

Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings

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Abstract

1. Local tree species distributions in tropical forests correlate strongly with soil water availability. However, it is unclear how species distributions are shaped by demographic responses to soil water availability. Specifically, it remains unknown how growth affects species distributions along water availability gradients relative to mortality.
2. We quantified spatial variation in dry season soil water potential (SWP) in the moist tropical forest on Barro Colorado Island, Panama, and used a hierarchical Bayesian approach to evaluate relationships between demographic responses of naturally regenerating seedlings to SWP (RGRs and first-year mortality) and species distributions along the SWP gradient for 62 species. We also tested whether species that were more abundant at the wet or dry end of the gradient performed better (a) at their “home end” of the gradient (“best at home” hypothesis) and (b) “at home” compared to co-occurring species (“home advantage” hypothesis).
3. Four and five species responded significantly to SWP in terms of growth or mortality respectively. Growth (but not mortality) responses were positively related to species distributions along the SWP gradient; species with a more positive (negative) growth response to SWP were more abundant at higher (lower) SWP, that is, at wetter (drier) sites. In addition, wet distributed species grew faster on the wet end of the SWP gradient than on the dry end (“best at home”) and grew faster on the wet end than dry distributed species (“home advantage”). Mortality rates declined with seedling size for all species. Thus, seedling growth responses to SWP indirectly shaped local species distributions by influencing seedling size and thereby mortality risk.
4. *Synthesis.* By demonstrating how growth responses to spatial variation in soil water availability affect species distributions, we identified a demographic process underlying niche differentiation on hydrological gradients in tropical forests. Recognizing the role of these growth responses in shaping species distributions should improve the understanding of tropical forest composition and diversity along rainfall gradients and with climate change.

KEYWORDS

Barro Colorado Island, Panama, demographic responses, habitat associations, home advantage, niche differentiation, plant population and community dynamics, seedling performance, soil moisture

1 | INTRODUCTION

The distributions of tropical forest tree species respond strongly to regional rainfall gradients (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Condit, Engelbrecht, Pino, Pérez, & Turner, 2013; Esquivel-Muelbert et al., 2017). At the local scale, species distributions are often associated with topographic or edaphic habitats that vary in soil water availability (Chuyong et al., 2011; Gunatilleke et al., 2006; Harms, Condit, Hubbell, & Foster, 2001), and these habitat associations tend to become stronger through ontogeny (Comita, Condit, & Hubbell, 2007; Paoli, Curran, & Zak, 2006; Webb & Peart, 2000). This is likely due to differential mortality responses to soil water availability among species, starting at the seedling stage (Comita & Engelbrecht, 2009; Engelbrecht et al., 2007). Yet, the exact mechanism by which demographic responses to soil water availability lead to spatial partitioning of soil water gradients (i.e., hydrological niche differentiation) remains unclear (Silvertown, Araya, & Gowing, 2015).

There are at least two possibilities by which seedling demography may shape species distributions along soil water gradients. Water shortage might shape species distributions directly by increasing drought-induced seedling mortality (Comita & Engelbrecht, 2009, 2014). Alternatively, water shortage might shape distributions indirectly by decreasing seedling growth, leading to smaller sized seedlings that suffer higher mortality rates (Delissio & Primack, 2003; Gilbert, Harms, Hamill, & Hubbell, 2001; Johnson, Condit, Hubbell, & Comita, 2017; Rose & Poorter, 2003). Our goal is to determine if mortality or growth responses to soil water availability (or both) shape local species distributions.

Recently, Fortunel et al. (2016) proposed a framework to understand how differential species performance (growth or mortality) among habitats with contrasting abiotic or biotic conditions shapes associations to those habitats. The authors posed two hypotheses. First, species might perform better in their “home habitat” than in other habitats (henceforth “best at home” hypothesis). Second, species might perform better “at home” than species that are not associated with that habitat (henceforth “home advantage” hypothesis).

With respect to water availability, reciprocal transplant experiments have implicitly tested these two hypotheses by comparing seedling growth and mortality of species common to dry and wet forests along a rainfall gradient in central Panama. Dry forest species tended to perform best in dry forests (i.e., “best at home”), and wet forest species had lower mortality in wet forests but showed no clear pattern for growth (Brenes-Arguedas, Coley, & Kursar, 2009; Gaviria & Engelbrecht, 2015; Gaviria, Turner, & Engelbrecht, 2017). Wet forest species generally grew faster than dry forest species not

only in wet forests (i.e., they had a “home advantage”) but also in dry forests, indicating that wet forest species have inherently higher growth rates. In contrast, dry forest species had a “home advantage” in terms of lower mortality, suggesting that they invest more in adaptations to survive drought than wet forest species, which might trade-off against their ability to achieve high growth rates (Brenes-Arguedas, Roddy, & Kursar, 2013).

