

# Edaphic factors, successional status, and functional traits drive habitat associations of trees in naturally regenerating tropical dry forests

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## Abstract

1. Many studies have examined individual environmental drivers of tropical tree species distributions, but edaphic and successional gradients have not been considered simultaneously. Furthermore, determining how functional traits influence species distributions along these gradients may help to elucidate mechanisms behind community assembly.
2. To assess the influence of environmental filtering on tropical dry forest (TDF) tree species distributions, we used forest inventory data from sites with large edaphic and successional gradients in NW Costa Rica. Our goals were to determine (1) whether edaphic or successional factors are more important determinants of the abundance of individual tree species in regenerating TDF, (2) how species-level functional traits are related to edaphic and/or successional niche associations of tree species and (3) correlations between species-level edaphic and successional niche associations.
3. The distributions of 82 focal tree species were strongly driven by both edaphic and successional gradients. Overall, 94% of species responded to soil chemistry, 89% to soil texture and 94% to stand age gradients. Some functional traits were correlated with the edaphic and successional niche associations of TDF tree species. Species that specialized on soils with high total nutrient concentrations had higher foliar nutrient concentrations (nitrogen and phosphorus) and lower leaf dry matter content (LDMC). Species with wider stand age niches had lower LDMC and wood density. There were no correlations between edaphic and successional niche optima of TDF tree species.
4. Our results indicate that successional and edaphic gradients concurrently drive community assembly in regenerating TDF. Moreover, our work underscores the importance of considering how the functional characteristics of TDF trees dictate species distributions across environmental gradients.

## KEYWORDS

Costa Rica, edaphic gradient, environmental filtering, forest succession, functional traits, natural regeneration, species distribution, tropical dry forest

## 1 | INTRODUCTION

Habitat specializations (niches) of plant species are closely associated with both environmental (Grime, 1977) and successional gradients (Pickett, 1976). Despite this, environmental and successional gradients are generally considered separately when examining species distributions over spatial scales. Both these gradients can filter the occurrence and abundance of plant species based on microclimatic conditions and/or resources available at a given location and species' multi-dimensional niche requirements (Hutchinson, 1957). Both environmental requirements (Whittaker, 1967) and regeneration niches (Grubb, 1976) of species can differ greatly, and can influence distributions of species along environmental gradients to varying extents. Gradient analysis has been used to explain how plant physiological requirements influence species distributions along continuous environmental gradients (Whittaker, 1967). Further extensions of gradient analysis have demonstrated that some species follow complex response shapes (Huisman, Olf, & Fresco, 1993), and that species-level niche optima and breadth can determine how abiotic and biotic factors influence tree habitat associations and community assembly (Olthoff, Martínez-Ruiz, & Alday, 2016). Tropical forests encompass enormous gradients in ecosystem state factors such as climate, soil parent material, weathering state (Townsend, Asner, & Cleveland, 2008) and land-use history (Chazdon, 2003). Recent studies have shown tropical tree species distributions are tied closely to both edaphic and successional gradients.

Tropical tree species distributions are linked to edaphic properties (Clark, Palmer, & Clark, 1999; Condit, Engelbrecht, Pino, Perez, & Turner, 2013; John et al., 2007; Toledo et al., 2012), climatic variables (Condit et al., 2013; Toledo et al., 2012) and successional age gradients (Chazdon et al., 2011; Letcher et al., 2015; Powers, Becklell, Irving, & Pérez-Aviles, 2009). The relative importance of these factors in determining tree species distributions may be context dependent. Some work suggests climate is more influential than edaphic factors (Toledo et al., 2012), while other studies conclude that edaphic properties and climatic variables are similarly important (Condit et al., 2013). Additionally, tree species may have different edaphic requirements. Tree species occurrence has been predicted with individual soil nutrients (Condit et al., 2013), while other studies show that complex edaphic requirements explain habitat associations (John et al., 2007; Toledo et al., 2012). While the combined evidence suggests tropical tree species distributions can be driven concurrently by many abiotic and biotic factors, additional research is necessary to explain the relative importance of these factors and how they interact. Functional traits related to life-history and resource-acquisition strategies of tree species could potentially clarify mechanisms behind species distributions along continuous environmental gradients, and help to further explain the relative importance of factors driving these patterns in tropical forests.

Moreover, the question of whether neutral or niche-based processes shape mature tropical forests and contribute to the maintenance of diversity has sparked much research and debate (Hubbell, 2005; Wright, 2002), and many studies have found niche-based

processes, rather than stochastic (neutral) processes, can strongly structure community assembly based on differences in species-level functional traits (Kraft, Valencia, & Ackerly, 2008; Lasky, Uriarte, Boukili, & Chazdon, 2014). Despite the established importance of niche-based process as drivers of species assembly in tropical forests, neutral theory is able to describe broad patterns of species abundance and richness in mature tropical forests (Rosindell, Hubbell, & Etienne, 2011). Therefore, both deterministic and stochastic factors potentially influence community assembly along successional trajectories in secondary tropical forests (Chazdon, 2008). Somewhat surprisingly in the light of the burgeoning literature on tropical secondary succession, the extent to which niche versus neutral processes or deterministic versus stochastic factors shape community composition over secondary forest succession is relatively understudied. While one study in Central and South American forests showed that patterns of change in successional dynamics were unpredictable and idiosyncratic (Norden et al., 2015), other studies have emphasized deterministic changes in functional traits and composition (Lohbeck et al., 2014; Muscarella et al., 2016). Much of the effort to understand how tropical tree communities assemble along successional pathways has focused on examining the influence of environmental conditions on the functional strategies of tree species, rather than focusing on the relative importance of niche versus neutral processes.

