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Shifts in taxonomic and functional composition of trees along rainfall and phosphorus gradients in central Panama

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Abstract

1. Environmental gradients act as potent filters on species distributions driving compositional shifts across communities. Compositional shifts may reflect differences in physiological tolerances to a limiting resource that result in broad distributions for tolerant species and restricted distributions for intolerant species (i.e. a nested pattern). Alternatively, trade-offs in resource use or conflicting species' responses to multiple resources can result in complete turnover of species along gradients.
2. We combined trait (leaf area, leaf mass per area, wood density and maximum height) and distribution data for 550 tree species to examine taxonomic and functional composition at 72 sites across strong gradients of soil phosphorus (P) and rainfall in central Panama.
3. We determined whether functional and taxonomic composition was nested or turned over completely and whether community mean traits and species composition were more strongly driven by P or moisture.
4. Turnover characterized the functional composition of tree communities. Leaf traits responded to both gradients, with species having larger and thinner leaves in drier and more fertile sites than in wetter and less fertile sites. These leaf trait–moisture relationships contradict predictions based on drought responses and suggest a greater role for differences in light availability than in moisture. Shifts in wood density and maximum height were weaker than for leaf traits with taller species dominating wet sites and low wood density species dominating P-rich sites.
5. Turnover characterized the taxonomic composition of tree communities. Geographic distances explained a larger fraction of variation for taxonomic composition than for functional composition, and community mean traits were more strongly driven by P than moisture.
6. *Synthesis*. Our results offer weak support for the tolerance hypothesis for tree communities in central Panama. Instead, we observe functional and taxonomic turnover reflecting trade-offs and conflicting species' responses to multiple abiotic factors including moisture, soil phosphorus and potentially other correlated variables (e.g. light).

KEYWORDS
leaf area, maximum height, meta-community analyses, nestedness, specific leaf area, tree species distributions, turnover, wood density

1 | INTRODUCTION

Tree community composition shifts along environmental gradients (Baldeck et al., 2013; Gentry, 1988; Givnish, 1999; Wright, 1992), particularly with changes in precipitation and soil fertility (Condit, Engelbrecht, Pino, Perez, & Turner, 2013; Esquivel-Muelbert et al., 2016; Gentry, 1988; Katabuchi et al., 2017; Vitousek, Porder, Houlton, & Chadwick, 2010). Although many studies have evaluated changes in taxonomic composition along environmental gradients, this provides limited information concerning the strategies and life histories that are optimal in different environments (Enquist et al., 2015; Grime, 2006; McGill, Enquist, Weiher, & Westoby, 2006; Swenson et al., 2012). Examining how different abiotic factors influence both ecological strategies and taxonomic composition of communities offers a holistic approach for understanding the drivers of shifts in tree communities along environmental gradients.

Changes in community composition in response to variation in abiotic conditions fall along a continuum, with endpoints of completely nested species distributions or complete turnover in species composition (Baselga, 2010, 2012; Harrison et al., 1992; Leibold & Mikkelson, 2002). Nested species composition emerges due to variation in physiological tolerances among species. Specifically, the local environment operates as a filter sorting species depending on their ability to withstand local abiotic conditions (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Keddy, 1992). Thus, species able to tolerate a relatively wide range of conditions would be broadly distributed, while less tolerant species would have relatively restricted distributions, nested within the ranges of widely distributed species. This physiological tolerance hypothesis (Janzen, 1967) predicts that local species richness and functional composition will be determined by how many and which species can tolerate local abiotic conditions. Thus, at the most stressful extreme of the gradient, species richness should be low and functional variation should be small. In contrast, at the least stressful extreme, species richness should be high and functional variation should be broad. This type of nested pattern has been found at the taxonomic level for tropical tree communities distributed along a gradient in drought seasonality in the Amazon (Esquivel-Muelbert et al., 2016). However, studies testing for nested composition within a functional framework are largely lacking.

In contrast to nested distributions, species and functional composition may show complete turnover across environmental gradients, with species replaced by others from one site to the next along the gradient (Engelbrecht et al., 2007; Pitman et al., 2002; Swenson, Anglada-Cordero, & Barone, 2011). This pattern might emerge as a result of life history trade-offs, such as tolerance to low resource conditions versus competitive ability under high resource conditions. For example, along light gradients, shade-tolerant species often survive well under low light but are outcompeted by light-demanding species under high light (Brokaw, 1987). Such trade-offs between performance at high versus low levels of a single resource can generate turnover in species composition along a resource gradient, as well as turnover in functional traits that underlie differences in life history strategies.