Despite our increasing understanding of performance differences between species from contrasting forest environments, the performance of naturally regenerating co-occurring seedlings with respect to soil water availability has only been compared once at a local scale (Comita & Engelbrecht, 2009). Moreover, studies linking local performance or species distributions to soil water status in tropical forests either used topographic or edaphic habitats as a proxy for soil water availability (see, e.g., Baltzer, Davies, Noor, Kassim, & LaFrankie, 2007; Chuyong et al., 2011; Comita & Engelbrecht, 2009; Daws, Pearson, Burslem, Mullins, & Dalling, 2005; Engelbrecht et al., 2007) or measured soil water content (Ashton, Gunatilleke, & Gunatilleke, 1995; Baraloto & Goldberg, 2004; De Gouvenain, Kobe, & Silander, 2007; Uriarte, Muscarella, & Zimmerman, 2018, but see Webb & Peart, 2000). However, soils with similar soil water contents can differ widely in their capacity to supply water to plants depending on their texture (Juo & Franzluebbers, 2003). Plants draw water from the soil along the soil–plant–atmosphere continuum of water potential (Lambers, Chapin, & Pons, 2008). Hence, soil water potential (SWP) is the most relevant measure of water status for plant–water relations and performance, especially during periods when water availability is limiting (Juo & Franzluebbers, 2003). Yet, few studies measured SWP at the spatial and temporal scales necessary to link SWP to performance or species distributions.

We explored how demographic responses to soil water availability shape species distributions. We constructed a detailed spatial gradient of SWP at 200 seedling census sites on Barro Colorado Island (BCI), Panama. We measured SWP during two dry seasons including a strong El Niño dry season, thereby capturing SWP during a drought event that could have severe effects on seedling dynamics (Comita & Engelbrecht, 2014). We used 21 years of annual seedling censuses to quantify local species distributions along the SWP gradient and to estimate species-specific growth and first-year mortality responses to SWP. Specifically, we ask:

1. Are species distributions along the SWP gradient related to growth and/or mortality responses to SWP? We expect that species differ strongly in their drought sensitivity (Brenes-Arguedas et al., 2009; Engelbrecht & Kursar, 2003), and that drought-sensitive species with positive demographic responses

to SWP are associated with wetter parts of the SWP gradient (Engelbrecht et al., 2007).

2. Do species perform “best at home”, that is, better at the end of the SWP gradient to which they are associated? We expect that species associated with wetter sites perform “best at home” (i.e., have higher growth and lower mortality rates under wetter conditions), whereas species associated with drier sites are drought tolerant and indifferent to SWP (Comita & Engelbrecht, 2009).
3. Do species have a “home advantage,” that is, better performance at their end of the SWP gradient than species associated with the other end? In terms of growth, we expect that wet distributed species have a “home advantage” over dry distributed species due to inherently higher growth rates (Brenes-Arguedas et al., 2009; Gaviria et al., 2017). In contrast, we expect that dry distributed species have a “home advantage” in terms of mortality, due to adaptations to cope with drought (Brenes-Arguedas et al., 2013).

By testing how growth and mortality responses to soil water availability are linked to species distributions, we explored the demographic underpinnings of niche differentiation on fine-scale soil moisture gradients in a tropical forest (Silvertown et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in a 50-ha Forest Dynamics Plot (Hubbell & Foster, 1983) located in old-growth, semideciduous lowland moist forest on Barro Colorado Island (BCI), Panama (9.15°N, 79.85°W). Annual rainfall averages 2,660 mm, 10% of which falls in the dry season from mid-December to late April (STRI, 2018). The intensity and length of the dry season vary greatly among years, with especially long dry seasons during some El Niño events (Condit et al., 2004). The 50-ha plot lies on a relatively flat plateau (elevation ranges from 120 to 155 m a.s.l., Hubbell & Foster, 1983). Soil water availability varies with topography within the 50-ha plot, with slopes being wetter than plateaus (i.e., SWPs are less negative, Becker, Rabenold, Idol, & Smith, 1988; Daws, Mullins, Burslem, Paton, & Dalling, 2002).

2.2 | Data collection

We focused on 200 permanent seedling census sites (henceforth sites) within the 50-ha plot (Wright, Muller-Landau, Calderón, & Hernández, 2005). The sites cover all topographic habitats within the 50-ha plot except streamsides (cf. Harms et al., 2001, see Supporting Information Figure S1.1 in Appendix S1). Each site has three 1-m² seedling plots (600 plots in total), located 2 m from the centre of the site. We tagged every seedling of woody species, identified them to species, measured their heights, and recorded mortality annually from 1994 to 2014 (see Wright et al., 2005, for methods).

To quantify spatial variation in soil water status, we took soil samples at 15 cm depth at each of the seedling census sites and measured SWP with a WP4C Dewpoint PotentialMeter (Decagon

Devices, Inc., Pullman WA, USA). We made these measurements in the dry season, when water availability becomes limiting for seedling growth and survival (Comita & Engelbrecht, 2009). We measured SWP three times in the 2015 dry season (February, March, and April) and once in the 2016 dry season (March). The 2016 dry season was the third longest dry season recorded on BCI since 1954 and was associated with the 2015–2016 El Niño (STRI, 2018). No rain occurred during sampling except in April 2015, and we excluded samples taken after the rain in that sampling round. After measuring SWP, we used the same soil samples to assess soil water content (SWC) gravimetrically from fresh mass (f) and dry mass (d) determined after 72 hr at 105°C ($SWC = (f - d)/d$). We excluded six outliers in SWP by comparing measured SWP and SWC with soil water retention curves we constructed for a subsample of the sites (see Supporting Information Appendix S2). We then calculated the median SWP for each site to characterize dry-season soil water status.