Changing environmental conditions along forest successional trajectories including decreases in light availability and air temperature, and increases in relative humidity, affect patterns of species-level functional traits in both tropical wet (Bazzaz & Pickett, 1980; Guariguata & Ostertag, 2001) and dry forest (Lebrija-Trejos, Perez-Garcia, Meave, Bongers, & Poorter, 2010; Lohbeck et al., 2013). In tropical dry forest (TDF) with strong rainfall seasonality, changes in functional strategies of tree species over succession explain community assembly (Lebrija-Trejos et al., 2010), and therefore species distributions along successional trajectories (Sanaphre-Villanueva et al., 2017). For example, stand age and edaphic properties were highly correlated with community-weighted values of foliar nutrient (nitrogen and phosphorus) and resource-acquisition traits (specific leaf area) in regenerating TDFs in NW Costa Rica (Becknell & Powers, 2014). However, this study did not discriminate where species' niche optima occurred in relation to functional trait values and strategies, and whether species can persist along ranges of edaphic and successional gradients, or if they specialize at specific points.

Hierarchical Poisson regression models, which produce species-level niche optima and breadth values (Jansen & Oksanen, 2013), allow for direct comparison between species-level functional traits and niche optima and breadth, and concurrently provide evidence of which deterministic factors, if any, contribute to environmental filtering of species' distributions and abundances. To further integrate functional trait theory into species distribution modeling, we conducted a study in Costa Rican TDFs to determine to what extent functional characteristics of tree species can be used to understand mechanisms behind species distributions along broad edaphic and successional gradients. We conducted novel

analyses using previously published forest inventory and soil data from chronosequences of naturally regenerating TDF in Costa Rica. This is an ideal system for our analyses linking functional traits to species' abundance patterns along edaphic gradients, as previous work has shown differences in soil parent material contribute to large edaphic gradients, but there are minimal climatic differences among sites in this region (Powers et al., 2009). Moreover, patches of land were abandoned from grazing or cropping at different times over the last eight decades, yielding a mosaic of forest stands in different stages of regeneration (Calvo-Alvarado, McLennan, Sánchez-Azofeifa, & Garvin, 2009) with differing micrometeorological conditions such as soil temperature and light availability (Derroire, Powers, Hulshof, Cárdenas Varela, & Healey, 2018). We combined distribution data with existing functional trait data collected in the same region (Powers & Tiffin, 2010) to examine how tree species distributions are influenced by edaphic and/or successional factors, and whether functional traits are correlated with species' habitat associations. The goals of our study were to determine: (a) whether edaphic or successional factors are more important determinants of tree species' distributions in regenerating TDF, (b) how species-level functional traits are related to edaphic and/or successional niche associations of tree species, and (c) whether species-level edaphic and successional niche associations are correlated.

Corresponding to our first goal, we hypothesized species distributions would be driven by both species-specific edaphic (Condit et al., 2013; Toledo et al., 2012) and successional (Chazdon et al., 2011; Letcher et al., 2015) conditions, but distributions would be driven more strongly by edaphic than successional gradients, because environmental gradients along TDF successional trajectories are not as extreme as those in tropical wet forest (Lebrija-Trejos et al., 2010). For our second goal, we hypothesized species-level functional traits would be correlated with the edaphic and successional niche optima and breadth of tree species. For edaphic associations, we hypothesized foliar nutrient traits would track edaphic gradients and species with low or high soil chemistry niche optima would have correspondingly low or high foliar nutrient values. In terms of successional gradients, we hypothesized species with late successional niche optima would have low values of traits associated with drought-tolerance (leaf dry matter content); by contrast, species with high values of these traits would have early successional niche optima. These relationships have been demonstrated in TDF at the community level when correlating community-weighted traits means with stand age (Becknell & Powers, 2014) and plot basal area (Lohbeck et al., 2013). Last, for our third goal, we hypothesized we would find species-specific correlations between the edaphic and successional niche associations of TDF trees. In particular, we expected the successional and edaphic niches of tree species would be positively correlated, and species with early successional niche optima would have niche optima in soils with low total soil nutrients, and vice versa. We developed this expectation because TDFs are generally more nutrient limited at early successional stages (Powers et al., 2015) and species persisting at those stages need to tolerate low total soil nutrient conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

We used data previously collected in two TDF conservation areas in NW Costa Rica: Sector Santa Rosa in the Área de Conservación Guanacaste (10.848°N, 85.628°W), and Parque Nacional Palo Verde in the Área de Conservación Tempisque (10.358°N, 85.358°W). These areas have similar mean annual precipitation, 1,764 mm at Santa Rosa, and 1,444 mm at Palo Verde, and a dry season of 5–6 months (Becknell & Powers, 2014). At these sites, the soils are typically Inceptisols, and some Vertisols, and differences in soil parent material have resulted in large edaphic gradients (Powers et al., 2009). The forests in these conservation areas are naturally regenerating following use for grazing and agricultural purposes (Calvo-Alvarado et al., 2009).

### 2.2 | Forest inventory plots

Plot installation methods were described in Powers et al. (2009) and Becknell and Powers (2014). In brief, 60 20 × 50 m (0.1 ha) plots were installed in 2007 (Powers et al., 2009), and 24 additional 0.1 ha plots were installed in 2010 (Becknell & Powers, 2014), along a 5–100 year forest age gradient. The successional age of each plot was determined using local knowledge and remote sensing (Powers et al., 2009). In each plot, every live tree ≥10 cm DBH (diameter at breast height) was measured (3,433 trees) and identified to species (146 species in 49 families).

