicates were analyzed per sample. Each replicate, weighing 11.74 ± 0.08 mg (mean ± standard error), was analyzed using a combustion analyzer (Flash EA 1112 Series NC Soil Analyzer, Thermo Electronic Corp., Waltham, MA, USA). Concentrations were calculated directly, using atropine as a standard reference material (70.56 % C, 4.84 % N).

D_{max} and WD were obtained from existing data sets with data collected at multiple sites across the Panama Canal Watershed, including the ASP (S.J. Wright, unpublished data; Condit et al. 2013). D_{max} was estimated as the 95th percentile DBH for individuals with DBH > 0.1 × maximum diameter for each species and is a robust measure of adult plant size because of its high correlation with maximum height (King et al. 2006). Wood samples were collected from tree stems of three to ten individuals per species, bark was removed, green volume was obtained using the water displacement method, and samples were oven-dried at 100 °C until a constant dry weight was attained. Samples were broken into smaller pieces to capture radial variation in WD (Nock et al. 2009; Plourde et al. 2014), and wood specific gravity was measured on each piece by dividing wet volume by oven-dried mass. WD was then estimated as an area-weighted average for each tree and averaged per species (Williamson and Wiemann 2010).

Data analysis

Although interspecific trait variation within a forest community usually represents the majority of trait variation (Swenson 2013), intra-specific trait variation can be significant along resource gradients or across ecological scales (Hulshof and Swenson 2010; Messier et al. 2010). To validate the use of species' means when calculating CWMs, we first assessed variation in leaf functional traits across the following levels: site, plot, species, light (inferred from crown-exposure), and tree. This nested design reflects our sampling design. We collected functional traits from multiple species in each plot (which are nested within sites); for each species, multiple trees in different light environments were selected, and two leaves were collected from each tree. For each trait, we fitted an intercept only linear mixed-effects model with a nested random effects structure (~1|Site/Plot/Species/Light/Tree) using restricted maximum likelihood (REML) and the 'lme' function in the 'nlme' package. The nested random effects structure differed for leaf toughness and leaf N; tree was excluded as a term for leaf toughness because only one leaf was measured per tree, and light and tree were excluded for leaf N as samples were pooled by plot. Variance partitioning was estimated using the 'varcomp' function in the 'nlme' package. The resulting variance partitions represent the amount of variation within each level, i.e., the variance partition for 'species' is equivalent to interspecific variation (Messier et al. 2010). For this analysis, LMA, A_{mass}, and leaf toughness were natural-log transformed and leaf N was logit transformed to meet normality assumptions.

CWMs represent trait values of the average plant in a community and can be weighted using different measures of relative abundance, including species frequency, percent cover, or basal area, to emphasize distinct ecological processes (Garnier et al. 2004; Lavorel et al. 2008). Here, we calculated CWMs of individual functional traits using data for the selected species and weighted them with relative abundance to emphasize community-level responses to disturbance, i.e., land clearance (Lavorel et al. 2008). For comparison, we also calculated CWMs based on relative basal area and provide the results in Online Resources 4a and b. Species' mean trait values were used when calculating CWMs. We calculated CWMs separately for two size classes, saplings and trees. We defined saplings as individuals <5 cm diameter at breast height (DBH) and trees as individuals >5 cm DBH.

Using the top-down approach described by Zuur et al. (2009), we fitted linear mixed-effects models with REML to evaluate variation in CWMs of individual functional traits during secondary succession using the 'lmer' function in the 'lme4' package (Bates et al. 2014). For each functional trait, we fitted separate models for CWMs weighted by relative abundance. In all models, size class and plot basal area were used as explanatory variables. Plot basal area is an integrated measure of changes in abiotic conditions during secondary succession (Fig. 1a; Lebrija-Trejos et al. 2010) and increases with time since abandonment (Fig. 1b; Breugel et al. 2007; Lohbeck et al. 2013; Whitfeld et al. 2014). To improve the interpretability of main effects and interactions, plot basal area was centered (Schielzeth 2010). Multiple random effects structures were tested for each model, allowing the response variables and the effects of plot basal area to vary across sites and plots (random intercept and slopes). We used AIC$_c$, a second-order bias correction to Akaike's information criterion for small sample sizes, to select the most parsimonious model (lowest AIC$_c$; Burnham and Anderson 2002). As well as visually assessing model residuals and homogeneity of variance, we estimated variance inflation factors (VIF) for all fixed effects to test for collinearity; across all models the maximum VIF was <2, suggesting that the fixed effects and their interaction were not correlated (Zuur et al. 2010). To evaluate model variation explained by fixed and random effects, marginal and conditional R^2 were calculated using the 'MuMin' package (Johnson 2014; Nakagawa and Schielzeth 2013). Marginal R^2 is model variation explained by a model's fixed effects, while the conditional R^2 is model variation explained by both fixed and random effects.