To determine whether spatial variation in SWP persisted over time, we evaluated correlations of site-specific SWP values across the four sampling rounds. To determine whether our measurements captured the peak of the dry season, which should be most limiting for seedling performance, we compared our SWC measurements with SWC measurements taken every 2 weeks at a second location on BCI, 1.25 km from the 50-ha plot (STRI, 2018). To determine whether our SWP measurements at 15 cm depth were representative of SWP in deeper soil layers, we took additional samples at 40 and 100 cm depth for 36 census sites and 66 sites adjacent to the 50-ha plot and correlated SWP at these depths with SWP at 15 cm.

2.3 | Species distributions along the SWP gradient

We quantified species distributions as distributional centres and spread along the SWP gradient for all 62 species included in the growth or mortality models (see Section 2.4). We defined centre and spread as the median and standard deviation (SD), respectively, of SWP at the sites where seedlings of a species occurred. We calculated centre and spread for each annual census individually and for all seedling observations across all censuses collectively. Values varied widely for individual censuses, especially for rare species that sometimes had only one individual in a census (Supporting Information Figure S1.2). For this reason, we believe values calculated over all censuses best represent species distributions, although we recognize that individuals that persisted across censuses have a stronger influence on this measure of species distributions than individuals that died quickly. We present distributions calculated over all censuses in the main text. Analyses using distributions calculated from single censuses (see Section 2.4) gave similar results (see Section 3.3).

To test whether species distributions along the SWP gradient differed significantly from random distributions, we compared the observed distributional centre and spread of each species with distributions generated by three increasingly conservative null models. In the first null model, we randomly assigned individuals of each species to sites 1,000 times, while keeping all observations of an individual together. In the second null model, we kept individuals

that occurred at the same site together and randomly assigned these individuals to sites 1,000 times, which retained site-level clumping of conspecifics. In the third null model, we preserved the spatial autocorrelation of species distributions by shifting all individuals from one site to the next along the trail network 200 times (because there are 200 sites). For each null distribution, we calculated distributional centres and spread of species as described above. If the observed distributional centre of a species was below the 2.5th or above the 97.5th percentile of the distributional centres of the null distributions, the species was associated with dry or wet sites respectively. Similarly, if the observed distributional spread was below the 2.5th or above the 97.5th percentile of the distributional spreads of the null distributions, the species distribution was more restricted or more widespread than expected by chance respectively.

We also determined whether species distributions with respect to soil water availability were consistent across life stages. To do this, we evaluated correlations between our distributional centres along the SWP gradient and associations with wet vs. dry habitats for larger seedlings and saplings (≥ 20 cm tall and < 1 cm dbh) and trees (≥ 1 cm dbh). Comita et al. (2007) determined the density of larger seedlings and saplings and trees in each 20×20 m quadrat in the 50-ha plot, calculated average densities for the five topographic habitats of Harms et al. (2001), and standardized by the average density across all 50 ha for each species. Following Engelbrecht et al. (2007), we used these data to calculate relative densities pooled over three wet habitats (slopes [sl], streamside [st], and the swamp [sw]) vs. two drier habitats (high plateau [hp] and low plateau [lp]). The calculation follows:

$$\ln \left(\sqrt{\frac{w_{sl} * d_{sl} + w_{st} * d_{st} + w_{sw} * d_{sw}}{w_{hp} * d_{hp} + w_{lp} * d_{lp}}} \right) \quad (1)$$

where d_{xx} is the standardized density in habitat xx and w_{xx} is the fraction of the pooled dry or wet habitat covered by habitat xx (e.g., w_{sl} equals the area in slope habitat divided by the sum of the areas in slope, streamside, and swamp habitats, data from Harms et al., 2001). Compared with the original calculation from Engelbrecht et al. (2007), we added the swamp to the wet habitats and log-transformed the habitat associations to reduce the influence of outliers with high relative densities in wet sites.

2.4 | Demographic responses to SWP and their link to species distributions

We quantified growth as annual relative height growth rate (RGR, henceforth growth):

$$\text{RGR} = \frac{\ln(\text{height}_2) - \ln(\text{height}_1)}{t_2 - t_1} \quad (2)$$

where height_2 and height_1 are the annual height measurements at times t_2 and t_1 respectively. We quantified mortality (dead/alive) in the census in the year after each seedling was first recorded (first-year mortality, henceforth mortality). We excluded seedlings that had

resprouted, that were visibly damaged by animals, fallen branches, or leaf litter, or that were infected by pathogens, because this damage likely affected their performance more than variation in SWP. Additionally, we excluded observations made in a census interval that deviated more than a month from a full year (365 ± 30 days). In the growth model, we excluded (a) extreme positive outliers in growth likely caused by high-light levels (Wright et al., 2010) using a modified z-score (Iglewicz & Hoaglin, 1993), (b) individuals ≥ 2 m height as their height could not be accurately measured, and (c) growth ≤ 0 (see below for details). We included all shrub and tree species with ≥ 100 growth observations in the growth model, and all species with ≥ 100 first-year seedlings in the mortality model. We excluded two species that had $> 50\%$ of their individuals at a single site. In total, we analysed demographic rates for 62 species; the growth model included 53 species with 16,834 individuals (50,901 growth observations) and the mortality model included 43 species with 31,246 individuals.