Turnover might also result from simultaneous variation in responses to several resources. Abiotic variables often covary in space, creating contrasting gradients of resource availability (e.g. sites having low availability of one resource, but high availability of another resource). For example, in the tropics, sites with high rainfall tend to have low nutrient availability due to leaching (Campo, Jaramillo, & Maass, 1998; Vitousek & Chadwick, 2013), which generates gradients from high nutrient/low rainfall to low nutrient/high rainfall sites. When a species cannot tolerate both low nutrient and low water availability (i.e. the two extremes of the gradient), conflicting stresses may select for trade-offs between the ability to tolerate these two different low resource states. In this case, we may observe a replacement of species along the gradient that is the outcome of some species being restricted to dry sites and other species restricted to nutrient-poor sites. While turnover in species composition is likely driven by whole plant responses to multiple resources, individual functional traits are likely to enhance performance with respect to specific limiting resources. This may lead to discrepancies between patterns of taxonomic and functional composition along environmental gradients. Examining such discrepancies may provide a more mechanistic understanding of how environmental variables drive spatial variation in plant community composition.

Gradients in environmental variables can also lead to gradients in biotic variables. For example, deciduousness declines with increasing rainfall intensifying competition for light in the understorey of wetter forests (Brenes-Arguedas, Broddy, Coley, & Kursar, 2011). Pest pressure also varies with rainfall (e.g. Weissflog, Markesteijn, Lewis, Comita, & Engelbrecht, 2018). Thus, shifts in functional composition across environmental gradients may reflect responses not only to changes in multiple abiotic variables but also to changes in biotic interactions.

In this study, we explore how taxonomic and functional composition changes over two-fold moisture and 300-fold soil phosphorus (P) gradients extending over the 65 km between the Pacific and Caribbean coasts of central Panama. There is a modest relationship between local moisture and P availabilities (r^2 = 0.30), allowing us to disentangle the effects of variation in these two critical resources (Condit et al., 2013). Both environmental factors have significant effects on plant species distributions (Condit et al., 2013; Engelbrecht et al., 2007; Prada et al., 2017; Turner, Brenes-arguedas, & Condit, 2018). We focus on four functional traits that reflect resource acquisition strategies and have been linked to responses to water and soil nutrient variation at the global scale: leaf mass per area (LMA), wood density (WD), leaf area (LA) and maximum height (MH; Table 1). Using data on these four functional traits, combined with data on the distribution of 550 lowland tropical tree species

TABLE 1 Functional trait descriptions and expected functional responses to moisture and soil P gradients

Trait	General description	Expected response for drier sites	Expected response for infertile sites	References
WD: wood density (g/cm^3)	Trade-offs between mechanical stability and transport efficiency and safety	High wood density trees are less susceptible to drought	High wood density trees display conservative resource-use strategies that allow them to succeed in infertile conditions	Chave et al. (2009) and Heineman, Turner, and Dalling (2016)
MH: maximum height (m)	Competitive ability for light	Taller trees are more susceptible to drought	Maximum tree height increases with nutrient supply	Ryan and Yoder (1997), Koch et al. (2004), Givnish, Wong, Stuart-Williams, Holloway-Phillips, and Farquhar (2014) and Bennett et al. (2015)
LMA: leaf mass per area (g/m^2)	Trade-off between carbon acquisition and conservation	Species with high LMA are more conservative in carbon use and better tolerate drought	Species with high LMA survive better in infertile soils	Wright et al. (2002), Wright et al. (2004) and Greenwood et al. (2017)
LA: leaf area (cm^2)	Display area for capturing light and transpiration	Smaller LA and transpirational area are advantageous in dry conditions	Unknown	Shields (1950), Ashenden (1978) and Poorter and Rozendaal (2008)

across 72 plots spanning the regional-scale gradients in moisture and soil P in central Panama, we ask:

1. Are species' distributions nested along the moisture and soil P gradients or do species exhibit turnover along these gradients? Do changes in functional composition across these gradients follow the same pattern as taxonomic composition?

Given the observed strong species-level responses to both moisture and soil P gradients in this system (Condit et al., 2013; Engelbrecht et al., 2007), we predicted that species turnover should play a larger role in determining patterns of taxonomic beta diversity in this system. For individual functional traits, we predicted that, if specific traits determine species tolerances, then certain trait values would be filtered out at low resource sites (dry or low-P sites), but not at less stressful sites (wet or rich-P sites). In this case, low resource sites would possess a subset of the species with trait values that confer tolerance and therefore a narrower range of functional trait values compared to higher resources sites, resulting in a nested pattern of functional composition.

2. Does moisture or soil P availability have a stronger influence on taxonomic and functional composition?

We predicted that moisture and soil P would be similarly important for driving taxonomic composition, given that individual species distributions have been shown to respond strongly to both water and soil P availability in this region (Condit et al., 2013). For functional composition, we predicted that moisture would be a stronger driver for wood density and maximum height because species with lower wood density and larger maximum size tend to be more susceptible to drought (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Falster & Westoby, 2005; Koch, Stillet, Jennings, & Davis, 2004; O'Brien et al., 2017; Ryan & Yoder, 1997). For leaf traits, we expected that both moisture and soil P should explain a high percentage of functional variation in LA and LMA (Shields, 1950; Wright, Westoby, & Reich, 2002).