Relationships among CWMs of individual functional traits were evaluated using Pearson's correlation coefficients for each life history stage separately and visualized with a weighted correlation network. CWMs of all traits met normality assumptions, with the exception of LMA, which was natural-log transformed. All analyses were performed using R 3.0.2 (R Development Team 2012).

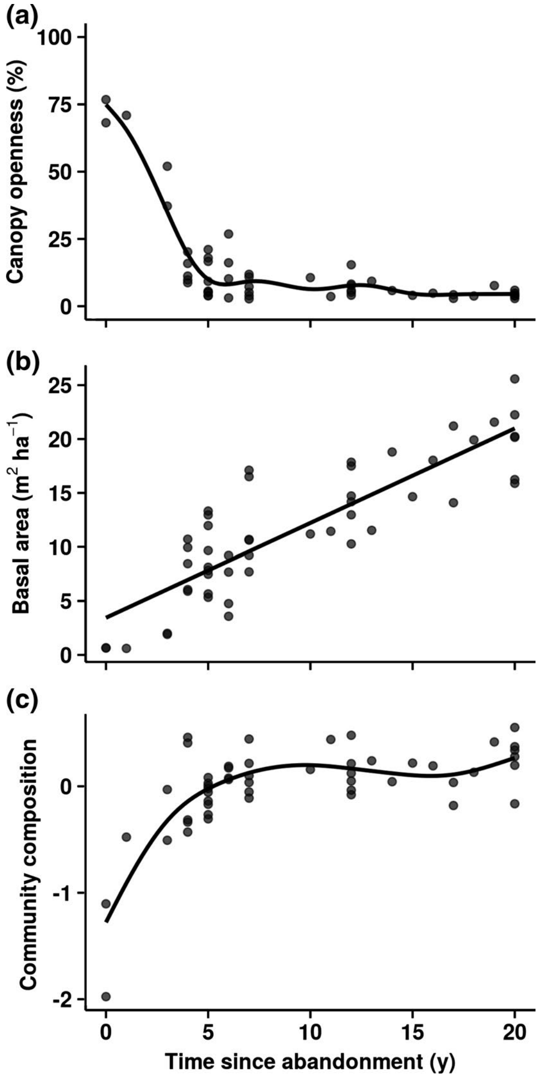


Fig. 1 Community characteristics in relation to successional age across a 20-year secondary forest chronosequence in central Panama (n = 51 0.5 ha plots), **a** canopy openness, **b** plot basal area, and **c** community composition. Community composition was calculated using non-metric multidimensional scaling based on the Jaccard index of dissimilarity. For **a** and **c** *lines* are generalized additive model fits; a linear model fit was used for **b**

Results

Inter- and intra-specific trait variation

Across all leaf functional traits, trait variation was consistently highest across species (Fig. 2; Online Resource