We assessed growth and mortality responses to SWP and their link to distributional centres with two-level Bayesian models. In the growth model, the first (individual-level) regression predicted growth across individuals for each species. Growth of individual i of species j at site s in year y ($\text{pred}_{i,j,s,y}$) was predicted from height at the beginning of the census interval ($H_{i,y}$) and median SWP ($\text{SWP}_{i,s}$) where the individual occurred:

$$\text{pred}_{i,j,s,y} = \beta_{0,j} + \beta_{1,j} \times \text{SWP}_{i,s} + \beta_{2,j} \times \ln(H_{i,y}) + u_i + u_s + u_y \quad (3)$$

where $\beta_{0,j}$, $\beta_{1,j}$, and $\beta_{2,j}$ described the species-specific mean log growth rate and the growth response to SWP and height, respectively, for species j . The model included random effects for individual (u_i), site (u_s), and year (u_y). We used a log-normal distribution to describe the variation in observed growth ($\text{obs}_{i,j,s,y}$) around predicted growth:

$$\text{obs}_{i,j,s,y} \sim \text{lognormal}(\text{pred}_{i,j,s,y}, \sigma_{p,j}) \quad (4)$$

Mortality responses to SWP were modelled using a logistic version of Equation 3 and a Bernoulli distribution in Equation 4. The mortality model did not include a random effect for individual, because we evaluated mortality just once for each individual. For each species, we assessed the fit of the model by plotting growth and mortality observations and model predictions against SWP and height. Species responses to SWP and height were significant when their 95% credible interval (CI) excluded zero. We tested for an interaction between the effect of SWP and height, but the added interaction term ($\beta_{3,j} \times \text{SWP}_{i,s} \times \ln(H_{i,y})$) was not significant for any species in the growth or mortality model.

The second (species-level) regression of the models related growth or mortality responses to SWP ($\beta_{1,j}$) to distributional centres observed along the SWP gradient (D_j) across species:

$$D_j \sim \text{normal}(\gamma_0 + \gamma_1 \times \beta_{1,j}, \sigma_d) \quad (5)$$

The Bayesian framework correctly accounts for uncertainty in $\beta_{1,j}$ (Clark, 2005; Ellison, 2004). To test if demographic responses were significantly related to the distributional centres (question 1,

see Section 1), we computed the 95% CI of the slope (γ_1). If the 95% CI did not include zero, the relationship was significant.

We ran additional Bayesian models to test if the link between demographic responses of species and their distributional centres (i.e., the species-level regression) was robust. To assess if relationships between growth responses to SWP and distributional centres emerged among first-year seedlings or only later, we ran a model with only first-year growth observations. This model also allowed for a more direct comparison with the first-year mortality results. We also tested for a potential bias in the relationship between demographic responses and distributions that might occur through an interaction between drought sensitivity of species and their vulnerability to pathogens or herbivory (Jactel et al., 2012; Oliva, Stenlid, & Martínez-Vilalta, 2014). To do this, we retained seedlings visibly damaged by animals or infected by pathogens in the growth and mortality models.

To detect a potential bias in the growth–distributions relationship resulting from excluding growth ≤ 0 , we ran all growth models including growth ≤ 0 . Negative growth can be caused by herbivory or falling debris (Delissio & Primack, 2003), die back caused by pathogens or drought (Gerhardt, 1996), or measurement error. Thus, many instances of negative growth are likely not a response to moisture availability. Positive growth most likely comes from faster growing seedlings that have a higher chance to survive and contribute to species distributions (Rozendaal, Brienen, Soliz-Gamboa, & Zuidema, 2010). Overall, models including only positive growth and models including growth ≤ 0 gave similar results, but as expected, including negative growth rates increased unexplained variation and diluted main effects (see Supporting Information Appendix S3).

Finally, we evaluated whether calculating distributional centres based on single censuses vs. all observations across all censuses affected relationships between demographic responses and distributional centres. To do this, we performed 10 growth and mortality models with distributional centres calculated from the 10 single censuses with the most individuals and included species with ≥ 20 individuals in the selected census. We also performed growth and mortality models for the median of distributional centres of all single censuses.

For each growth and mortality model, we calculated the proportion of explained variance (R^2) following Gelman and Hill (2007) (Supporting Information Appendix S4.1). Additionally, we evaluated possible phylogenetic signal among the residuals of the species-level regression between distributional centres and demographic responses for each model. As there was no phylogenetic signal except for the first-year growth models, we did not consider it further (see Supporting Information Appendix S4.2 for details). Supporting Information Appendix S4.1 provides implementation procedures and model code. The Bayesian models were implemented in the Bayesian inference software package RSTAN version 2.16.2 (Stan Development Team, 2017).

2.5 | Testing the “best at home” and “home advantage” hypotheses

To evaluate the “best at home” and “home advantage” hypotheses (question 2 and 3, see Section 1), we first used our models to

calculate growth and mortality for each species at a standardized size (10 cm height) at dry and wet sites. We defined dry and wet sites as the 10th percentile driest and wettest site along the SWP gradient, having median SWP of -0.75 MPa and -0.06 MPa respectively. We then classified species using three different thresholds. We classified species with a distributional centre among the 25%, 33%, or 50% of driest (or wettest) distributional centres as dry (or wet) distributed (see Figure 1). This classification does not imply that these species were significantly associated with the SWP gradient, which we tested separately using null models (see Section 2.3). To evaluate the “best at home” hypothesis, we compared performance “at home” (e.g., at dry sites for dry distributed species) and performance “away from home” (e.g., at wet sites for dry distributed species), using a paired *t*-test. For the “home advantage” hypothesis, we compared performance “at home” with performance “away from home” for the same sites (e.g., performance of dry distributed species and wet distributed species for dry sites respectively), using Welch's unequal variances *t*-test. We weighted both *t*-tests by the uncertainty in the calculated growth or mortality rates. For each species j , we determined these weights ($weight_j$) by drawing 1,000 random samples from the posterior distribution of $\beta_{0,j}$, $\beta_{1,j}$, and $\beta_{2,j}$ and calculating growth or mortality 1,000 times with these estimates as described above. We used the difference between the 2.5th and 97.5th percentile of these randomly fitted growth or mortality rates ($width_j$) as a measure of uncertainty and determined weights as:

$$weight_j = 1 - \frac{width_j}{\max(width)} \quad (6)$$

The weight of the species with the largest uncertainty (i.e., largest $width_j$) was set to half the weight of the species with the second largest uncertainty (instead of zero). All analyses were conducted in R version 3.4.1 (R Core Team, 2017).

3 | RESULTS

3.1 | Soil water potential

SWP measurements ranged from -2.45 MPa to 0.00 MPa (saturation), and the medians per site ranged from -1.57 MPa to 0.00 MPa. Measurements taken at the same sites but during different sampling rounds were positively correlated among all rounds (February, March, April 2015, and March 2016, $p < 0.001$, Supporting Information Figure S1.3). Thus, relative differences in SWP were temporally consistent across sites and therefore likely reflected spatial variation throughout the seedling census period (1994–2014). Comparison of our SWC values with those from a nearby location where SWC is measured once every 2 weeks showed that we captured the peaks of the 2015 and 2016 dry seasons (Supporting Information Figure S1.4). SWP measurements were positively correlated across depths (15, 40, and 100 cm, $p < 0.001$, Supporting Information Figure S1.5), indicating that measurements at 15 cm depth represented variation in deeper soil layers.

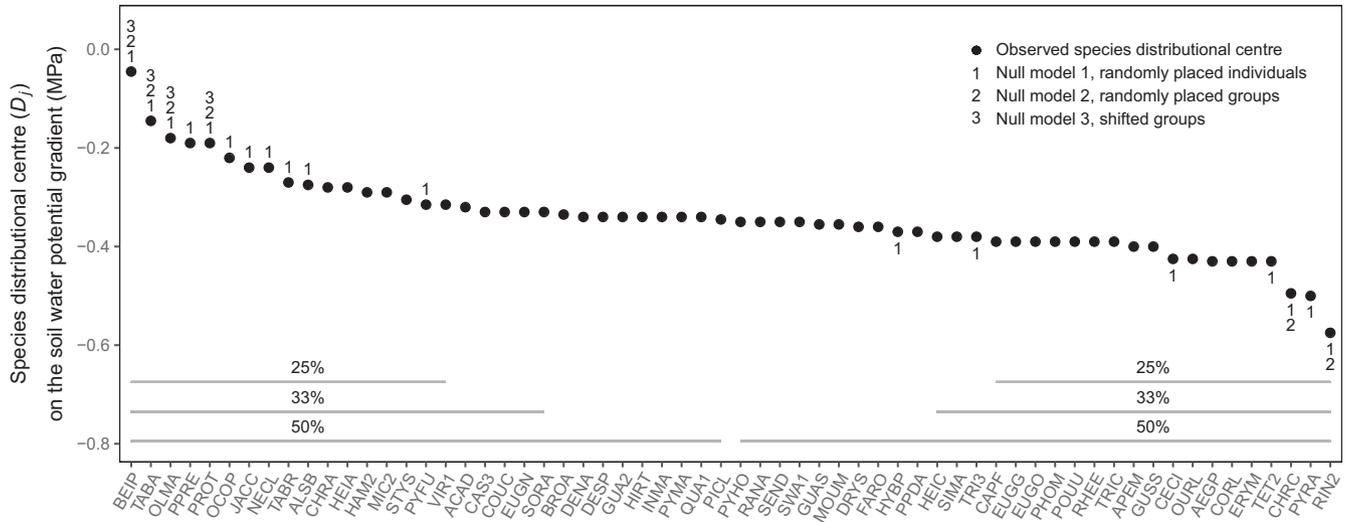


FIGURE 1 Distributional centres (D_j) of species on the local soil water potential (SWP) gradient. Species on the left side (SWP less negative) occur mostly on the wetter end of the gradient and species on the right side (SWP more negative) occur mostly on the drier end. Distributional centres are the median SWP of the sites where the seedlings of the respective species occurs. Numbers indicate species that have distributional centres outside of the 95% confidence interval of randomized values (see Section 2.3). Horizontal lines identify species with the wettest or driest 25%, 33%, or 50% of distributional centres. The 62 species each had ≥ 100 positive growth and/or ≥ 100 mortality records. Table S4 provides a key to full species names for the four-letter mnemonics along the horizontal axis