### 2.3 | Plot-level edaphic properties

We focused specifically on particle size distribution (sand, silt, clay %), and total soil nutrient data (Ca, K, Mg, Na, P and N) collected previously in the 84 plots by Powers et al. (2009). In this study, 10 samples of mineral soil were collected with a soil corer (four samples at each corner, and six samples down each plot centre) in the 84 plots and bulked for analyses. Soil particle size distribution was determined with a hydrometer (Bouyoucos, 1962), and total rock-derived Ca, K, Mg, Na and P (mg/kg) were determined with ICP-AES following hot nitric acid digestion at the Research Analytical Laboratory at the University of Minnesota. Total soil N (% oven dry) was determined using an elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of California, Davis. Because soil nutrient concentrations can change along succession (Powers & Marin-Spiotta, 2017), we used total element concentrations, rather than labile or extractable nutrients, and assumed they were a better reflection of differences among plots due to parent material and soil weathering status. Previous work in this system suggests total soil elements are generally good proxies for available nutrients as well (Waring, Adams, Branco, & Powers, 2016).

### 2.4 | Plant functional traits

To link functional trait data with tree species occurring in the plots, we used previously published databases of functional traits (Powers & Tiffin, 2010), seed mass (Smith-Martin et al., 2017) and wood anatomy traits (Werden, Waring, Smith-Martin, & Powers, 2018)

all collected in the same region using standard methods (Pérez-Harguindeguy et al., 2013). From (Powers & Tiffin, 2010), we collected mean species-level values of specific leaf area (SLA;  $\text{cm}^2/\text{g}$ ), leaf area ( $\text{cm}^2$ ), leaf dry matter content (LDMC;  $\text{g}/\text{g}$ ), wood density ( $\text{g}/\text{cm}^3$ ), foliar  $\delta^{13}\text{C}$  (‰), foliar phosphorus (P; %) and nitrogen (N; %) and carbon (C; %), leaf type (simple or compound) and habit (deciduous, semi-deciduous and evergreen). Additional trait data were gathered for mean seed mass (g; Smith-Martin et al., 2017), maximum adult tree height (m; J.S. Powers, unpublished), wood vessel diameter (mm) and xylem vessel density ( $\# \text{ vessels}/\text{cm}^2$ ; Werden, Waring, et al., 2018). Finally, we considered species-level dispersal syndrome (animal, wind or gravity, both; Powers et al., 2009; Hilje, Calvo-Alvarado, Jiménez-Rodríguez, & Sánchez-Azofeifa, 2015).

## 2.5 | Statistical analysis

### 2.5.1 | Reducing data dimensionality

Using data from Powers et al. (2009) and Becknell and Powers (2014), we built an abundance matrix for tree species identified in the 84 plots (146 species total) to use as a response matrix. We also created a plot-level edaphic (soil particle size distribution and total nutrients) and successional (stand age) property matrix, to define species' abundance predictors. We removed rare tree species (occurring in <5% of plots) from further analysis, narrowing our focus to 82 species in 37 families. This yielded species occurring in 5 to 55 plots. We then performed a principal components analysis (PCA; R *psych* package) on the plot-level edaphic property and stand age matrix to summarize all edaphic (soil particle size distribution and total nutrients) and successional (stand age) variables into several axes, as prior exploratory analysis using Gaussian logistic regression following Condit et al. (2013) showed no evidence species had associations with individual soil properties. We included stand age in the matrix, in addition to edaphic variables, to determine whether we could define orthogonal axes associated with distinct edaphic and successional characteristics to use as predictors of species abundance in the 84 inventory plots. The first PCA axis loadings were associated primarily with total soil nutrient concentrations (Ca, K, Mg, Na, P and N); the second axis loadings were associated with soil particle size distribution; and the third axis loadings were associated with stand age. We therefore used the first PCA axis as a predictor of plot-level total soil nutrient concentrations (soil chemistry), the second axis as a predictor of plot-level soil particle size distribution (soil texture) and the third axis as a predictor of plot successional status (stand age). Accordingly, our metrics of soil chemistry, soil texture and soil age were not confounded and largely independent.

### 2.5.2 | Determining the influence of edaphic and successional factors on species distributions

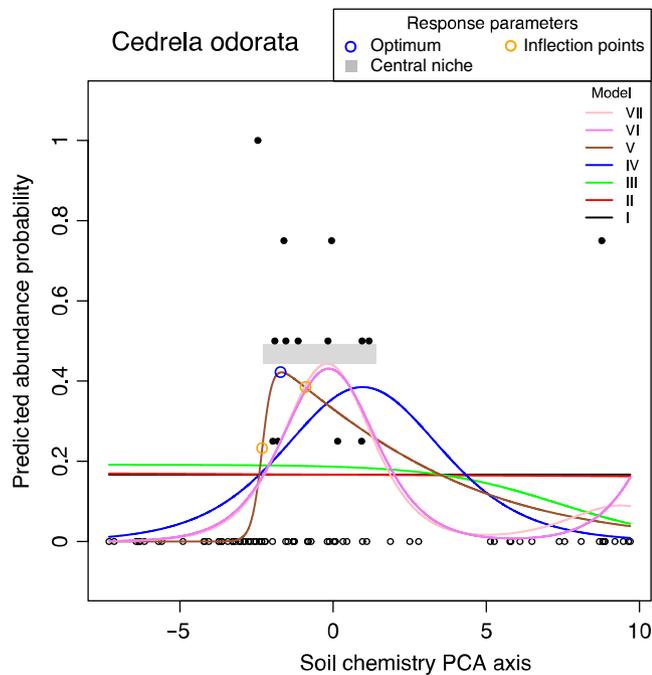
To determine how edaphic and stand age factors contributed to the prediction of species distributions, we built multiple Poisson