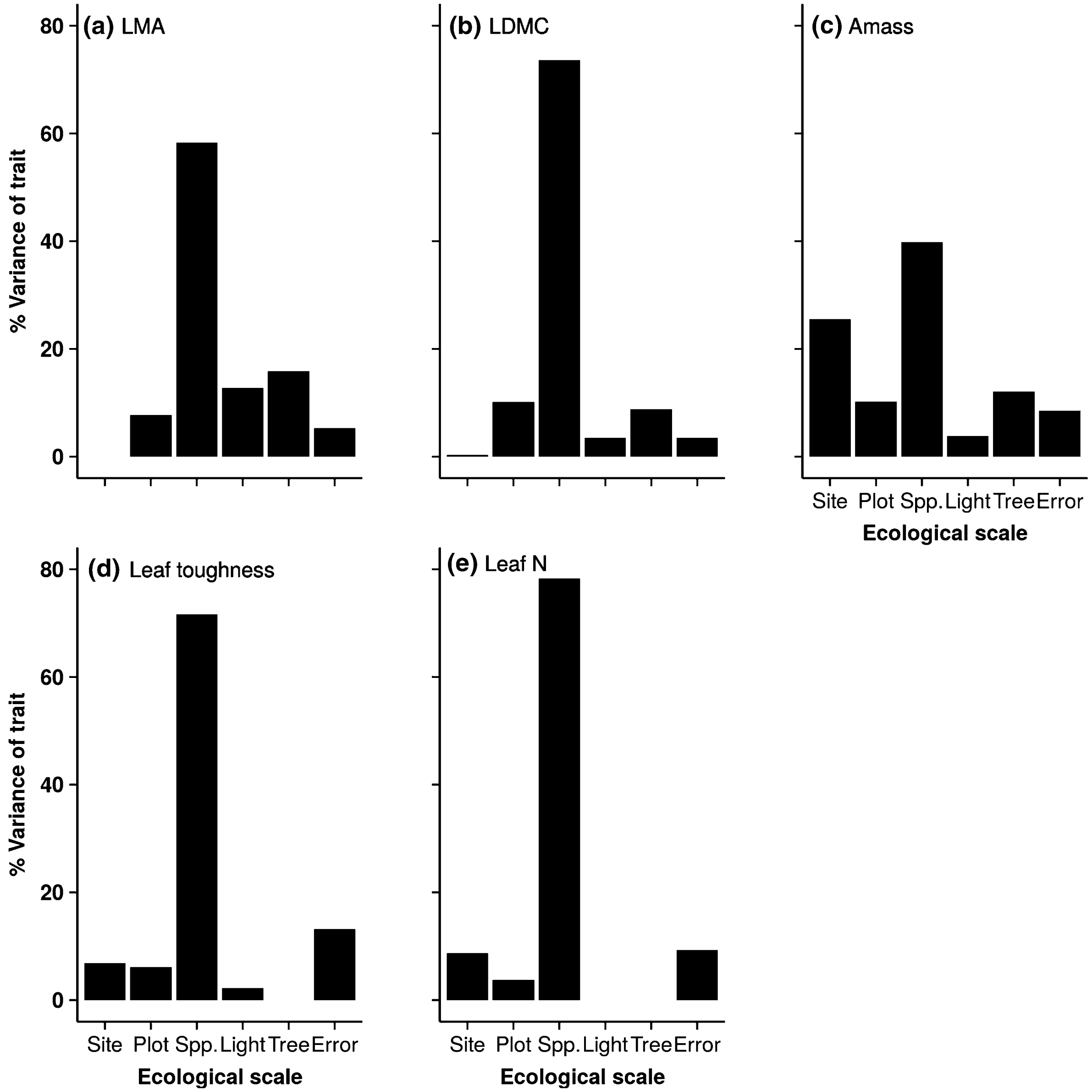


Fig. 2 Variance partitions of leaf functional traits for 55 woody species sampled from a young secondary forest in central Panama. Variance partitions for 'tree' were not calculated for leaf toughness and for 'light' and 'tree' for leaf N. See Table 1 for trait abbreviations

2a). Interspecific variation ranged from 40 % for A_{mass} to 80 % for leaf N. Variation within other levels was generally lower than 20 %, with the exception of cross-site variation for A_{mass}. Intra-specific variation, i.e., the sum of trait variation at levels below species, was markedly lower than inter-specific variation and ranged from 9.30 % for leaf N to 33.95 % for LMA (Online Resource 2b).