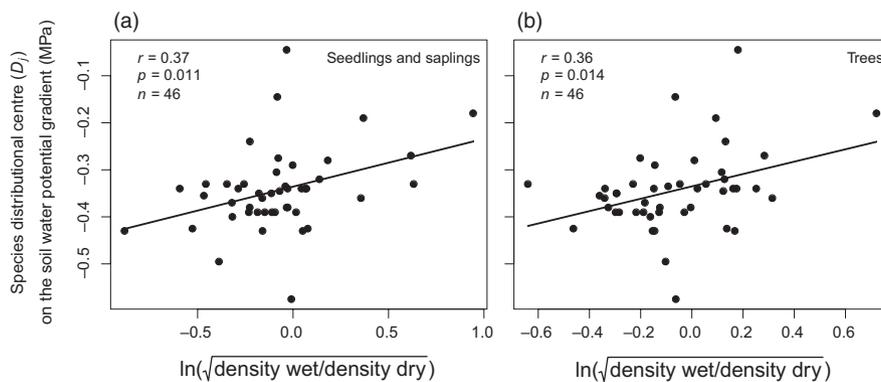


FIGURE 2 Relationships between relative densities of (a) seedlings and saplings (≥ 20 cm tall and < 1 cm dbh) and (b) trees (≥ 1 cm dbh) in wet vs. dry habitats and seedling distributional centres on the soil water potential (SWP) gradient (i.e., median species distribution, D_j , see Section 2.3). Relative densities were calculated from densities in wet habitats (slopes, streamsidcs, and swamp combined) relative to dry habitats (high and low plateau combined, data adapted from Comita et al., 2007, see Equation 1 in Section 2.3). Solid lines represent significant relationships ($p < 0.05$).

3.2 | Distributional associations and demographic responses to SWP

Species' distributional centres along the SWP gradient ranged from -0.58 to -0.05 MPa (Figure 1, Supporting Information Table S4). Distributional centres of 18 of the 62 species (29.0%) differed significantly from random expectations using the first null model based on random shuffling of individuals, with 11 species being more abundant at wetter sites and seven species at drier sites (Figure 1). Likewise, 18 species exhibited significantly narrower or wider distributional spread along the SWP gradient (i.e., lower or higher SD) than expected, with 14 species being more restricted and four more widespread (Supporting Information

Figure S1.6). Using the second and third null model, six and four species, respectively, had observed distributional centres that differed significantly from random distributions (Figure 1). Observed distributional spreads differed significantly from random expectations for four species in the second as well as in the third null model (Supporting Information Figure S1.6). Distributional centres of seedlings along the continuous SWP gradient were positively correlated with the relative densities of larger seedlings and saplings (≥ 20 cm tall and < 1 cm dbh) and trees (≥ 1 cm dbh) in wet vs. dry habitats across the 50-ha plot (Figure 2, data from Comita et al., 2007).

Nine of the 62 species (14.5%) showed a significant demographic response to SWP (Supporting Information Figures S4