Addressing these questions reveals whether functional trait–environment relationships underlie patterns of species distributions and changes in taxonomic community composition along the moisture and soil P gradients spanning central Panama. Using four traits important for different functions (see Table 1) offers new insights into the interplay of multiple functions in response to complex resource gradients. More broadly, we seek a more mechanistic understanding of species and community responses to shifts in abiotic conditions along environmental gradients.

2 | MATERIALS AND METHODS

2.1 | Study area

We used tree species occurrence data for individuals ≥1 cm DBH distributed across the Isthmus of Panama. Forty sites contained

1-ha plots in which all individuals were tagged and identified, yielding data on species presence/absence and abundance. At the remaining 32 sites, all species were recorded in 1-day surveys, but individuals were not counted and therefore only presence/absence data were available. The sites are arranged along moisture and soil P gradients that extend from the Caribbean Sea to the Pacific Ocean in forests near the Panama Canal with a total range in mean annual temperature of 23.0 and 26.1°C (Condit et al., 2013; Figure 1). Of the 890 species recorded, 779 (87%) were identified to species, 88 to genus and 23 remained unidentified. We used 550 species that were fully identified, present in at least three of the 72 sites and that had data for at least one of the four functional traits.

2.2 | Moisture and soil resin P predictors

To estimate drought stress at each site, we used the dry-season moisture deficit index (D_m) described by Condit et al. (2013), which is a measure of the difference between precipitation and potential evapotranspiration. The precipitation information was obtained from 47 gauges distributed along the Panama Canal. The evapotranspiration information was obtained from Barro Colorado Island and corrected for elevation (Condit et al., 2013). For P, we used information on soil resin P that quantifies the amount of inorganic phosphate available to trees. Soil resin P (henceforth soil P) was determined for anion-exchange membranes placed in the upper 10 cm of the soil profile during the wet season (Condit et al., 2013; Turner et al., 2018; Turner & Romero, 2009). The dry-season moisture deficit index ranged from −579 to −370 mm (Figure 1). Soil P ranged from 0.07 to 22.80 mg P/kg (Figure 1).

2.3 | Functional traits

We measured LMA (g/m^2) and LA (cm^2) for leaves collected from adult individuals (~3 individuals per species) located close to the Barro Colorado Island (BCI) 50-ha forest dynamics plot (9.15°, −79.85°) or to canopy cranes in the Bosque Protectora San Lorenzo (9.27°, −79.98°) and the Parque Natural Metropolitano (8.99°, −79.54°). These three sites are located near the centre and the wet Caribbean and dry Pacific ends of the rainfall gradient respectively. Fully expanded and sun-exposed leaves were collected from canopy branches. Leaf area was calculated for entire leaves. MH (mm) was measured for up to the six largest individuals of each species in the BCI 50-ha plot. WD (g/cm^3) was measured from adult individuals (~5 individuals per species) located within 15 km of the BCI 50-ha plot. Wright et al. (2010) describe methods for all traits fully. We obtained WD for 58 species from a global dataset (https://datadryad.org/stash/dataset/doi.org/10.5061/dryad.234, Zanne et al., 2009). When species-level wood density data were unavailable, we substituted genus or family means (20% and 7% of the species respectively). Data were available for 67%, 65%, 76% and 100% of the 550 species for LMA, LA, MH and WD respectively. Table S1 lists the proportion of species for which data were available for each site used in the analyses. Table S2 shows all pair-wise correlations between traits.

2.4 | Analyses

Functional and taxonomic beta diversity—We implemented the framework of Baselga (2010, 2012) to disentangle the contributions of turnover and nestedness for changes in taxonomic and functional