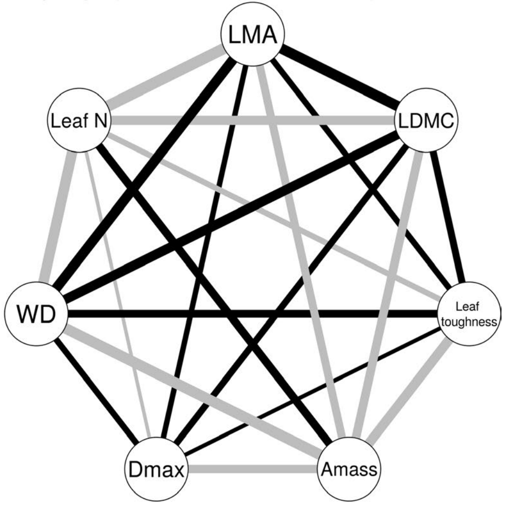
Relationships among functional traits (CWMs)

In line with expectations, CWMs of individual functional traits exhibited strong and statistically significant correlations for both size classes (Fig. 3a, b; Online Resource 3). Traits related with leaf structure and mechanical properties, LMA, LDMC, and leaf toughness were significantly positively correlated with one another, WD, and D_{max}, but were significantly negatively correlated with A_{mass} and leaf N. While A_{mass} was significantly negatively correlated with D_{max} and WD, it was significantly positively correlated with leaf N. Leaf N was significantly negatively correlated with WD, yet was not correlated with D_{max}. D_{max} also was significantly positively correlated with WD.

Variation in functional composition during secondary succession

Along the successional gradient in forest structure and between size classes, we found consistent changes for

(a) Saplings (individuals < 5 cm DBH)



(b) Trees (individuals > 5 cm DBH)

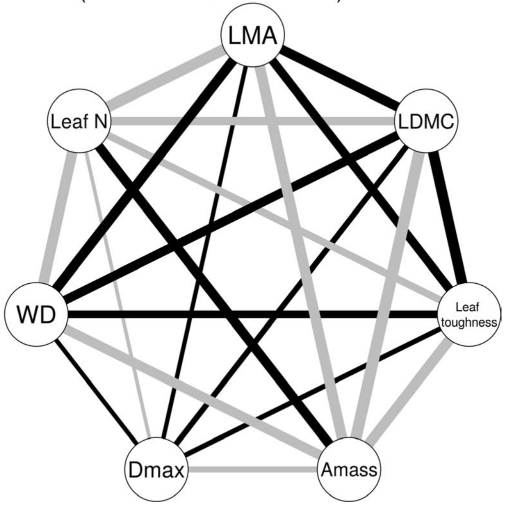


Fig. 3 Weighted correlation networks of community-weighted means of functional traits for two size classes of trees sampled from a young secondary forest in central Panama, **a** saplings and **b** trees. *Black lines* represent positive correlations and *gray lines* represent negative correlations; line width was scaled by Pearson's correlation coefficients (provided in Online Resource 3). For both tree size classes, all correlations were statistically significant at $\alpha = 0.05$ except for leaf N ~ $D_{\max}$. See Table 1 for trait abbreviations

CWMs of most functional traits. CWMs of leaf N, leaf toughness, and $D_{\max}$ increased significantly and that of A_{mass} decreased significantly with increasing plot basal area (Fig. 4d, f, g; Table 2). For LMA, LDMC, WD, and $D_{\max}$, the tree size class had significantly greater CWMs than the sapling size class, while the sapling size class had a significantly larger CWM of A_{mass} than the tree size class (Fig. 4a–c, e, g; Table 2). CWMs of LMA, A_{mass}, leaf N, and WD also exhibited contrasting responses to changes in plot basal area between tree size classes (BA × SC interactions; Fig. 4a, c–e; Table 2). For LMA, the CWM of the sapling size class remained constant during succession, while that of the tree size class decreased markedly and converged with the CWM of the sapling size class (Fig. 4a). CWMs of A_{mass} for both tree size classes declined during succession, yet the CWM of the sapling size class decreased more rapidly than that of the tree size class (Fig. 4c). In contrast, the CWM of leaf N of the tree size class increased more rapidly than that of the sapling size class, which showed a marginal increase with increasing plot basal area (Fig. 4d). Initially lower than the CWM of WD of the tree size class, the CWM of WD of the sapling size class increased sharply during succession and had a larger CWM than that of the tree size class at the end of the successional gradient (Fig. 4e).

Across CWMs of functional traits, the explanatory power of the two fixed effects varied widely. Plot basal area and tree size class explained 41.17 % of model variation for the CWM of A_{mass}, yet explained only 6.12 % of model variation for WD (Table 2). Random effects, which accounted for variation in CWMs across sites and plots, added a considerable amount of explanatory power to the fitted models. With their inclusion, conditional R^2 (variation explained by fixed and random effects) ranged between 64.18 and 84.44 % across CWMs of all traits (Table 2).