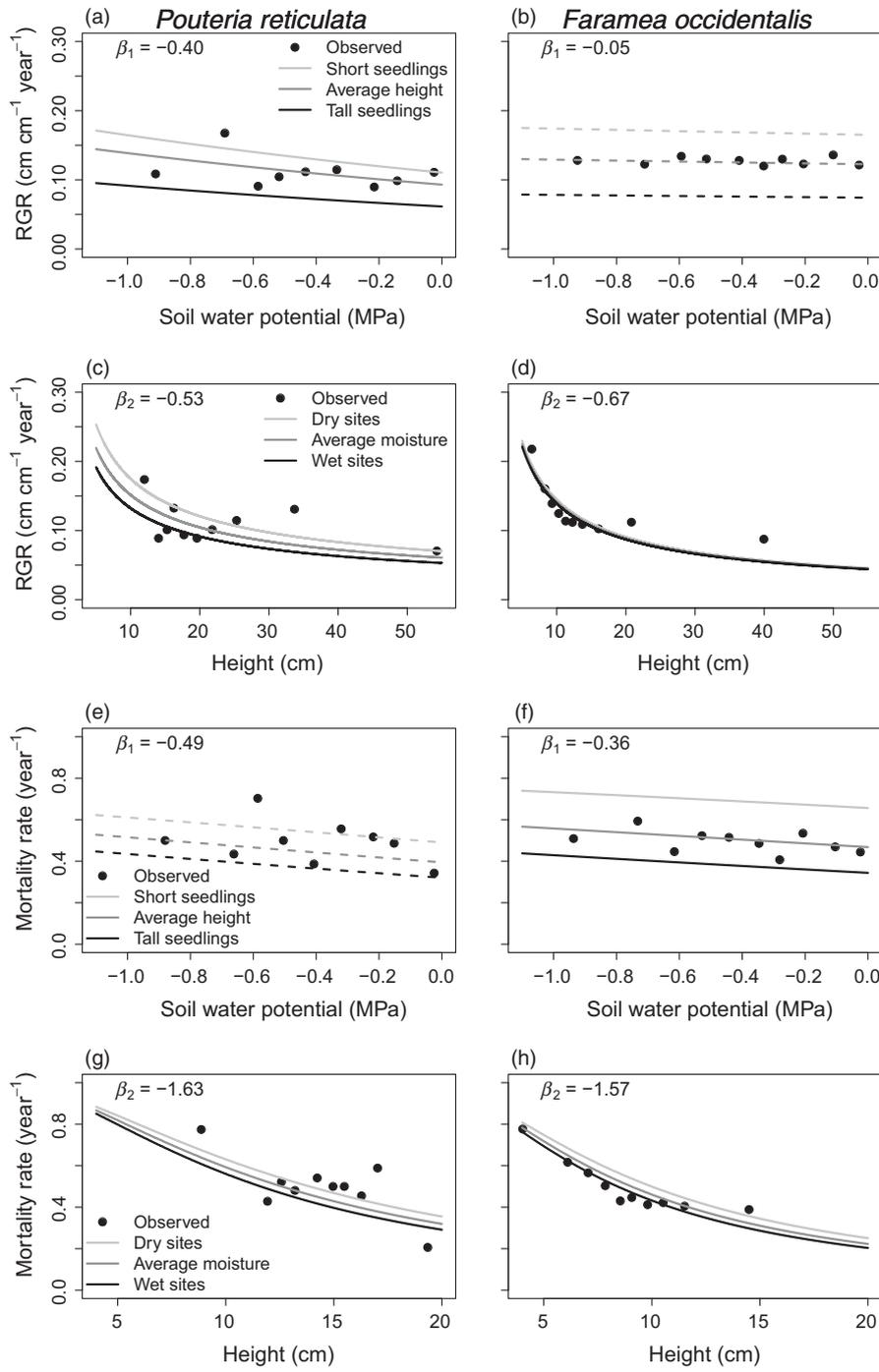


FIGURE 3 Relationships between RGRs (a–d), first-year mortality rates (e–h), and dry-season soil water potential (SWP; a, b, e, f) and seedling height (c, d, g, h) for seedlings of *Pouteria reticulata* (left panels) and *Faramaea occidentalis* (right panels). Dots represent mean observed growth or mortality for 10 moisture (a, b, e, f) or 10 height (c, d, g, h) classes, each containing 10% of the individuals of the species. Lines show fitted growth and mortality responses to SWP for three levels of seedling height (short, average, tall; a, b, e, f), and responses to seedling height for three levels of SWP (dry, average, wet; c, d, g, h). Levels correspond to the 10th, 50th, and 90th percentile of height or SWP for each species. Solid lines indicate significant responses and dashed lines indicate non-significant responses. Each panel presents the fitted slope of the response (β_1 or β_2)

and S5). Four species responded significantly to SWP in terms of growth; three grew significantly slower with increasing moisture and one grew significantly faster (Supporting Information Table S5). Five species had significant mortality responses; four had lower mortality and one had higher mortality with increasing moisture (Supporting Information Table S6). None of the species responded significantly to SWP for both growth and mortality. In all species, growth and mortality decreased significantly with seedling height (Supporting Information Tables S5 and S6). Figure 3 illustrates demographic responses to dry season SWP and seedling height for two common species, one with significantly

slower growth (*Pouteria reticulata*, Figure 3a) and one with significantly lower mortality (*Faramaea occidentalis*, Figure 3f) at wetter sites. Over all species, the variation explained (R^2) was 0.30 for the growth model and 0.12 for the mortality model.

3.3 | The link between demographic responses and species distributions

The distributional centres of species along the SWP gradient were significantly positively related to growth responses to SWP (Figure 4a; γ_1 in Equation 5). Species with positive growth responses

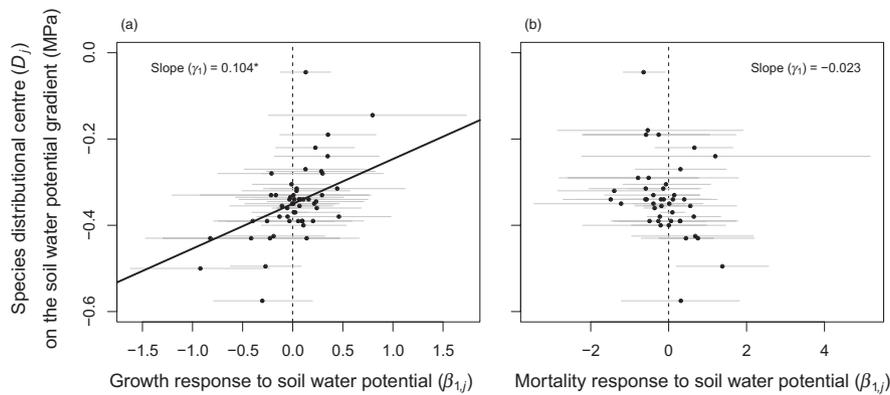


FIGURE 4 Relationships between distributional centres on the local soil water potential (SWP) gradient and (a) growth and (b) mortality responses of seedlings to SWP. Distributional centres on the SWP gradient are the median SWP of the sites where the species occurs (D_j , see Section 2). The growth and mortality responses are fitted species-specific slopes for relationships between SWP and each demographic rate ($\beta_{1,j}$, see text Equation 3). Horizontal grey lines represent the 95% credible intervals (CI) of $\beta_{1,j}$. The relationship between distributional centres and SWP responses is the slope of a linear regression fitted in the Bayesian models (γ_1 , see text Equation 5), which is significant for growth rates (a) but not for mortality rates (b)

to SWP tended to have their distributional centres at wetter sites (higher SWP), and species with negative growth responses tended to have their distributional centres at drier sites (lower SWP).

In the models with only first-year growth, the positive relationship between distributional centres and growth responses was marginally significant (i.e., the 90% CI of γ_1 did not include zero, see Supporting Information Table S1.1). In the growth model that included observations with fungal infections or damage by animals, the relationship was significantly positive (Supporting Information Table S1.1). When including growth ≤ 0 , the relationship was significant (and marginally significant) when seedlings affected by pathogens and herbivores were included (and excluded) and non-significant for only first-year growth (Supporting Information Figure S3.1, Supporting Information Table S1.1). Distributional centres were not related to first-year mortality responses to SWP (Figure 4b, Supporting Information Table S1.1).