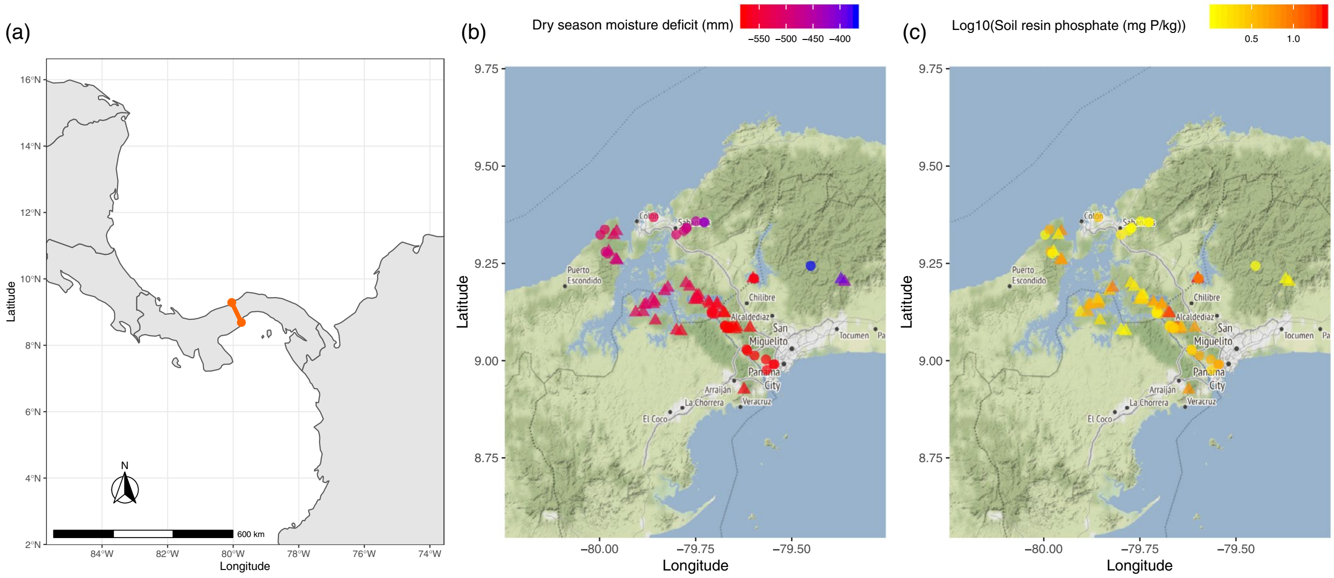

FIGURE 1 Map of Panama showing the distribution of sites along the moisture and soil resin P gradients. (a) Shows the study site location in Panama. (b) Shows a regional map where dark blue represents wetter sites, while red represents drier sites. (c) Shows a regional map where red represents sites rich in soil resin P, while yellow represents sites poor in soil resin P. Triangles indicate plots with abundance data and circles indicate plots with occurrence data

composition along the moisture and soil P gradients. Baselga (2010) decomposed taxonomic beta diversity (β_{sor}) into two additive components due to turnover (β_{sim}) (replacement) and nestedness (β_{nes}), such that $\beta_{sor} = \beta_{sim} + \beta_{nes}$. β_{sor} is calculated as the Sørensen index and β_{sim} is calculated as the Simpson dissimilarity index.

We first assessed the turnover and nestedness components at the meta-community-level calculating multiple-site dissimilarity using the functions 'betapart.core' and then 'beta-multi' from package BETAPART version 1.5.1 (Baselga & Orme, 2012). The meta-community-level analysis reveals the relative contribution of turnover versus nested to beta diversity across this region, but not the degree to which such patterns are related to environmental gradients. Therefore, we then examined if there was a relationship between the degree of turnover for a given pair of plots and a difference in moisture, soil P and geographic distance (pair-wise environmental analysis). To do this we first calculated taxonomic dissimilarity (turnover) between all pairs of plots along the gradients, again using the functions 'betapart.core' and 'beta.pair'. Next, we evaluated changes in taxonomic dissimilarity between pairs of plots with moisture or soil P, accounting for geographic distance using partial Mantel tests, with the function 'mantel.partial' in the package VEGAN version 2.5-6 in R (Oksanen et al., 2019).

We extended this framework to functional beta diversity by decomposing the UniFrac metric in turnover and nestedness components in the same way as described above (Baselga, 2010, 2012; Swenson, 2014). Unifrac is a distance-based metric that uses trait dendrograms and quantifies the fraction of the dendrogram that is shared between two communities. To calculate functional nestedness and turnover, we used a modification of the function 'betapart.core' from package BETAPART (see code in Supplementary Methods). Since functional beta diversity and species richness might be correlated, we implemented a null model to determine whether shifts in functional beta diversity were higher or lower than expected given observed species richness (see Supplementary Methods for details). The standardized values of beta diversity were then used to evaluate whether changes in standardized beta diversity were related to dissimilarity in moisture and soil P accounting for geographic distance, using partial Mantel tests as described above. We compared standardized and non-standardized beta diversity results to examine whether the shifts in functional dissimilarity along both gradients were mainly associated with shifts in species richness.

Shifts in community mean trait values along the gradients—We used community mean trait values (CM) to quantify community functional structure. We calculated CM with species weighted equally for all 72 plots. We also calculated community weighted mean trait values (CWM) with species weighted by their abundances for the 40 plots with abundance data. However, we focus on the non-weighted metric to make our results comparable to Condit et al. (2013).

To examine changes in CM values along the moisture and soil P gradients, we fit separate linear models for each trait where the response variable was CM and the predictor variables were D_m and soil P. We also fit models using CWM for the subset of sites that had species abundance information.

Contribution of spatial and environmental factors—We used variance partitioning analyses (Legendre, 2008; Legendre, Borcard, & Peres-Neto, 2005) to assess the relative contributions of moisture, soil P and space (i.e. the geographic distance between sites) to differences in community mean trait values and taxonomic composition (see Supplementary Methods for details).

All analyses were performed in R version 3.6.1 (R Development Core Team, 2017).

3 | RESULTS

Taxonomic beta diversity—Meta-community-level analyses showed that shifts in taxonomic composition were mostly the result of turnover and less due to nestedness ($\beta_{sim} = 0.96$, $\beta_{nes} = 0.014$). In the pair-wise environmental analysis, we found a significant increase in taxonomic turnover with dissimilarity in both moisture and soil P (Table 2).

