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**Title: Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest**

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## Abstract

**Question(s):** Successional shifts in biodiversity are key drivers of the recovery of ecosystem functioning following disturbances. Identifying mechanisms that enhance or limit the ecological processes that drive these successional patterns can strengthen efforts to manage biodiversity-dependent ecosystem functions across human-dominated landscapes. Here, we examine successional patterns of multiple aspects of functional diversity in a seasonally wet tropical secondary forest and changes in the strength of environmental filtering during secondary succession.

**Location:** central Panama

**Methods:** We calculate functional richness (FRic) and dispersion (FDis) across a secondary forest chronosequence ( $n = 51$  0.1 ha plots) using nine functional traits related to resource acquisition and conservation. Functional diversity indices are calculated using all traits and each trait individually. Using a null model approach, we test the effects of environmental filtering during secondary succession.

**Results:** FRic and FDis exhibit saturating relationships with time since abandonment, reaching their maxima after seven and ten years respectively. Overall, we find evidence that environmental filtering reduces FDis to a greater extent than FRic and that the strength of environmental filtering on both FDis and FRic increases during succession. The impacts of environmental filtering on functional diversity of individual traits are consistent; the mean standardized effect sizes (SES) of FRic and FDis of at least six of the nine studied traits are lower than expected. Notably, environmental filtering on FRic and FDis of particular traits associated with light and nutrient

acquisition increases significantly along the secondary forest chronosequence, suggesting that functional convergence of multiple resource acquisition strategies strengthens in parallel.

**Conclusions:** We find that successional shifts in environmental conditions limit trait variation in seasonally wet tropical secondary forests. Our results suggest that the increasing strength of environmental filtering shifts abundance of trait combinations towards a subset of functionally convergent species that compete for light and nutrients in similar ways.

**Keywords:** functional diversity; functional divergence; functional convergence; functional traits; environmental filtering; secondary succession

**Nomenclature:** iPlant Collaborative TNRS v3.1

**Abbreviations:** FRic = functional richness, FDis = functional dispersion; SLA = specific leaf area; LDMC = leaf dry matter content;  $A_{\text{mass}}$  = net photosynthetic capacity;  $D_{\text{max}}$  = maximum DBH; WD = wood density; SES = standardized effect size

**Running head:** Successional shifts in functional diversity

## Introduction

Secondary forests are recognized as important for provisioning a wide array of ecosystem functions across tropical regions, including above- and belowground C sequestration, N cycling, and water cycling (Davidson et al. 2007; Hassler et al. 2011; Neumann-Cosel et al. 2011; Martin et al. 2013; Batterman et al. 2013; Ogden et al. 2013; Zimmerman et al. 2013; Poorter et al. 2016). However, the capacity of tropical secondary forests to provide ecosystem functions is constrained by climate, previous land-use type and intensity, and habitat fragmentation (Chazdon et al. 2009; Poorter et al. 2016). The extent to which ecosystem functions are biodiversity dependent may further limit the provisioning capacity of tropical secondary forests (Balvanera et al. 2014). Identifying ecological processes that drive successional patterns of biodiversity has the potential to provide insights to factors underlying recovery of ecosystem function following anthropogenic disturbances in tropical landscapes.

In tropical secondary forests, composition and diversity shift rapidly along successional gradients, from young forests dominated by fast-growing, pioneer species to older forests dominated by shade tolerant, slow-growing species (Chazdon et al. 2010). Secondary forests are initially dominated by species with trait values associated with resource acquisition, such as high photosynthesis and specific leaf area (SLA) and low wood density, and later by species with trait values related to resource conservation, such as high wood density, leaf toughness, maximum adult height, low SLA, and photosynthesis (e.g., Dent et al. 2013; Lohbeck et al. 2013; Lasky et al. 2014; Craven et al. 2015; Muscarella et al. 2016; Boukili & Chazdon 2017). In parallel, taxonomic diversity of secondary forests typically increases following land abandonment (Chazdon et al. 2007). At local and landscape scales, variation in environmental conditions, previous land-use history, and landscape connectivity also mediate deterministic changes in both diversity and composition (Chazdon et al. 2007, Harvey et al. 2008, but see Norden et al. 2015) through their effects on niche-based species replacement and dispersal limitation (Rees et al. 2001, van Breugel et al. 2013).