regression models for each of the 82 focal species (Goal 1). For each model, we used species abundance as the response and included all three PC axes (soil chemistry, soil texture and stand age) as predictors. We performed a separate analysis using plot-level species occurrence as the response variable and found similar results (not shown). We extracted the z-scores for each of the three predictors from each model (82 species  $\times$  3 predictors  $\times$  1 z-score per predictor = 246 z-scores total). To test for differences in the relative importance of each predictor, we made pairwise comparisons between the mean absolute values of z-scores of each predictor (least square means with Tukey adjustment; R *lsmeans* package).

### 2.5.3 | Testing for evidence of environmental filtering and trait syndrome/habitat associations

To determine how edaphic factors and successional stages predicted niches of our 82 focal tree species, we constructed hierarchical Poisson regression Huisman–Olf–Fresco (HOF) models (Huisman et al., 1993; Jansen & Oksanen, 2013) using abundance data for individual tree species as the response, and three separate predictors (first three PCA axes) representing soil edaphic (chemistry and texture) and stand age for the 84 plots. As before, using plot-level species occurrence as the response produced similar results for chemistry and stand age predictors, however, the predictive power of soil texture differed (see Results). The advantage of using HOF models, over standard Poisson regression, is that a species can be fit to a number of ecologically relevant responses of increasing complexity (see Figure 1 for model shapes and descriptions), beyond normal or unimodal distributions. Additionally, this approach yields species-level niche optima and breadth parameters for each predictor.

To model species abundance, we used three predictors: soil chemistry, soil texture and stand age (i.e., the three PCA axes) for each plot. Three separate HOF models (*eHOF* package in R) per species were created, one each for each predictor (82 tree species  $\times$  3 predictors = 246 models total). To robustly select HOF model shapes for each species, we bootstrapped model runs 1,000 times and selected best-fit model types for each predictor using AICc (Akaike information criterion corrected for finite sample sizes). Following the selection of best-fit models for each predictor and tree species, we extracted the best-fit HOF model type (I–VII) and the niche optima and breadth corresponding to the three predictors (soil chemistry, soil texture and stand age) for the 82 focal species. For models with two optima (VI, VII), we extracted the optima associated with the highest predicted abundance (VII), or took the mean of the two optima for species with two equivalent abundance probabilities (VI). To determine whether functional traits were correlated with habitat association niche optima and breadth (Goal 2), we calculated Pearson correlation coefficients for continuous species-level traits and species niche optima and breadth extracted from the HOF models for all



**FIGURE 1** Huisman-Olff-Fresco (HOF) hierarchical Poisson regression model types and parameters (niche optima, niche breadth, etc.) for the abundance of *Cedrela odorata* in 84 forest inventory plots predicted by plot-level soil chemistry data (soil chemistry PCA axis). HOF models increase in complexity from no response (I) to models with two niche optima (VI and VII). In this example, the optimal model type selected by AICc (1,000 bootstrapped iterations) was V (skewed unimodal response). The HOF model type (I–VII) corresponds to the following responses observed for each species: I: no response; II: increasing or decreasing trend (monotone sigmoid) with a peak at one end of the predictor range; III: increasing or decreasing trend (monotone sigmoid) with a plateau at one end of the predictor range; IV: symmetric unimodal response; V: skewed unimodal response; VI: response with two niche optima corresponding to equivalent abundance probabilities; and VII: response with two niche optima corresponding to different abundance probabilities (Huisman et al., 1993; Jansen & Oksanen, 2013)

three species abundance predictors (soil chemistry, soil texture and stand age).

#### 2.5.4 | Correlations between edaphic and successional niche associations

To determine whether species-level edaphic and successional niche associations at our site were correlated (Goal 3), we calculated Pearson correlation coefficients between species-level soil chemistry, soil texture and stand age niche optima from the HOF models. To examine overall patterns in the niche optima and breadth of our focal tree species, we used the species-level niche optima and breadth values in three separate PCAs, one for each predictor (soil chemistry, soil texture and stand age). Last, we created biplots for each PCA to concurrently visualize the niche optima and breadth of our focal species (*R psych* package). All analyses were conducted using R version 3.4.0 (R Development Core Team, 2017).

## 3 | RESULTS

### 3.1 | Summary of edaphic and stand age factors

Total soil nutrients varied over several orders of magnitude, underscoring the large differences in parent material and soil weathering status among sites (Table 1). The first three PCA axes explained 77% of the variance of these predictors. 85% of the first axis variance was explained by total soil nutrient variables; 74% of the second axis variance was explained by soil texture variables; and 55% of the third axis variance was explained by stand age (Table 1). We therefore defined PC1 as an axis of soil chemistry, PC2 as an axis of soil texture, PC3 as an axis of stand age, and used plot-level PC loadings as predictors in the HOF models.

### 3.2 | Which edaphic or successional factors have more influence on species distributions?

Both soil chemistry and stand age had similar relative importance when considering all three edaphic and successional factors as predictors of species-level abundance (Figure 2). While soil chemistry was predicted to have a greater impact on species abundance than soil texture ( $t = 2.86$ ,  $p = 0.013$ ), there was only a marginally significant difference between the contributions of stand age and soil texture ( $t = -2.30$ ,  $p = 0.056$ ). Furthermore, both soil chemistry and stand age generally had greater magnitudes of influence on species-level abundances when considering the distributions of effect sizes (z-scores) for each predictor (Supporting Information Figure S1).