Functional beta diversity—Meta-community-level analyses showed that shifts in functional composition were mostly determined by turnover and less by nestedness ($\beta_{simWD} = 0.97$, $\beta_{nesWD} = 0.002$; $\beta_{simMH} = 0.97$, $\beta_{nesMH} = 0.002$; $\beta_{simLMA} = 0.97$, $\beta_{nesLMA} = 0.004$; $\beta_{simLA} = 0.97$, $\beta_{nesLA} = 0.003$). For pair-wise environmental analysis, we found that comparisons for non-standardized functional beta diversity showed that functional turnover increased with moisture dissimilarity for WD and LMA and increased with soil P for WD and MH (Table 2). However, when using standardized values of functional turnover along the soil P and moisture gradients, these relations were not significant (Table 2).

Shifts in community mean trait values along the gradients—Relationships between moisture availability and CM trait values were significantly positive for LMA and MH, significantly negative for LA and not significant for WD (Figure 2; Table S3). For the subset of plots with species abundance data, relationships between

TABLE 2 Partial mantel tests to evaluate relationships between taxonomic or functional turnover (β_{sim}) and dissimilarity in moisture, or soil P while controlling for geographic distance. Bold numbers indicate significant relationships (alpha = 0.05)

	Turnover	
	Moisture	**P (resin)**
Taxonomic	**0.329**	**0.204**
WD	**0.205**	**0.181**
MH	−0.007	**0.232**
LMA	**0.307**	0.105
LA	−0.098	0.141
SES WD	0.043	0.090
SES MH	0.001	−0.018
SES LMA	−0.012	−0.002
SES LA	0.016	0.003

Abbreviations: LA, leaf area; LMA, leaf mass per area; MH, maximum height; SES, standardized effect size; WD, wood density.

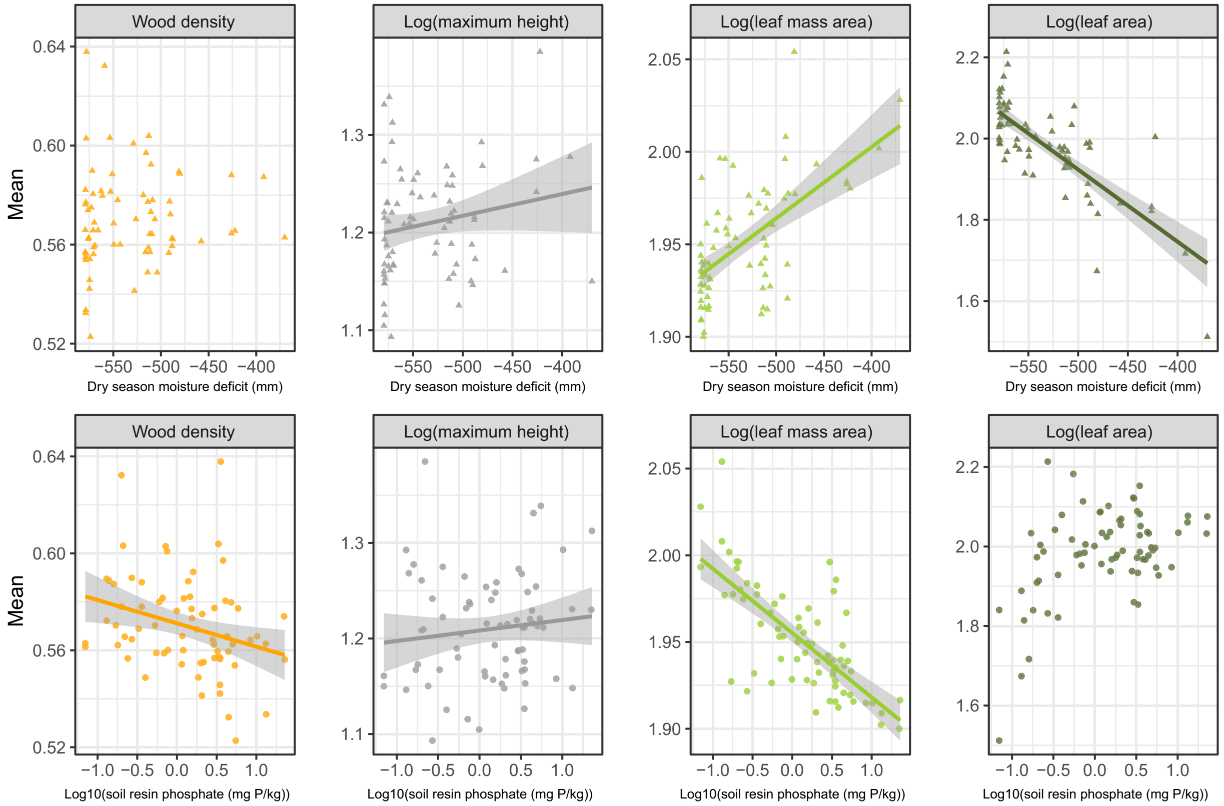

FIGURE 2 Relationships between community mean (CM) trait values and dry-season moisture deficit (D_m; top row) and soil resin P (bottom row) across 72 sites in Panama. Units are g/cm^3 for wood density, m for maximum height, g/m^2 for leaf mass per area, and cm^2 for leaf area. The lines show significant relationships and the shaded area represents the 95% confidence intervals (alpha = 0.05)