Factors thought to drive patterns of community composition and diversity do so by shaping the range and distribution of functional traits (Kraft et al. 2008, Cornwell & Ackerly 2009, Swenson & Enquist 2009). Consequently, tropical secondary forests are also expected to exhibit successional patterns of functional diversity that emerge in response to changes in environmental conditions, forest structure, and dispersal limitation (Lohbeck et al. 2012, Bhaskar et al. 2014, Becknell et al. 2014, Whitfeld et al. 2014, Muscarella et al. 2016). These patterns have been used to test fundamental hypotheses related to trait-based community assembly following disturbances, principally the 'functional convergence/divergence' hypothesis (Boersma et al. 2016). This hypothesis posits that functional diversity will either increase ('divergence') or decrease ('convergence') following land abandonment by altering the range and distribution of trait values (e.g. Lohbeck et al. 2012, Muscarella et al. 2016, Boukili & Chazdon 2017). For example, functional diversity in secondary forests may be initially low because high light availability and air temperatures (Lebrija-Trejos et al. 2011), the absence of local propagule sources (Holl 1999; Lebrija-Trejos et al. 2011), and the slow rate at which large-seeded, resource conservative species recruit (van Breugel et al. 2013) limit the range of trait values, resulting in communities composed of functionally similar species. As succession progresses and the strength of these filters weaken, the arrival of species with different trait combinations may expand trait space and, thus, increase functional diversity. Conversely, low intensity disturbances generally leave multiple regeneration pathways intact and high landscape connectivity facilitates seed dispersal, which may allow species from a diverse array of ecological strategies to quickly re-colonize disturbed areas (Kammesheidt 1998; Boucher et al. 2000; Dent & Wright 2009; Carreño-Rocabado et al. 2012). Functional diversity could therefore decrease during succession as lower light availability may result in the local disappearance of resource acquisitive species and an increase in the abundance of functionally similar resource conservative species (van Breugel et al. 2013). Given the diversity of possible successional patterns of functional diversity in tropical secondary forests, it is therefore essential to identify their

underlying mechanisms to facilitate comparisons across environmental contexts, e.g. wet and dry tropical forests, and disturbance regimes, e.g. logging, agriculture, and cattle ranching.

Environmental filtering is perhaps the primary deterministic mechanism that underpins successional patterns in functional diversity (Rees et al 2001; Chazdon et al. 2007). By altering the presence and abundance of viable ecological strategies, environmental filtering may shape the magnitude of functional convergence or divergence along successional gradients (Cadotte & Tucker 2017). Abiotic filters may directly exclude species with non-adaptive values of morphological, structural, or physiological traits or confer a competitive advantage to species with traits that are adaptive in a particular environment (Cornwell & Ackerly 2009), resulting in communities where co-occurring species have trait values that are more similar than expected ('functional convergence'). Alternatively, the diversifying effects of disturbance on seedling communities (Grime 2006) or biotic interactions, e.g. competition (Cadotte & Tucker 2017) or plant-soil feedbacks (Mangan et al. 2010), may decrease functional similarity of co-occurring species ('functional divergence') and thus enable co-occurring species to partition resource gradients (Kraft et al. 2008; Swenson & Enquist 2009). In tropical secondary forests, the strength of environmental filtering may change during secondary succession (Lohbeck et al. 2014, Muscarella et al. 2016) due to shifts in the availability of growth-limiting resources, particularly light in wet tropical forests (Montgomery and Chazdon 2002) and water in dry tropical forests (Eamus & Prior 2001). However, environmental filtering may act upon individual traits non-uniformly (Spasojevic & Suding 2012), as traits vary in their responses to changes in the availability of different resources. Therefore, testing for environmental filtering on individual traits may identify resources that limit functional diversity during secondary succession.

In this study, we describe successional patterns of multiple aspects of functional diversity, e.g. range and abundance of trait combinations, in a seasonally wet tropical secondary forest. We then test for successional changes in the strength of environmental filtering using a null model approach. We hypothesize that environmental filtering may have stronger impacts on trait space

during the initial years of succession because high light and air temperatures (Lebrija Trejos et al. 2011) and the limited availability of local propagules (Harvey et al. 2008; Dent & Wright 2009) constrain trait range and variation. Alternatively, environmental filtering may strengthen during succession as decreasing light availability will progressively exclude or lower the abundance of trait combinations, particularly those of resource acquisitive species (Muscarella et al. 2016; Boukili & Chazdon 2017). Lastly, we evaluate the effects of environmental filtering on individual traits to detect successional shifts in acquisition strategies associated with different resources, e.g. light, nutrients, and tolerance to herbivory and mechanical damage. We hypothesize that environmental filtering on individual traits will act more strongly upon traits related to light acquisition, as it is usually the most limiting resource along wet tropical forest successional gradients (e.g., van Breugel et al. 2013, Boukili & Chazdon 2017), although biomass accumulation rates following land clearance also may be nutrient limited and thus driven by nutrient acquisition strategies (Batterman et al. 2013; Nagy et al. 2017).