### 3.3 | How do individual species respond to edaphic and stand age characteristics?

HOF models were considered successful in characterizing species' habitat associations if a species responded significantly to edaphic (soil chemistry and texture) or successional (stand age) factors, for example if a HOF model other than type I (no response) was selected by AICc after bootstrapping. HOF models were able to characterize responses of most species. In total, 94% of tree species abundances responded to soil chemistry (PC1), 89% of species responded to soil texture (PC2) and 94% of tree species responded to stand age (PC3; Table 3). Table S2 (Supporting Information) lists species-level responses. All species were associated with at least one of the three predictors. Using species presence/absence rather than abundance as the response yielded similar patterns, albeit with slightly fewer species showing responses (84%, 71% and 87% to soil chemistry, soil texture and stand age, respectively).

### 3.4 | Are species with specific edaphic and/or successional requirements functionally distinct?

Values for continuous functional traits of the 82 native or naturalized tree species had comparatively large interspecific ranges, and coefficients of variation ranged from 3.9% for foliar  $\delta^{13}\text{C}$  to 200% for seed

**TABLE 1** Mean, minimum, maximum and coefficients of variation (CV) of predictor variables in the hierarchical Poisson regression models. The correlations of variables with each PC axis are shown with the proportion of variance explained in parentheses

Variable	Mean	Min.	Max.	CV (%)	Correlation with PC1 (chemistry) (%)	Correlation with PC2 (texture) (%)	Correlation with PC3 (stand age) (%)
<b>Soil chemistry</b>							
Ca (mg/kg)	9,639	1554	29,368	77.4	0.93 (18.4)	0.14 (1.1)	-0.17 (2.4)
K (mg/kg)	1,181	375	4,122	72.0	0.81 (14.0)	0.19 (1.9)	0.34 (10.2)
Mg (mg/kg)	3,199	772	18,196	116.2	0.75 (12.0)	0.44 (10.7)	0.05 (0.2)
Na (mg/kg)	875	221	3,136	66.9	0.73 (11.6)	-0.13 (1.0)	-0.45 (17.2)
P (mg/kg)	301	30	1,273	89.0	0.89 (17.0)	-0.13 (0.9)	0.15 (2.1)
N (%)	0.34	0.11	0.71	30.3	0.76 (12.5)	-0.12 (0.8)	0.16 (2.2)
<b>Soil texture</b>							
Sand (%)	40.27	24.8	56.9	17.2	0.35 (2.6)	-0.87 (40.5)	-0.23 (4.7)
Silt (%)	30.28	17.3	47.8	21.6	-0.64 (8.9)	0.25 (3.3)	0.26 (6.0)
Clay (%)	29.47	16.4	45.5	19.9	0.31 (2.2)	0.75 (30.0)	-0.02 (0.1)
<b>Successional stage</b>							
Stand age (years)	31.83	5	100	69.8	0.21 (0.9)	-0.43 (9.8)	0.80 (54.9)

mass (Table 2). The proportions of categorical traits follow: leaf habit (semi-deciduous—15.8%; evergreen—18.2%; deciduous—65.8%), leaf type (compound—45.1%; simple—54.9%), seed dispersal syndrome (both animal and wind—6.1%; wind or gravity—39.0%; animal—54.9%). The three dominant tree families, based on species richness within a family, were Fabaceae (23.2% of species), Rubiaceae (6.1%) and Meliaceae (4.95%; see Supporting Information Table S1). Functional traits were correlated with tree species niche associations defined by soil chemistry or stand age niches, but not soil texture (Table 4). Species specializing on soils with higher total soil nutrient values were likely to have lower LDMC ( $r = 0.27, p = 0.023$ ), and higher foliar P ( $r = 0.37, p = 0.002$ ) and N concentrations ( $r = 0.30, p = 0.013$ ; Table 4). Interestingly, the only two traits correlated with niche breadth were LDMC and wood density; species with a wide stand age niche had lower LDMC ( $r = -0.28, p = 0.017$ ) and wood

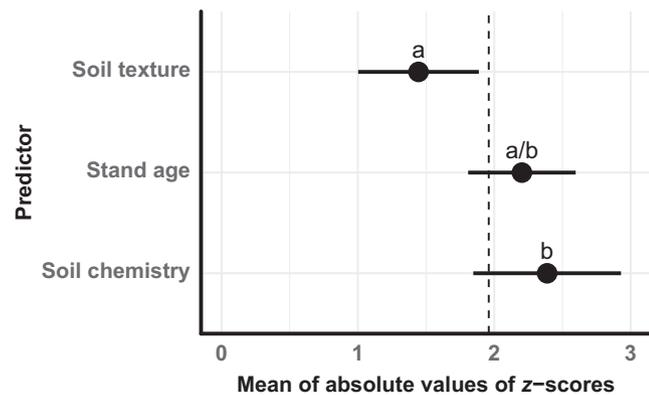
density ( $r = -0.32, p = 0.006$ ; Table 4). None of the categorical traits differed in terms of niche optima or breadth (data not shown).