When weighted by relative basal area, CWMs of $D_{\max}$ and leaf N increased and A_{mass} decreased significantly along the successional gradient in forest structure (Online Resources 4a, b). For LMA, LDMC, and $D_{\max}$, CWMs of the tree size class were significantly larger than those of the sapling size class. In contrast, the sapling size class had a significantly greater CWM of WD than the tree size class. We also found evidence that size classes responded differently along the successional gradient for CWMs of A_{mass}, leaf N, and WD. For A_{mass}, the sapling size class initially had a greater CWM than the tree size class and declined sharply during succession, while the CWM of the tree size class was constant. CWMs of leaf N for both size classes increased during succession, but the CWM of the tree size class increased more rapidly than that of the sapling size class. Both size classes showed contrasting patterns for WD, where the CWM of the sapling size class increased and the CWM of the tree size class decreased with increasing plot basal area. Leaf toughness was the only functional trait whose CWM was not sensitive to changes in forest structure and did not differ significantly between size classes.

Models fitted using CWMs weighted by relative basal area explained similar amounts of variation in functional composition as when using CWMs weighted by relative

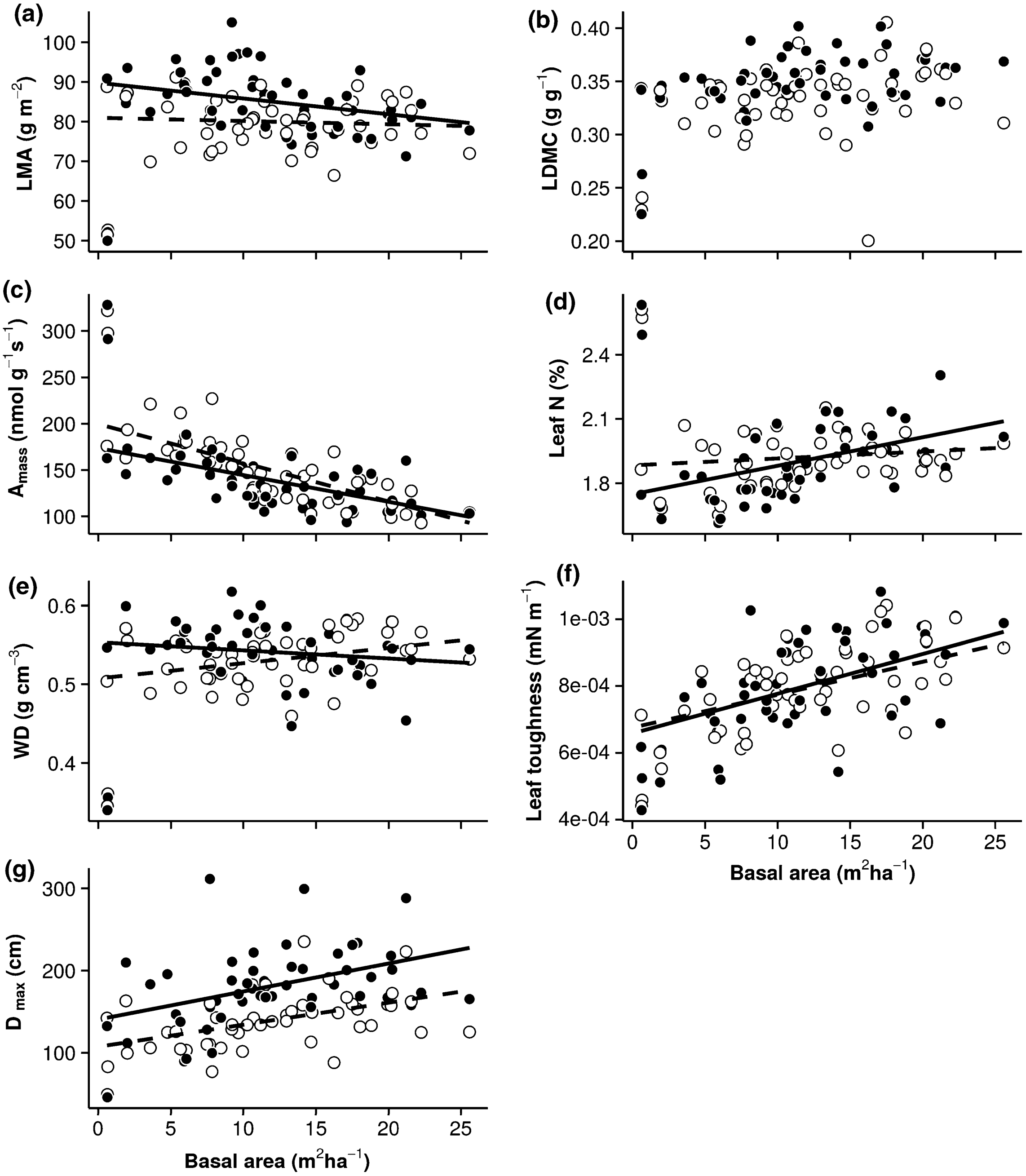


Fig. 4 Variation in community-weighted means (CWMs, weighted by abundance) of functional traits for two size classes of trees predicted by plot basal area during succession in young secondary forests in central Panama. *Lines* are linear mixed-effect model fits and were plotted if either plot basal area or the interaction of fixed effects was statistically significant; *dashed and solid lines* correspond to sapling (<5 cm diameter at breast height, DBH) and tree (>5 cm DBH) size classes, respectively. *Empty and filled symbols* represent plot-level CWMs of sapling and tree size classes, respectively. See Table 2 for model fit information and fixed effect tests

abundance with two exceptions: A_{mass} and leaf toughness (Online Resource 4a). In these two cases, the fixed effects explained considerably less model variation when CWMs were weighted by relative basal area than when weighted by relative abundance. While both fixed effects explained 41.17 % of model variation when the CWM of A_{mass} was weighted by relative abundance, they explained 14.20 % of model variation when weighted by relative basal area. Similarly, 22.42 % of variation in the CWM of leaf toughness when weighted by relative abundance was explained by both fixed effects, yet only 4.11 % when weighted by relative basal area.