## Methods

### *Site description*

The study was done in the Agua Salud Project (ASP), Panama (9°13' N, 79°47'W, 330 masl) in a landscape mainly comprising active and abandoned cattle pastures, agricultural fields, and seasonally wet tropical secondary forests. Soils are mostly silt clay to clay (van Breugel et al. 2013) and mean annual precipitation for the site is 2700 mm yr<sup>-1</sup>, with a dry season lasting from mid-December until early May (Ogden et al. 2013).

We use a chronosequence approach to infer temporal trends from static vegetation plot data. To address potential limitations of this approach (e.g., Johnson & Miyanishi 2008), we use a high number of replicates over a short chronosequence (20 years). In 2008 and 2009, 108 plots, each

measuring 20 x 50m (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 study area 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. Time since abandonment of these secondary forests ranged from 0 to 32 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, labeled, and measured DBH. In one half of each plot, all stems  $\geq 1$  cm DBH were treated similarly.

#### *Functional trait sampling and measurement*

We selected 55 of the most abundant tree and shrub species for functional trait measurement (Table S1). The analysis was restricted to 51 plots where the selected species represent at least 80% of plot basal area (Pakeman & Quested 2007) and had been abandoned for 0 to 20 years. Across the selected plots, the sampled species represent  $88.3 \pm 0.7$  % (mean  $\pm$  standard error) of basal area and  $86.7 \pm 1.2$  % of individuals.

We selected nine functional traits that represent the two principal dimensions of variation in plant form and function (Díaz et al. 2016) using standardized measurement protocols (Pérez-Harguindeguy et al. 2013). These traits include specific leaf area (SLA,  $\text{m}^2 \text{g}^{-1}$ ), leaf dry matter content (LDMC,  $\text{g g}^{-1}$ ), net photosynthetic capacity per unit leaf mass ( $A_{\text{mass}}$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ), leaf toughness ( $\text{mN m}^{-1}$ ), foliar C:N, C:P, and N:P, maximum DBH ( $D_{\text{max}}$ , cm), and wood density (WD,  $\text{g cm}^{-3}$ ). Selected traits are related to resource acquisition and conservation strategies, as well as tolerance to drought, shade, mechanical damage, and herbivory (Reich 2014). More specifically,  $A_{\text{mass}}$ , SLA, and  $D_{\text{max}}$  capture interspecific variation in light acquisition, foliar C:N, C:P, and N:P are associated with soil

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nutrient acquisition, and WD, leaf toughness, and LDMC are associated with tolerance to herbivory and mechanical damage (Pérez-Harguindeguy et al. 2013). We use an intensive species-based sampling approach to precisely estimate species' means (Lavorel et al. 2008; Baraloto et al. 2010). Previous analysis of trait data used in this study indicate that inter-specific trait variation is consistently higher than intra-specific trait variation (Craven et al. 2015). Samples were collected during the wet season (June – November 2010). We collected leaves from and measured the selected functional traits on 8- 32 trees per species distributed across at least four plots (Appendix S2 provides details for trait data collection). For leaf C, N, and P content, we analyzed leaves using pooled samples from four individuals per species per plot in four plots.

#### *Functional diversity indices*

We calculate two functional diversity indices: functional richness (FRic) and dispersion (FDis). FRic, which is not weighted by abundance, describes the multi-dimensional volume in trait space occupied by communities and is suitable for testing the functional divergence/convergence hypothesis because it reflects increases (or decreases) in the range of trait values in response to environmental conditions (Boersma et al. 2016). FDis provides insight to changes in the abundance of trait combinations and is calculated as the mean distance of species from the centroid of a community (Laliberté & Legendre 2010). We calculate FRic and FDis in each plot for all traits together and individual traits separately using the 'FD' package in R (Laliberté & Legendre 2010).

#### *Null model*

To test for environmental filtering, we use a null model that randomizes functional trait data while conserving species richness and relative abundance (Gotzenberger et al. 2016). This randomization breaks the link between trait values and relative abundances by randomly assigning

trait values from the 55 species sampled for functional traits to the species that occur in each plot.