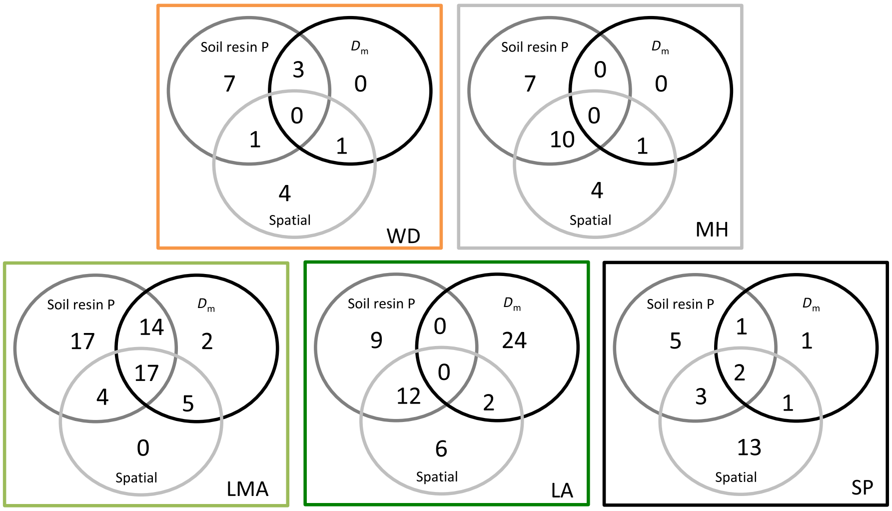

FIGURE 3 Percentages of variation in community mean trait values (LA, leaf area; LMA, leaf mass per area; MH, maximum height; WD, wood density) and taxonomic composition (SP) explained by soil resin P, dry-season moisture deficit index (D_m) and space (Spatial). The combined effects of soil resin P, D_m and/or space explain percentages enclosed by two or three circles

moisture availability and CWM trait values were significantly negative for LA and not significant for LMA, MH and WD (Figure S1).

Relationships between soil P availability and CM trait values were significantly negative for LMA and WD, significantly positive for MH and not significant for LA (Figure 2; Table S3). Relationships between soil P and CWM trait values were significantly negative for LMA, significantly positive for MH and not significant for WD and LA (Figure S2).

Contribution of spatial and environmental factors—Soil P alone explained a larger percent of variation than moisture availability for community means of WD, LMA and MH, as well as for taxonomic composition. In contrast, moisture availability explained more variation in community mean LA. Space alone explained a smaller percentage of variation in functional trait means (0%–6%) compared to taxonomic composition (13%; Figure 3). Table S4 gives the total percentage of variation explained by each trait.

4 | DISCUSSION

We examined changes in taxonomic and functional composition of tree communities distributed along moisture and soil P gradients in Panama. These changes are dominated by a replacement of species and functional trait values (turnover) rather than nestedness. We hypothesize that species are unable to tolerate the full range of both moisture availability and soil P observed across our sites preventing nested taxonomic distributions. Likewise, we hypothesize that functional trade-offs prevent nested distributions of functional traits across the moisture and soil P gradients. In addition, we observed significant shifts in community mean traits along both gradients, with the strength of these functional responses varying among traits (WD, LMA, LA and MH) and resources (either moisture or soil P). Combined these results suggest that shifts in species and functional composition are not dominated by a single abiotic factor, but that instead, moisture, soil P, and possibly other factors generate conflicting responses of species.

4.1 | Dominance of taxonomic and functional turnover

At the meta-community level, we found a prevalence of functional and taxonomic turnover suggesting the simultaneous action of multiple environmental constraints generating conflicting responses on species and their traits. This is consistent with the results reported by Condit et al. (2013), who found strong species-specific associations with both high and low soil P and moisture levels, and provides further insights into the functional responses underlying these compositional shifts. The integration of functional trait information indicated that the extremes of the gradient that are either limiting in P or in water constrain the number of species able to persist at those sites generating the observed functional turnover. These results agree with the idea of environmental harshness as the main factor limiting species richness via restrictions in species ranges (Kleidon & Mooney, 2000), with restricted species distributions resulting from multiple environmental stressors.