### 3.5 | Are edaphic and successional niche associations correlated?

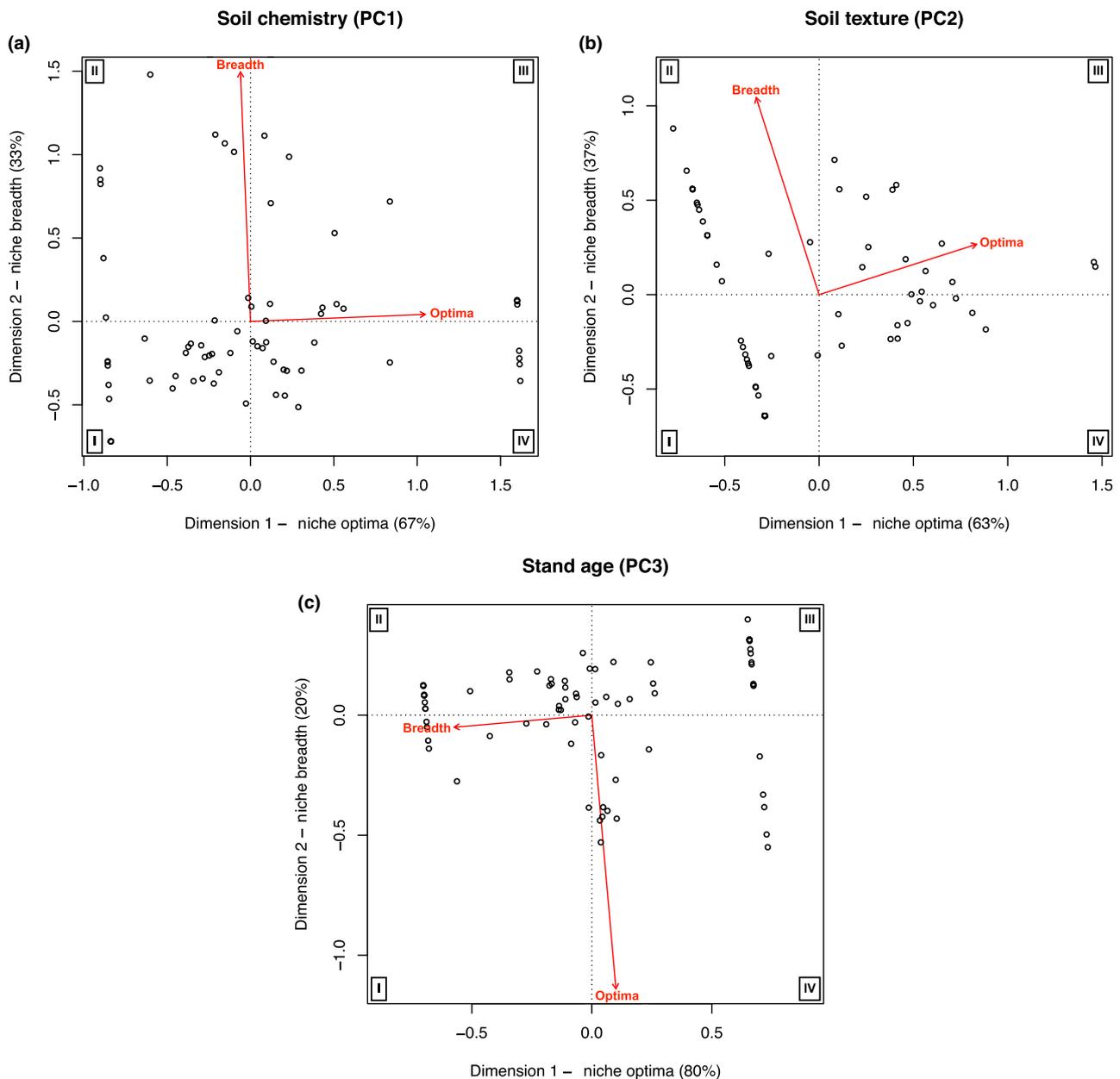
There were no significant correlations between the soil chemistry, soil texture or stand age niche optima of TDF tree species. The niche optima of the focal species explained a majority of the variance for

**TABLE 2** Mean, minimum, maximum and coefficients of variation (CV) of species-level functional traits for 82 tropical dry forest species

Trait	Mean	Minimum	Maximum	CV (%)
SLA (cm <sup>2</sup> /g)	102.9	54.8	229.5	33.7
Leaf area (cm <sup>2</sup> )	124.9	15.1	572.1	91.6
LDMC (g/g)	0.42	0.26	0.6	16.2
Wood density (g/cm)	0.63	0.18	0.88	24.9
Foliar δ <sup>13</sup> C (‰)	-29.3	-32.7	-27.2	3.87
Foliar P (%)	0.11	0.06	0.2	30.6
Foliar N (%)	2.34	1.17	3.63	27.2
Foliar C (%)	46.1	37.6	52.3	6.38
C:N	21.6	12.3	37.7	30.3
N:P	22.9	12.6	43.5	28.0
C:P	465.0	216.7	837.1	28.5
Seed mass (g)	0.31	0.01	3.49	200.3
Max height (m)	19.7	6.8	42.1	40.2
Wood vessel diameter (mm)	0.25	0.07	0.61	65.4
Xylem vessel density (#/cm <sup>3</sup> )	8.11	1.6	31.5	104.4



**FIGURE 2** Mean absolute values of z-score for multiple Poisson regression model predictors of the abundance of 82 tropical dry forest tree species. Error bars are 95% confidence intervals, and letters indicate significant differences among predictors (pairwise least squared means comparisons with Tukey corrections). The dotted line horizontal line is the critical z-score at 95% confidence ( $\alpha = 0.05$ )



**FIGURE 3** Biplots of principal components analysis of niche parameters (optima and breadth) for 82 tropical dry forest species separated by predictor: (a) soil chemistry, (b) soil texture and (c) stand age. The four quadrants represent distinct combinations of parameters: I = low niche optima/narrow niche breadth, II = low niche optima/wide niche breadth, III = high niche optima/wide niche breadth and IV = high niche optima/narrow niche breadth. The points in a vertical line on the left and right side of each figure represent species with niche optima at the lowest and highest end of the range, respectively

all three predictors (Figure 3). Furthermore, species were widely distributed along both niche axes, ranging from having low niche optima and narrow niche breadth (*quadrat I* in Figure 3) to high niche optima and wide niche breadth (*quadrat III* in Figure 3).