We create 1,000 null communities for each plot and subsequently calculate FRic and FDis using all traits and for each trait separately. To evaluate the magnitude and direction of the deviation of each plot from the null distribution, we calculate standardized effect sizes (SES) using probit-transformed  $p$ -values following Lhotsky et al. (2016) because FRic and FDis (for all and individual traits) of the null communities are not normally distributed and right skewed (Fig. S1-S2). More negative SES values indicates stronger environmental filtering, i.e. less variation in trait range, spacing or abundance of trait combinations than expected, while more positive SES values indicate greater niche complementarity, i.e. more variation in trait range or abundance of trait combinations than expected (Bernard-Verdier et al. 2012, Lhotsky et al. 2016).

#### *Data analysis*

To test for shifts in FRic, FDis, and SES of FRic and FDis (using all traits and for each trait separately) during secondary succession, we fit generalised additive mixed-effects models with a Gaussian distribution using the 'gamm4' package in R (Wood & Scheipl 2017) that accommodate for multiple functional forms, e.g. linear, uni-modal, and saturating. In all models, time since abandonment (years) is used as an explanatory variable; plots were nested within sites, which is treated as a random intercept.

We calculate 95 % confidence intervals of SES of FRic and FDis with all traits and for individual traits from 1,000 bootstrapped replicate samples using the percentile method. All analyses are performed with R 3.4.2 (R Core Team 2017).

## Results

### *Changes in functional diversity during secondary succession*

FRic and FDis exhibit saturating relationships with time since abandonment along the tropical secondary forest chronosequence (Fig. 1), reaching their respective maxima between seven and ten years following land abandonment. Similarly, FRic and FDis of individual traits generally increase during secondary succession (Fig. S3 & S4). FRic of  $D_{\max}$ , foliar C:N, foliar C:P, WD, and leaf toughness increases significantly and nonlinearly with time since abandonment. FRic of  $A_{\text{mass}}$ , SLA, and foliar N:P do not vary significantly along the secondary forest chronosequence. FDis of foliar C:N, WD, and LDMC increase significantly with time since abandonment. FDis of SLA,  $D_{\max}$ , foliar C:P, and leaf toughness also increases during secondary succession but not at statistically significant levels ( $P > 0.05$ ). In contrast to FDis of other individual traits, FDis of  $A_{\text{mass}}$  shows a significant and linear decrease during secondary succession.

### *Directional changes in environmental filtering during secondary succession*

The effects of environmental filtering are, on average, stronger on FDis than on FRic and strengthen during succession in young, tropical secondary forests. SES of FRic is lower than expected (mean = -0.47; 95% CI = -0.72, -0.25 ) and decreases significantly with time since abandonment (Fig. 2a). SES of FDis is also lower than expected (mean = -2.58; 95% CI = - 2.94, - 2.14) and exhibits a marginally significant ( $P = 0.07$ ), nonlinear decrease during secondary succession (Fig. 2b).

Environmental filtering strongly impacts FRic and FDis of individual traits during secondary succession (Fig. S5). For FRic, mean SES of  $A_{\text{mass}}$ , SLA, foliar C:P, foliar N:P, WD, and leaf toughness are lower than expected, while mean SES of  $D_{\max}$ , foliar C:N, and LDMC do not deviate from expectations. SES of  $A_{\text{mass}}$ , SLA,  $D_{\max}$ , and foliar N:P decrease and the SES of LDMC increases significantly with time since abandonment (Fig. 3, Table S1). For FDis, mean SES of all individual traits

are lower than expected (Fig S5). SES of  $A_{\text{mass}}$ , foliar C:N, and foliar C:P decrease significantly during secondary succession (Fig. 3, Table S1).

## Discussion

We find that seasonally wet tropical secondary forests become more functionally diverse during the first twenty years of succession. Trait space increases because the progressive arrival and establishment of species with unique trait combinations expand trait range and increases abundance-weighted trait variation. We also find evidence that environmental filtering on the abundance of trait combinations (FDis) and multidimensional trait space (FRic) strengthens during secondary succession. Our results reveal that light and soil nutrient availability in young seasonally wet tropical forests, by limiting the range of viable ecological strategies, determines shifts in community assembly during secondary succession.