Our results contrast with taxonomic nestedness along a pronounced seasonal drought gradient in the Western Amazon (Esquivel-Muelbert et al., 2016) and with nested distributions of plant growth forms with respect to soil fertility in lowland forests of South America (Gentry & Emmons, 1987). We suggest that this discrepancy is related to variation among study systems in the strength of abiotic filters and the length of the gradients, as well as differences in the factors that covary with the environmental gradients being studied (Ruokolainen et al., 2002). For example, the range of variation in soil P across the studied gradient in Panama is larger than the range reported for the lowland Amazon forest (Quesada et al., 2010). Also, in a tropical dry forest in Florida, temperature was detected as a major factor driving nested taxonomic patterns for tree communities (Ross, Sah, Ruiz, Spitzig, & Subedi, 2016).

4.2 | Functional turnover in response to moisture

We examined whether the degree of functional turnover in pair-wise comparisons across all plots was related to dissimilarity in environment (i.e. moisture or soil P) accounting for spatial distance (pair-wise environmental analysis). We found evidence for functional turnover of LMA and WD along the moisture gradient (Table 2). However, these patterns disappear when we standardized the metric suggesting that a great part of the observed directional trends in functional turnover along the moisture gradient are the result of differences in species richness.

At the same time, when examining community mean (CM) trait values, we found that leaf traits and maximum stature (MH) respond significantly to dry-season severity. Species with higher LMA, lower LA, and taller MH are more prevalent in wetter sites. While the results for MH agree with our predictions, the leaf trends contradict the pattern expected by environmental filtering due to drought (e.g. more conservative leaf traits in drier sites; Figure 2; Table S3). We believe this is due to additional factors that covary with moisture. For example, in our study system, light availability varies along the moisture gradient, with wet sites being more light-limited than dry sites due to more dense canopies, fewer drought-deciduous species and more cloudy days (Brenes-Arguedas, Roddy, & Kursar, 2013). This variation in light should play an important role in determining photosynthetic strategies of plants and, therefore, should influence traits involved in light-use strategies (Brenes-Arguedas et al., 2013). Similarly, pest pressure might contribute to the observed shifts in leaf traits given that pathogens and herbivores vary along environmental gradients and influence species distributions and diversity (Brenes-Arguedas, Coley, & Kursar, 2009; Fine, Mesones, & Coley, 2004; Gaviria & Engelbrecht, 2015). Pest pressure is also thought to be stronger in wetter sites (Givnish, 1999; Leigh et al., 2004) (but see Weissflog et al., 2018) and should lead to leaves with higher LMA to deter herbivore attack (Poorter et al., 2009). Thus, our results suggest that the observed functional turnover along the rainfall gradient may be predominantly driven not by moisture directly but by variation in light availability and/or pest pressure along the gradient. Given the modest correlation between moisture and soil P ($r^2 = 0.30$), functional changes along the moisture gradient may also be weakly influenced by soil P availability (see below).

An additional, but not mutually exclusive explanation for the observed trends in leaf traits is that many species in dry sites respond via drought avoidance strategies such as dropping their leaves during the dry season to minimize water loss (Brenes-Arguedas et al., 2013; Comita & Engelbrecht, 2014; Markesteijn & Poorter, 2009). These deciduous species tend to have thin leaves characterized by low LMA and are more dominant in dry sites (Eamus, 1999). In fact, across our study sites, we find a higher predominance of deciduous species at drier than at wetter sites (Figure S3), which may also contribute to the observed trends in leaf traits.

4.3 | Functional turnover in response to soil P

We found that functional turnover for WD and MH increases along the soil P gradient when accounting for differences in spatial distance (Table 2). However, as with moisture, these trends disappear when accounting for differences in species compositional turnover (Table 2). Combined, these results indicate that the directional changes in observed functional turnover across the soil P gradient are largely due to changes in taxonomic richness.

We also examined if there were directional trends in community-level trait means (CM) along the soil P gradient. We found significant shifts in community mean traits, with species having more conservative resource-use strategies (i.e. high LMA high WD) at sites with lower soil P (Figure 2). The decreasing trend of LMA towards high soil P sites may be explained by the distribution of deciduous species, which tend to have acquisitive strategies, and increase in proportion towards high soil P sites (Figure S4). Similar negative relationships between LMA and soil P have been found in previous studies (Fyllas et al., 2009; Hidaka & Kitayama, 2011; Reich, Uhl, Waiters, & Ellsworth, 1991), but, in most cases, the relationships reported are modest (reviewed by Poorter et al., 2009). We suggest these differences in the responses to soil P are related to the variation in the magnitude of the variation in soil P along gradients. In the case of the gradient in central Panama, soil P varies 300-fold across sites and is a key environmental factor influencing species distributions in this region (Condit et al., 2013; Prada et al., 2017; Zalamea et al., 2016). Thus, soil P appears to be a major factor determining ecological strategies of species related to LMA in this system. Species with low LMA exhibit acquisitive resource-use strategies (Wright et al., 2004) and may be at a competitive advantage over species with high LMA under high soil P conditions.