## 4 | DISCUSSION

Our results indicate that edaphic and successional gradients concurrently drive habitat associations of TDF tree species, providing strong support for deterministic factors as drivers of tree species distributions

in this region. Furthermore, tree species in this region have distinct functional strategies at the extremes of both edaphic and successional gradients. Thus, integrating functional traits into species abundance modelling helps to clarify the functional mechanisms behind tree species distributions along both abiotic and biotic gradients.

### 4.1 | Edaphic and successional gradients concurrently drive species distribution patterns

Contrary to our hypothesis that edaphic gradients would be the strongest filters of tree species distributions (Goal 1), the abundance

**TABLE 3** Hierarchical Poisson regression model (Huisman, Olff, Fresco: HOF) shapes selected for 82 tropical dry forest tree species (bootstrapped 1,000 times with AICc selection) for each predictor. Table S2 shows species-level model predictions, and Figure 1 shows model shapes and includes descriptions

Predictor	Bootstrapped model choice (%)						
	I	II	III	IV	V	VI	VII
Chemistry (PC1)	5 (6)	5 (6)	4 (5)	18 (22)	19 (23)	11 (13)	20 (25)
Texture (PC2)	9 (11)	3 (4)	5 (6)	11 (13)	14 (17)	4 (5)	36 (44)
Stand age (PC3)	5 (6)	7 (8)	9 (11)	13 (16)	16 (20)	7 (8)	25 (31)

of individual tree species at our study sites was strongly influenced by both soil chemistry gradients (94%) and successional trajectories (94%; Table 3). When considering all predictors simultaneously, soil chemistry was the strongest predictor of species abundance at our sites, although its effect was not statistically distinguishable from stand age (Figure 2).

These findings contribute to a growing body of literature indicating that niche partitioning is an important driver of species assembly in tropical forests along edaphic gradients, and that neutral theory cannot thoroughly explain tree species distributions when growth and survival are limited by many resources (Condit et al., 2013; John et al., 2007; Wright, 2002). Soil texture was also a reliable predictor of species abundance (89%; Table 3), although it was not the best predictor (Figure 2). Our findings are therefore similar to a study in Bolivian tropical forests that found soil texture and soil chemistry were equally important predictors of species distributions across edaphic gradients (Toledo et al., 2012). A caveat is that when considering species occurrence rather than abundance as the response, the approach taken by Toledo et al. (2012), soil texture only explained 71% of species' occurrence at our sites. Therefore, while our study sites fall along a large soil texture gradient (Table 1), texture may have been a more important determinant of species' occurrence in Toledo et al. (2012) because of the wider range of soil texture at their sites.

Our data also underscore the strong and independent role of forest age in determining species occurrences and abundances. Environmental conditions may not change as drastically along successional trajectories in regenerating TDFs when compared to wet tropical forests (Lebrija-Trejos et al., 2010), but our results suggest TDF tree species are very sensitive to successional gradients at our sites. Further effort will be necessary to determine whether mechanisms such as dispersal limitation and past land-use history at our sites (Powers et al., 2009) are also important drivers of species distributions. In summary, our results corroborate the emerging consensus that both edaphic and successional predictors are highly correlated with tree species distributions in this system, and they add nuance to help understand how individual species distributions and traits contribute to previously identified community-level patterns. However, one potential limitation of our study is that our plots likely do not encompass a large or even modest climatic gradient (although we do not have plot-specific climatic data to verify this); thus, we cannot make inferences about the relative magnitude of edaphic and successional versus climatic factors. Other studies have found

climate (Toledo et al., 2012) and drought (Condit et al., 2013) to be important environmental filters of tree species distributions over large geographic scales. Additionally, in some cases, climatic factors have been found to outweigh the importance of edaphic factors in predicting species' occurrence (Toledo et al., 2012). Regardless, our results provide strong support that edaphic factors are important drivers of tree species distributions in our study system that is marked by high soil heterogeneity, as almost all species responded to soil chemistry (Table 3).

#### 4.2 | Species-level functional traits are associated with soil chemistry and successional gradients

We found correlations between species-level functional traits and successional and edaphic niche optima and breadth of tree species (Goal 2). Species specializing on soils with high total soil nutrient values had distinct resource-use and life-history traits. For the edaphic factors, we examined, foliar P and N tracked soil chemistry gradients as hypothesized, as tree species occurring on soils with low total soil nutrients had low foliar nutrients and those preferentially distributed on soils high in total nutrients had high foliar nutrients (Table 4). This finding suggests foliar nutrients are possible proxies for species-level resource requirements in this system. A study in tropical wet forest showed that tree species with edaphic specializations do not perform well when transplanted into soils where they do not specialize (Baltzer, Thomas, Nilus, & Burslem, 2005), and another showed that below-ground resource-acquisition strategies increase as edaphic conditions change during ecosystem development in Mediterranean shrubland (Zemunik, Turner, Lambers, & Laliberté, 2015). Our findings are therefore consistent with the hypothesis that functional specializations are an important mechanism behind edaphic niche associations of TDF tree species.