### *Successional patterns of functional diversity*

Our analysis shows that functional diversity increases rapidly across a twenty-year tropical secondary forest chronosequence. This finding suggests a congruent shift among multiple aspects of trait diversity, from secondary forests with species where co-occurring species occupy a narrow range of functional niches and utilize resources similarly to secondary forests where co-occurring species occupy a wider range of functional niches and utilize resources differently (Lohbeck et al 2012; Whitfield et al 2014; Becknell & Powers 2014, Bhaskar et al. 2014). Moreover, this pattern of increasing multidimensional functional diversity coincides with patterns of functional diversity for most individual traits (Figs. S4 & S5). Where functional diversity is low, recent work from our study site (Craven et al. 2015) and others (Alvarez-Añorve et al. 2012; Becknell & Powers 2014; Dent et al. 2013; Lasky et al. 2014; Lebrija-Trejos et al. 2010; Lohbeck et al. 2013; Whitfield et al. 2014; Boukili &

Chazdon 2017) shows that young secondary forests are dominated by species with trait values associated with fast resource acquisition, such as high photosynthesis and low adult plant size and leaf toughness (Fig. S6). Over time, the establishment of species with functionally unique trait combinations increase FRic and FDis to their maxima while also shifting functional composition towards secondary forests dominated by species with trait values associated with resource conservation, e.g. high adult plant size and leaf toughness and low photosynthesis (Fig. S6; Alvarez-Añorve et al. 2012; Becknell & Powers 2014; Dent et al. 2013; Lasky et al. 2014; Lebrija-Trejos et al. 2010; Lohbeck et al. 2013; Whitfeld et al. 2014; Craven et al. 2015; Boukili & Chazdon 2017). Thus, our results suggest that increasing functional diversity during secondary succession occurs in parallel with a shift in functional composition towards resource conservative species.

Our results provide evidence that functional diversity saturates quickly in young seasonally wet tropical forests in a human-dominated landscape where connectivity is high. This pattern suggests that successional changes in functional diversity slow down markedly seven to ten years after land abandonment and likely occurs because species with unique trait combinations, such as large-seeded, shade tolerant species, either recruit slowly (or failed to recruit) due to the low abundance or absence of mammal dispersers (Tabarelli & Peres 2002; Cramer et al. 2007), are unable to tolerate environmental conditions in secondary forests (Lebrija-Trejos et al. 2010), or are locally rare in older secondary forests (Martin et al. 2013). Along a 100 year secondary forest chronosequence on nearby Barro Colorado Island, Dent et al. (2013) found gradual recruitment of slow-growing, shade tolerant species, which suggests that changes in functional diversity beyond 20 years of secondary succession may be moderate in magnitude.

#### *Increasing strength of environmental filtering during secondary succession*

We use a null model approach to examine how environmental filtering may underlie successional shifts in functional diversity and find that SES of FDis and FRic decrease during secondary succession. The contrasting trends of increasing absolute functional diversity and

decreasing SES of functional diversity during succession are likely due to non-linear increases in species richness and diversity during succession (Fig. S7), which increase the expected values of functional diversity. The increasing strength of environmental filtering on FRic and FDis supports the idea that secondary forests become increasingly functional convergent, which is consistent with previous studies in wet and dry tropical secondary forests (Bhaskar et al. 2014, Muscarella et al. 2016) and intact wet tropical forests (e.g., Kraft et al. 2008, Swenson and Enquist 2009). Successional shifts in environmental conditions (e.g. from high to low light availability; Nicotra et al. 1999) likely reduce trait variation by increasing the competitive advantage of particular trait combinations (Cornwell & Ackerly 2009). However, the weaker impacts of environmental filtering on FRic (relative to FDis), suggest that environmental filters may not be sufficiently strong to alter stabilizing mechanisms leading to species coexistence (Chesson 2000), such as asymmetric competition for light in tropical secondary forests (van Breugel et al. 2012). The stronger impacts of environmental filtering on FDis (relative to FRic) indicates that successional shifts in environmental conditions influence the abundance distribution of trait combinations that underlie the shift in dominance from resource acquisitive to resource conservation species.

#### *Convergence of resource acquisition strategies*

While multi-trait measures of functional diversity capture whole-plant responses to environmental conditions (Laughlin and Messier 2015), they frequently obscure mechanistic links between community assembly and trait diversity because individual traits may not respond congruently to changes in the availability of different resources (Spasojevic and Suding 2012). We find that multiple aspects of functional diversity are lower than expected for most individual traits, indicating that environmental filtering constrains functional diversity across individual traits thought to be related to different resource acquisition strategies. On average environmental filtering on the functional diversity of traits associated with light acquisition, such as SLA and  $A_{mass}$ , was equally strong as that on the functional diversity of traits associated with nutrient acquisition, such as foliar

C:P or N:P, or herbivory and pathogen tolerance, such as leaf toughness and wood density. Notably, the strength of environmental filtering on trait range and variation of individual traits shifts and usually strengthens during secondary succession, particularly for traits associated with light, e.g., SLA,  $A_{\text{mass}}$ , and  $D_{\text{max}}$ , and nutrient acquisition, e.g., foliar C:N, C:P, and N:P.