In addition to the results for leaf traits, we found that CM for WD and MH were also related to the soil P gradient, with harder wooded and shorter species characterizing less fertile sites. This result agrees with our predictions and with previous studies across other Neotropical lowland forests that found negative correlations between WD and soil fertility (Muller-Landau, 2004; Patiño et al., 2009). Low soil fertility may favour species exhibiting resource conservative life history strategies (i.e. high WD) that are more tolerant to adverse conditions.

4.4 | Explained variation in taxonomic and community mean functional composition along the environmental gradient

Among all traits analysed, CM leaf traits showed the strongest responses to both moisture and soil P gradients, with variation in LA mainly associated with the moisture gradient and LMA mainly associated with soil P. These results were also reflected in the variance partitioning analyses where variation in CM LMA was better explained by the soil P gradient, and variation in CM LA was better explained by the moisture gradient (Figure 3). WD and MH showed less dramatic shifts in our study system and had lower percentages of variance explained by both gradients (between 0% and 10%). Combined, our results indicate that variation among sites in mean functional traits is more strongly driven by deterministic factors associated with moisture and soil P than by spatial location of plots alone (Figure 3). This indicates that functional composition of tree communities in central Panama is strongly determined by environmental filters that change over space. In terms of taxonomic composition, we found that soil P explained a higher percentage of variance (5%) than moisture (1%). Condit et al. (2013) found that moisture was a stronger predictor of species distributions than soil P in central Panama, but this discrepancy may be due to differences in statistical approaches (e.g. community vs. individual species-level analyses). Also, space explained a larger percentage of variance in taxonomic composition than for functional trait composition, suggesting that there are additional factors, such as dispersal limitation, that drive shifts in species composition but that may be less important for shaping functional composition. Ultimately, we found that soil P and moisture explained relatively small amounts of taxonomic variation (~13% combined; Figure 3; Table S4), suggesting that additional environmental factors likely also contribute to the observed taxonomic turnover.

4.5 | Caveats

While this study offers a comprehensive examination of the effects of resource gradients on functional composition of tree communities in central Panama, there are several caveats. First, although the trait data used in the study represent the most complete dataset available, information is missing for ~35% of species for at least one trait. Most of the species missing trait information are rare, with restricted distributions in wet and infertile sites (Figure S5). This missing information could have a sizeable effect on community-level and functional turnover results obtained, particularly given that previous studies have shown that rare species can make an important contribution to local functional diversity (Leitaõ et al., 2016; Umaña et al., 2017). For example, functional turnover results were mostly significant for WD (Table 2), which was the only trait with information for all species in the dataset. However, CM trait relationships remained consistent when we excluded plots with leaf trait data for less than 30% of species (Table S5). Nonetheless, collecting trait data for rare species at wet and infertile sites along these gradients should be a priority for future studies of functional composition and diversity. Further, we only considered a handful of above-ground traits that might not represent the multifunctional nature of tree species. Root traits should provide further insights into species and functional responses to below-ground resources (Zemunik, Turner, Lambers, & Laliberté, 2015). Finally, we did not consider intraspecific trait variation, even though trait variation within species can be substantial (Albert et al., 2010; Messier, McGill, & Lechowicz, 2010; Siefert et al., 2015; Umaña, Zhang, Cao, Lin, & Swenson, 2018).

5 | CONCLUSIONS

Changes in functional and taxonomic composition of tree communities along environmental gradients result from the simultaneous influence of multiple factors on tree species. Our results reveal that shifts in species composition over these gradients are dominated by a replacement of species and functional trait values instead of nestedness, which suggests conflicting responses of species and their traits to different factors. In addition, we found that despite considerable variation in rainfall and previously documented strong species' responses to seasonal drought (Condit et al., 2013; Engelbrecht et al., 2007), community-level responses in leaf traits did not match the expected patterns. Instead, soil P appears to be a main determinant of community mean leaf trait distributions. Finally, variation in moisture and soil P explained a higher percentage of variation for CM leaf traits than for WD and MH, suggesting that leaf traits are more strongly shaped by these gradients than the other traits. A full understanding of the underlying mechanisms driving shifts in tree community composition along gradients will require accounting for multi-dimensional responses of species to multiple factors that simultaneously covary along gradients and exert potent selective forces.

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AUTHORS' CONTRIBUTIONS

M.N.U. and L.S.C. conceived the idea; R.C., R.P., B.T. and S.J.W. collected the data; M.N.U. analysed and wrote the first draft of the manuscript with input from L.S.C. All authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Survey and census data are available from Dryad https://doi.org/10.15146/mdpr-pm59 (Condit, Pérez, Aguilar, & Lao, 2019) and https://doi.org/10.15146/R3FH61 (Condit, Pérez, Aguilar, Lao, Foster, et al., 2019).

Trait data are available from Dryad and TRY or through previously published archives: maximum height (Dryad https://doi.org/10.5061/dryad.85k53v8), wood density and LMA (supplementary files from Wright et al., 2010) and LA (from try-db.org, Panama trait databased by S.J. Wright, database ID 112).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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