Other studies in the same region have shown community-weighted mean foliar traits are associated with successional gradients (Becknell & Powers, 2014; Buzzard, Hulshof, Birt, Violle, & Enquist, 2016), but have not demonstrated that these relationships may also be partially driven by edaphic characteristics. Interestingly, we also found species with high soil chemistry niche optima had low LDMC (Table 4). This suggests that species occurring on soils with high total soil nutrients generally have acquisitive, less drought-tolerant traits (Kitajima & Poorter, 2010). Our results therefore directly validate recent studies indicating LDMC is a better predictor of soil chemistry than specific leaf area, because LDMC values should be

Trait	Chemistry		Texture		Stand age	
	Optima	Breadth	Optima	Breadth	Optima	Breadth
SLA (cm <sup>2</sup> /g)	0.26	-0.19	-0.01	-0.10	-0.11	0.10
Leaf area (cm <sup>2</sup> )	0.04	-0.11	-0.10	-0.07	-0.08	0.15
LDMC (g/g)	<b>-0.27</b>	<0.01	-0.17	0.16	0.11	<b>-0.28</b>
Wood density (g/cm <sup>3</sup> )	-0.04	-0.22	-0.07	-0.09	0.03	<b>-0.32</b>
Foliar δ <sup>13</sup> C (‰)	-0.04	0.05	-0.01	-0.03	-0.07	-0.10
Foliar P (%)	<b>0.37</b>	-0.03	0.23	-0.11	0.06	0.05
Foliar N (%)	<b>0.30</b>	-0.16	-0.13	-0.07	-0.03	0.03
Foliar C (%)	-0.17	-0.18	-0.25	-0.17	0.05	-0.02
Seed mass (g)	-0.10	0.15	0.01	-0.01	0.18	-0.05
Max height (m)	-0.12	0.06	-0.07	-0.12	-0.18	-0.18
Wood vessel diameter (mm)	-0.15	0.29	0.02	0.26	-0.23	0.21
Xylem vessel density (#/cm <sup>3</sup> )	0.01	-0.18	0.32	-0.18	0.23	-0.06

**TABLE 4** Pearson correlations tests of species-level traits and species niche optima and breadth from Poisson regression HOF models. Pearson correlation coefficients are shown with two-tailed Bonferroni corrected significance ( $\alpha = 0.05/2$  tests: cut-off  $p < 0.025$ ) indicated with bold text

independent of shade (Hodgson et al., 2011; Reich, 2014), and match findings in other ecosystems that LDMC is negatively correlated with soil chemistry (Hodgson et al., 2011). While our hypothesis that leaf traits would track edaphic gradients was generally supported, our predictions for how species' traits would vary along successional gradients did not align with our findings.

For successional gradients, based on observational studies in tropical dry and wet forest (Buzzard et al., 2016; Lohbeck et al., 2013), we hypothesized species with conservative LDMC values (high values indicative of drought-tolerance) would have early successional niche optima. However, we did not find any correlations between species-level traits and successional niche optima. Species occurring at our sites that had wider stand age niches had lower LDMC and wood density, both acquisitive strategies (Table 4). Few studies have focused on determining trait syndromes of generalist TDF species, but a study in Mexican TDF found generalist species encompass wide ranges in trait syndromes (Sanaphre-Villanueva et al., 2017). Furthermore, a study in Mexican wet forest showed that dominant species become less similar in terms of key resource-acquisition functional traits over succession (Lohbeck et al., 2014), and our finding that TDF species with acquisitive traits have wider stand age niches indicates that species' trait syndromes may also influence how species dominance shifts along tropical forest succession. Overall, these findings further underscore how functional drivers can explain patterns of species assembly along edaphic and successional gradients, and they point to the utility of integrating functional ecology into species distribution modelling.

#### 4.3 | Edaphic and successional niches of the focal species are not associated

Both total soil nitrogen and phosphorus concentrations increase over succession in our plots (data not shown), following the

expectation that nutrients are more limiting at earlier successional stages (Powers et al., 2015). Despite this general trend, we found no evidence to support our expectation that species with early successional niche optima would also have low soil chemistry niche optima (Goal 3). A study in Mexican TDF showed that changes in air temperature strongly predicted TDF community assembly (Lebrija-Trejos et al., 2010), and it is possible that changes in microclimatic conditions, rather than edaphic factors, are stronger drivers of shifts in species distributions along succession. Further effort is necessary to determine the relative importance of microclimate and edaphic factors in structuring TDF communities. Furthermore, because we found species were widely distributed with respect to their niche optima and breadth (Figure 3), it will be important to consider how the interaction of these parameters acts to structure TDF communities along edaphic and successional gradients.

## 5 | CONCLUSIONS

Our study underscores how successional and edaphic gradients interact to drive community assembly in regenerating TDFs, and also provides evidence that functional traits can explain some mechanisms behind these patterns and processes. Furthermore, the niche optima and breadth of tree species were associated with some key resource-acquisition traits along these gradients. Our work is an important step towards considering the functional mechanisms driving tree species distributions along environmental gradients.

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## AUTHORS CONTRIBUTIONS

L.K.W. and J.S.P. conceptualized the study; J.S.P. and J.M.B. designed and implemented field surveys and collected data; L.K.W. conducted statistical analyses; L.K.W. and J.S.P. interpreted results and wrote the manuscript. All authors contributed to revisions.

## DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.kv2002g> (Werden, Becknell, & Powers, 2018).

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