The present study is the first to our knowledge that shows strengthening of functional convergence across traits associated with different resource acquisition strategies in tropical secondary forests. While previous studies in tropical wet and dry secondary forests have found evidence of increasing functional convergence in traits associated with light acquisition (Bhaskar et al. 2014, Muscarella et al. 2016), none have found functional convergence in traits related to nutrient acquisition (but see Mason et al. 2012 for an example from a temperate forest). The strong decline in light availability during secondary succession in our study site (van Breugel et al. 2013) and others (Nicotra et al. 1999, Lebrija-Trejos et al. 2011) supports the idea that low variation in light availability may exclude or reduce the abundance of species with trait values associated with high resource acquisition. Similarly, soil nutrient availability is remarkably stable throughout our secondary forest chronosequence (van Breugel et al. 2013), which may explain the consistently negative SES values of FDis (and FRic to a lesser extent) of foliar C:N, C:P and N:P (Fig. 3). This finding highlights the intimate linkages between community ecology and the nutritional limitations that constrain biomass accumulation during secondary succession (Batterman et al. 2013, Nagy et al. 2017). Thus, the strengthening impacts of environmental filtering during secondary successional appears to reduce the number of viable ecological strategies to a group of abundant species that compete for light and nutrients in similar ways.

## Conclusions

By examining patterns of multiple facets of functional diversity and factors limiting functional diversity in a seasonally wet tropical secondary forest, our study provides unique insights to shifts in the relative importance of environmental filtering during succession. We find that

absolute measures of functional diversity increase rapidly in the initial stages of secondary succession and that environmental filtering strengthens during succession and progressively reduces trait variation. We show that rapid saturation in multidimensional functional diversity is likely due to the strengthening of environmental filtering across individual traits associated with different resource acquisition strategies.

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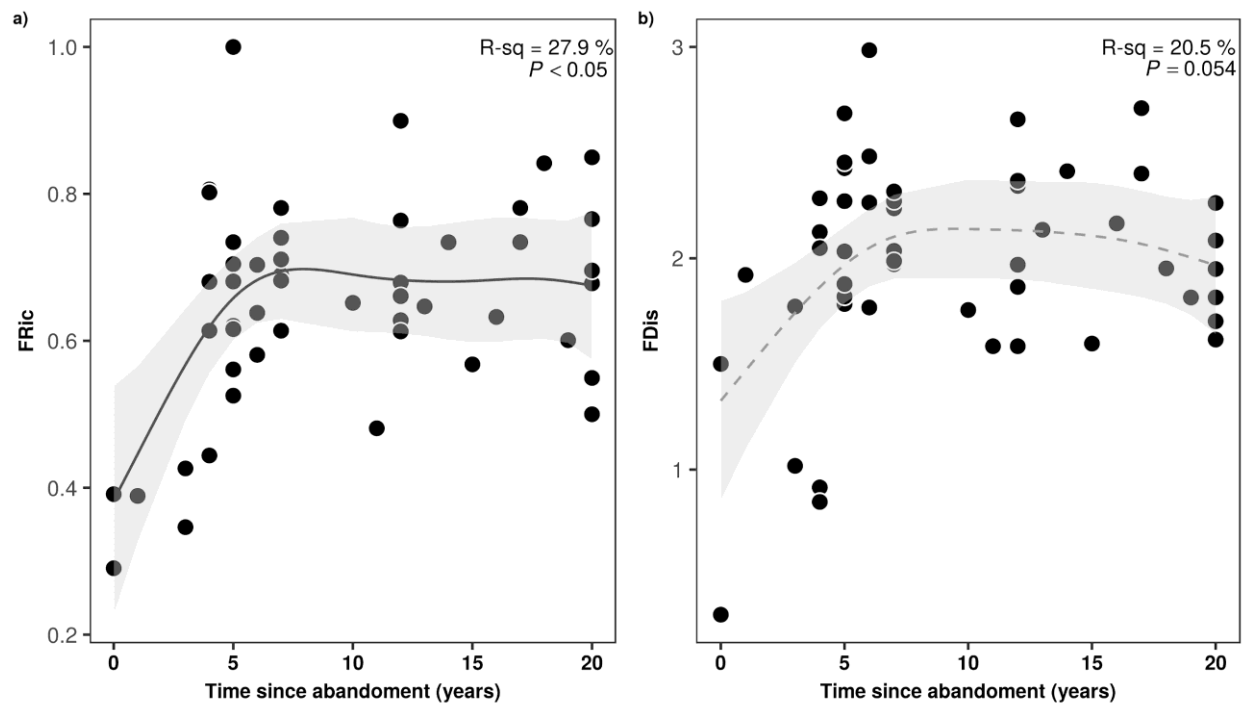
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## Appendices