Table 2 Summary of linear mixed-effects models evaluating variation in community-weighted means (weighted by abundance) of individual functional traits predicted by plot basal area in young secondary forests in central Panama

Functional trait	AIC_c	Marginal R^2 (%)	Conditional R^2 (%)	Fixed effects		
				Basal area (BA)	Size class (SC)	BA × SC
LMA	679.27	13.16	66.22	2.05	22.60*	3.84*
LDMC	−399.98	11.91	67.82	1.63	19.67*	0.32
A_{mass}	910.3	41.17	84.44	15.10*	11.79*	6.69*
Leaf N	−136.19	12.59	84.33	4.04*	1.21	18.96*
Leaf toughness	−1,505.19	22.42	77.88	7.78*	0.25	0.97
WD	−367.84	6.12	76.16	0.08	5.39*	16.56*
D_{max}	1,010.24	35.14	64.18	40.43*	12.19*	0.64

AIC_c is the small-sample-size corrected version of Akaike's information criterion; marginal and conditional R^2 represent model variation explained by fixed effects and the combination of fixed and random effects, respectively. For both fixed effects and their interaction, values are χ^2 for likelihood ratio tests; values with asterisks are statistically significant at $\alpha = 0.05$. See Table 1 for trait abbreviations

Discussion

This study assesses the extent to which successional changes in forest structure parallel variation in functional composition along a highly replicated chronosequence in a tropical secondary forest. Our study provides strong evidence of a consistent shift in the relative importance of contrasting functional strategies during the most dynamic phases of secondary succession. The results further suggest that stochastic processes related to dispersal, previous land-use history, and abiotic factors also influence variation in the functional composition of secondary forests.

Successional shifts in functional strategies

Variation in functional composition along the successional gradient in forest structure confirms the hypothesis that functional strategies shift from resource acquisition to resource conservation during tropical secondary forest succession. While small, the number of studies addressing similar questions has increased rapidly in recent years (e.g., Alvarez-Añorve et al. 2012; Becknell and Powers 2014; Dent et al. 2013; Lasky et al. 2014; Lebrija-Trejos et al. 2010; Lohbeck et al. 2013; Whitfeld et al. 2014). In general, results from the present and previous studies provide increasingly strong evidence for the validity of this hypothesis across different tropical regions. Later in this section, we will also discuss some exceptions.

Along the successional gradient in forest structure, we found significant decreases in CWMs of A_{mass} and increases in D_{max}, leaf toughness, leaf N, and WD (for the sapling size class). The shifts in functional strategies within size classes for A_{mass} and WD further indicate that changes in functional composition are shaped by environmental conditions. In open-canopy, young secondary forests, the sapling size class exhibited faster A_{mass} and lower WD, later shifting to lower A_{mass} and higher WD as light became more limiting with increasing plot basal area. Our findings substantiate the predictions of resource-driven models of secondary succession in tropical and temperate forests (e.g., Bazzaz and Pickett 1980; Ewel 1980; Finegan 1996; Huston and Smith 1987), in which species turnover is driven by species-specific responses to shifting resource availability along the successional gradient. Later in succession, CWMs were closely associated with a resource conservation strategy, i.e., high D_{max}, WD (for the sapling size class), and leaf toughness and low A_{mass} (Reich 2014). Trait values associated with this functional strategy are strongly correlated with greater shade and herbivory tolerance (Kitajima and Poorter 2010; Lasky et al. 2014; Onoda et al. 2011; Reich et al. 2003), thus facilitating persistence in abiotic and biotic conditions in which resource acquisitive species would not survive (Kitajima 1994; Rees et al. 2001; Wright 2002).

Counter to expectations, CWMs of leaf N and LMA did not shift from values associated with resource acquisition to resource conservation. CWMs of leaf N for both tree size classes increased during succession, which apparently contradicts the decrease in the CWM of A_{mass}. Previous studies (Becknell and Powers 2014; Whitfeld et al. 2014) also have reported either anomalous variation or increases in the CWM of leaf N, possibly due to an increase in the abundance of N-fixing species (Batterman et al. 2013) or increases in soil pH. The expectation that leaf N will decrease during succession is predicated upon its positive correlation with A_{mass} (Wright et al. 2004), although recent studies have demonstrated that this relationship is also mediated by leaf structural attributes, density, and thickness, which comprise LMA (Poorter et al. 2009; Shipley et al. 2005, 2006). When controlling for variation in LMA, we found that correlations between leaf N and A_{mass} for both size classes were conditionally independent (Online Resource 5). These findings suggest that the increase in CWMs of leaf N during succession is likely related to changes in leaf structural traits.

The CWMs of LMA for both size classes exhibited unexpected patterns during succession that contrasted with patterns reported in Mexico and New Guinea (Alvarez-Añorve et al. 2012; Lohbeck et al. 2013; Whitfeld et al. 2014). However, our results for the tree size class coincide with those reported by Becknell and Powers (2014) in Costa Rica, where the CWM of specific leaf area (1/LMA) increased during succession. One potential explanation for the weak response in the CWM of LMA along the successional gradient was its high intra-specific variation across light environments and sampled individuals (33.95 %; Online Resource 2b). In the present study, variation in LMA and LDMC in response to successional changes in forest structure (or lack thereof) highlights the potential problems of relying uniquely on ‘soft’ traits as proxies to detect shifts in ecological strategies (Wright et al. 2010). The ‘hard traits’ used in the present study have direct, mechanistic links with different aspects of plant performance: A_{mass} produces C used for growth (e.g., Poorter 1999; Walters et al. 1993), and leaf toughness determines tolerance to herbivory or mechanical damage, which affects survival (Alvarez-Clare and Kitajima 2007). Furthermore, these ‘hard’ traits exhibited a greater ability to detect successional changes in forest structure, which was reflected by their high marginal R^2 values (Table 2). Thus, our findings support the use of ‘hard’ traits to capture variation in plant- and community-level responses along successional gradients associated with the acquisition and conservation of light, nutrients, and water.