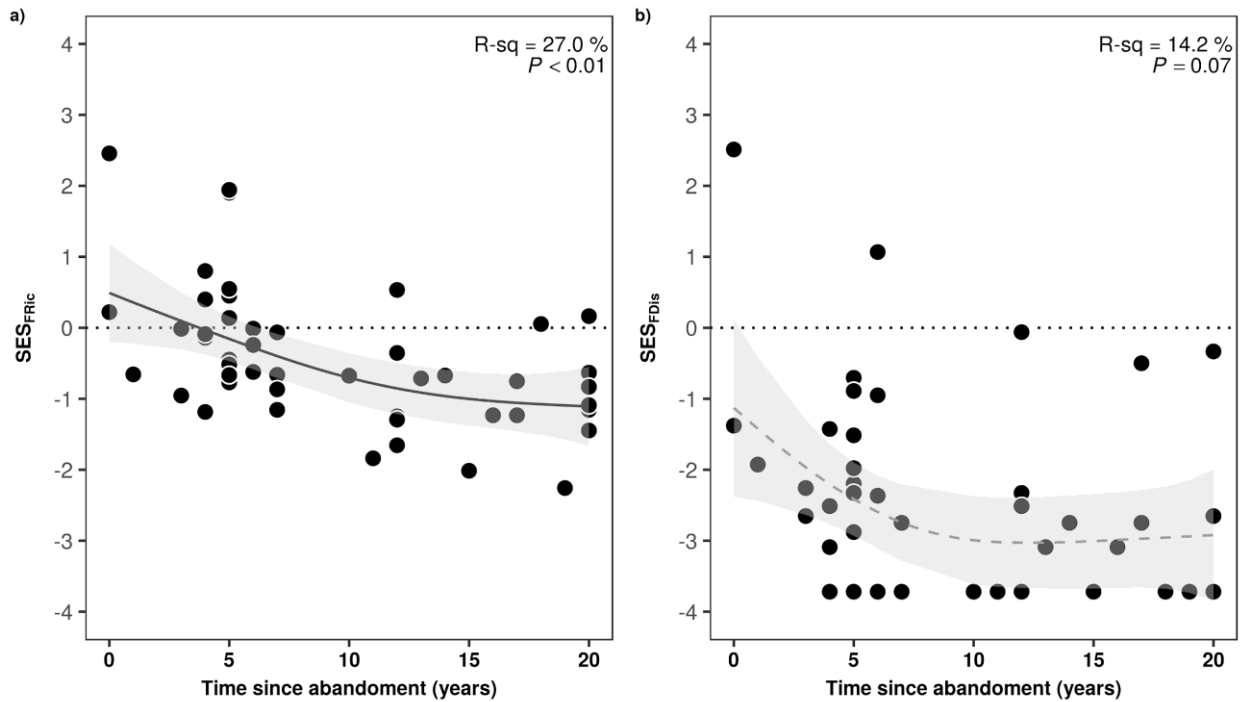
**Appendix S1.** List of 55 species used in this study.