Stochastic processes in young secondary forests

Beyond mechanisms affecting interspecific variation in performance or shade tolerance (Pickett et al. 1987; van Breugel et al. 2013), our data also suggest that changes in functional composition during secondary succession are determined by stochastic processes, e.g., dispersal limitation and previous land-use history. Following the framework of Pickett et al. (1987), competition for growth-limiting resources is conditional upon site and species availability. That is, propagules must be both present within the landscape and capable of dispersing into and establishing in new sites. The linear mixed-effects models used in the present study account for cross-site variation in species composition through the specification of random effects; their inclusion in the fitted models substantially increased the amount of explained model variation compared to that explained by fixed effects alone (see Table 2; Johnson 2014). This finding illustrates that the configuration of the landscape matrix weakened the extent to which variation in functional composition was determined by shifts in successional gradients. Differences in species composition likely arose from dispersal or recruitment limitation due to the configuration of the landscape matrix, which previous studies have identified as a key factor influencing seed rain diversity in human-dominated landscapes (Dent and Wright 2009; Harvey et al. 2008; Holl 1999). Additionally, the random effects used here possibly capture cross-site variation in soil nutrient availability and pH, which also modulates successional patterns of functional composition in tropical secondary forests (Becknell and Powers 2014).

The lack of a consistent pattern of successional change in CWMs of A_{mass} and leaf toughness—when weighted by relative basal area—suggests another possible factor that plays a role in succession: previous land-use history. In areas previously subjected to frequent cattle grazing, resource conservative species with mechanistically tough, less palatable leaves would have been favored prior to land abandonment (Griscom et al. 2009; Guevara et al. 1986; Norden et al. 2011b) and likely persisted in the early stages of secondary succession because of their initial size advantage (van Breugel et al. 2012). Moreover, isolated trees are abundant in the pastures in the study region, and many are functionally dissimilar to early colonizing species (van Breugel and Hall, unpublished data). Given their large size at the onset of succession (Sandor and Chazdon 2014), these trees will strongly affect the basal-area-weighted functional composition of young secondary forests. Therefore, our results indicate that multiple functional strategies were present during the initial stages of secondary succession, supporting recent work in our study site (van Breugel et al. 2013) and classical models of old-field succession (Egler 1954).

Conclusions

Our results suggest that there was a significant and consistent shift in functional strategies shift along the successional gradient in forest structure. These shifts were markedly more pronounced when using ‘hard’ traits, as they are more directly linked with key aspects of plant performance: growth and survival. This suggests that ‘soft’ traits should be used with greater caution when interpreting ecological processes in tropical secondary forests. It is also important to note that interspecific variation in both ‘hard’ and ‘soft’ traits was higher than intraspecific variation (Swenson 2013), which validates our use of species’ means when calculating CWMs. However, the high intra-specific variation of LMA and the lack of the expected successional shift from low to high LMA values suggest that species’ means might not be appropriate for functional traits with high intra-specific variation (Albert et al. 2011; Violle et al. 2012). Our study also indicates that stochastic processes related to dispersal limitation and previous land-use history shape the functional composition of tropical secondary forests. Including data on dispersal vectors and distance and landscape configuration in future models will greatly enhance our ability to determine the relative importance of resource-driven mechanisms and stochastic processes in driving successional patterns of functional patterns across tropical secondary forests.

Author contribution statement DC and MvB designed field sampling, DC collected and analyzed data, and DC, MvB, MSA, GPB, and JSH wrote the manuscript.

Acknowledgments This paper is a scientific contribution to the Agua Salud Project (ASP), a collaboration between the Smithsonian Tropical Research Institute (STRI), the Panama Canal Authority (ACP), and the National Environmental Authority of Panama (ANAM) and part of the Smithsonian Institution Forest Global Earth Observatory (ForestGEO). This study complies with the current laws of Panama, where the study was performed and samples collected. At the time of this study, the ASP was supported by the HSBC Climate Partnership, STRI, the ACP, the Frank Levinson Family Foundation, and the Motta Family Foundation. DC received financial support from the Tropical Resources Institute, STRI, the Lewis B. Cullman Fellowship, and sDiv, the Synthesis Centre for Biodiversity Sciences—a unit of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). We thank the staff and personnel of the ASP for logistical support. Without the help of the following people, this project would not have been possible: Nathaly Guerrero Ramirez, Daniela Weber, Federico Davis, Demetrio Hernandez, S. Joseph Wright, Julian Moll-Rocek, Grant Tolley, Michele Abbene, Mario Bailon, Anabel Rivas, and Guillermo Fernandez. The authors also thank Walter Carson and two anonymous reviewers for helpful comments that significantly improved this manuscript.

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