**Appendix S2.** Extended methods for functional trait measurements.

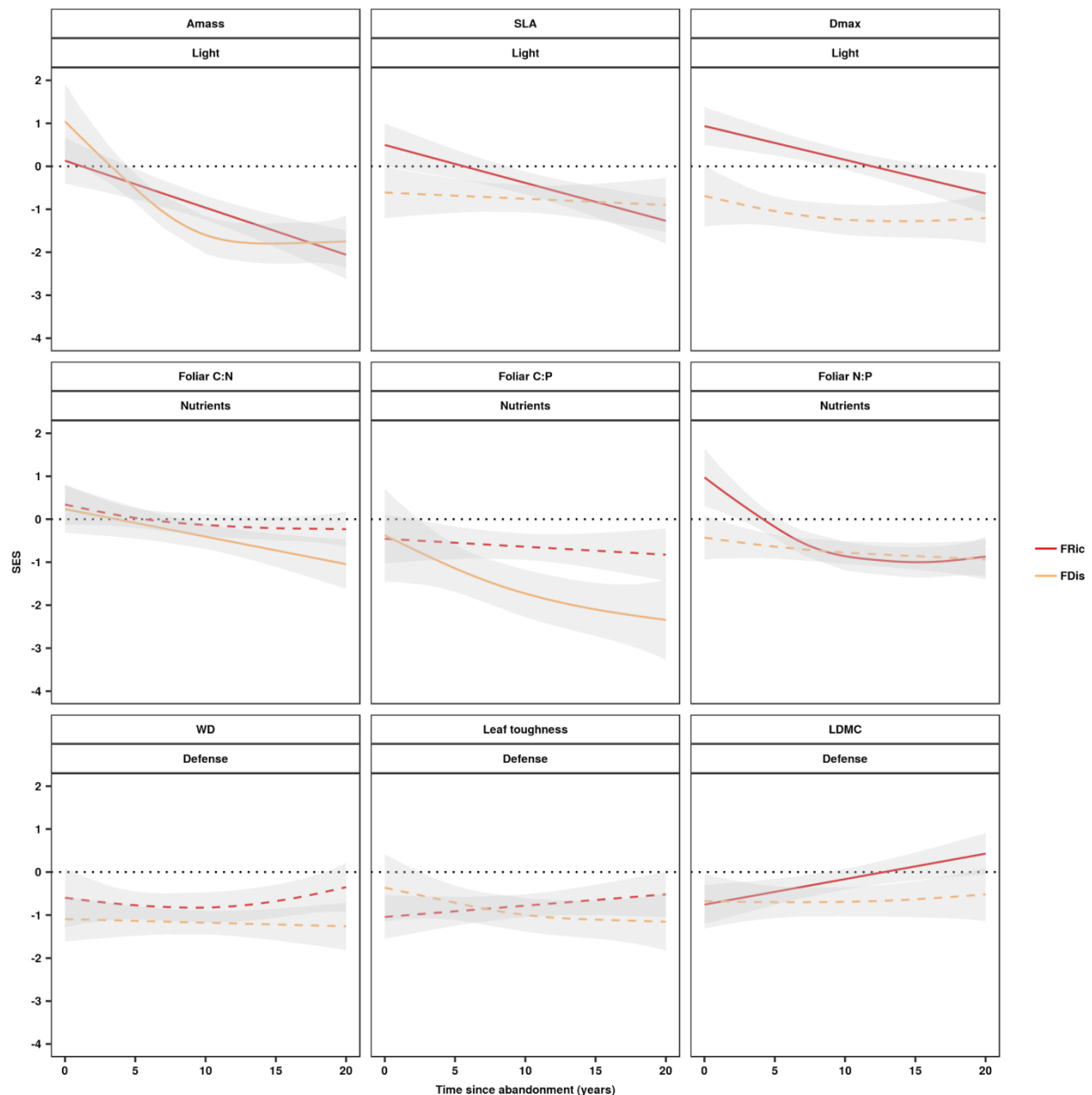
## Figures



**Figure 1.** Changes in functional **a)** richness (FRic) and **b)** dispersion (FDis) since land abandonment in seasonally wet tropical secondary forests in central Panama. Regression lines are estimated using generalised additive mixed effects models; adjusted  $R^2$  values (%) represent model variation explained by smoothed fixed effects. Solid black lines indicate that smoothed fixed effects are statistically significant ( $P \leq 0.05$ ) and grey dashed lines indicate that smoothed fixed effects are not statistically significant. Grey bands indicate 95% confidence intervals.



**Figure 2.** Changes in standardized effect sizes of functional **a)** richness ( $SES_{FRic}$ ) and **b)** dispersion ( $SES_{FDis}$ ) during succession in seasonally wet tropical secondary forests in central Panama. Positive standardized effect sizes indicate that functional diversity indices are greater than expected and negative standardized effect sizes indicate that functional diversity indices are lower than expected. Regression lines are estimated using generalised additive mixed effects models; adjusted  $R^2$  values (%) represent model variation explained by smoothed fixed effects. Solid black lines indicate that smoothed fixed effects are statistically significant ( $P \leq 0.05$ ) and grey dashed lines indicate that smoothed fixed effects are not statistically significant. Grey bands indicate 95% confidence intervals.



**Figure 3.** Changes in standardized effect sizes (SES) of functional richness (FRic) and functional dispersion (FDis) for individual traits during succession in seasonally wet tropical secondary forests in central Panama. Below each trait is the resource with which each trait is associated. Positive SES indicate that functional diversity indices are greater than expected and negative SES indicate that functional diversity indices are lower than expected. Regression lines are estimated using generalised additive mixed effects models; adjusted  $R^2$  values represent model variation explained by smoothed fixed effects. Solid lines indicate that smoothed fixed effects are statistically significant ( $P \leq 0.05$ ) and dashed lines indicate that smoothed fixed effects are not statistically significant. Grey bands indicate 95% confidence intervals. See Table S1 for model fit information.