Distributional centres based on single censuses were significantly or marginally significantly positively related to growth responses for seven of 10 censuses (Supporting Information Table S1.2). The relationship between mortality responses and distributional centres based on single censuses was only once marginally significantly negative, that is, species with a more negative mortality response to SWP expectedly tended to be more abundant at wetter sites (Supporting Information Table S1.2). The median of the distributional centres of all single censuses was significantly positively related to growth but not related to mortality (Supporting Information Table S1.2).

3.4 | The “best at home” and “home advantage” hypotheses

Wet distributed species grew significantly faster at wet sites than at dry sites (for all distribution thresholds; Figure 5a, Table 1). This is consistent with the “best at home” hypothesis. Dry distributed species did not grow faster at dry sites (Figure 5a, Table 1). The wettest

distributed 33% and 50% of species grew significantly faster at wet sites than the driest distributed 33% and 50% of species, and the wettest distributed 25% of species grew marginally faster at wet sites than the driest distributed 25% of species (Figure 5b, Table 2). This is consistent with the “home advantage” hypothesis. Dry distributed species did not have a “home advantage” in terms of growth (Figure 5b, Table 2). Patterns weakened when negative growth was included (see Supporting Information Tables S3.1–S3.2 for details). For mortality, only the wettest distributed 50% of species performed marginally significantly better “at home” (Figure 5c, Table 1). We found no evidence for a “home advantage” for mortality (Figure 5d, Table 2).

4 | DISCUSSION

We explored the roles of growth and mortality responses to SWP in shaping local species distributions of naturally regenerating seedlings. Growth responses to SWP were positively related to distributional centres of species along the SWP gradient. Species that were more abundant at wetter sites grew faster there (“best at home”) and outgrew species that were more abundant at drier sites (“home advantage”). In contrast, we found little evidence that first-year mortality responses to SWP affected species distributions. Instead, we propose that growth responses to SWP indirectly shape local species distributions, because growth advantages increase seedling size and thereby decrease mortality risk in later seedling stages. In this way, growth responses to SWP promote niche differentiation along gradients of soil water availability.

4.1 | Growth responses to soil water potential contribute to species distributions

As expected, we found that species with a more positive (negative) growth response to SWP were more abundant at wetter (drier) sites

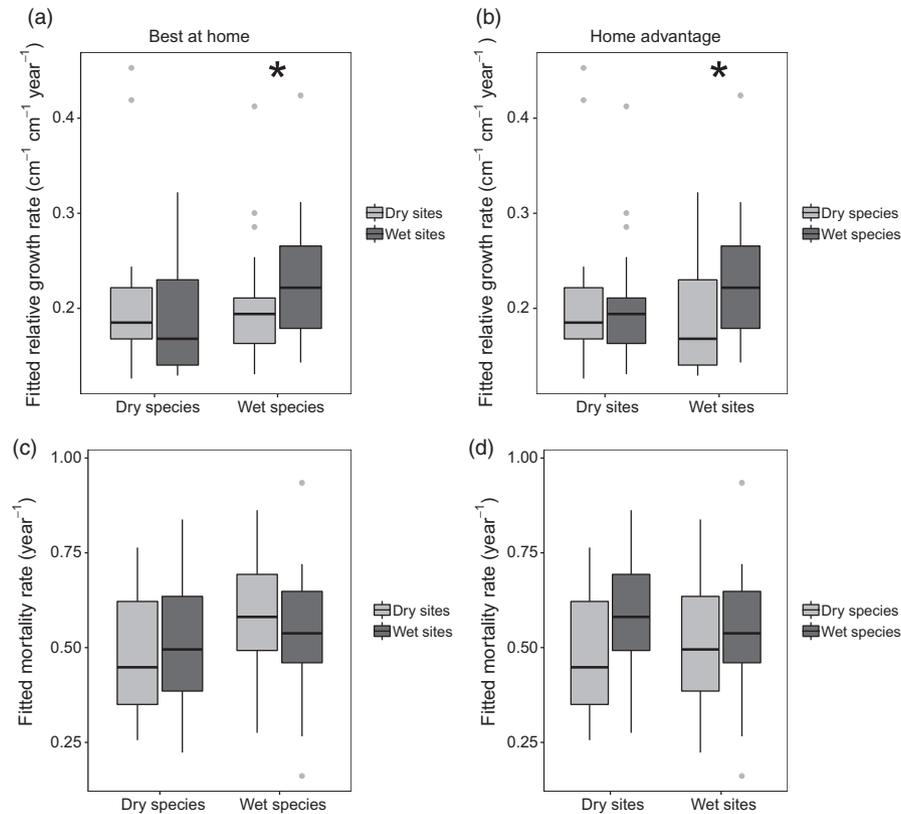


FIGURE 5 Tests of the “best at home” and “home advantage” hypotheses. For the “best at home” hypothesis (a, c), the box and whisker plots are for dry and wet distributed species (separated along the horizontal axis) and compare performance at dry vs. wet sites (light vs. dark shaded boxes, respectively). For the “home advantage” hypothesis (b, d), the box and whisker plots are for performance at dry or wet sites (separated along the horizontal axis) and compare performance of dry vs. wet distributed species (light vs. dark shading respectively). Shown is performance of dry and wet distributed species, which have a distributional centre that is among the 33% of driest or wettest distributional centres respectively (see Figure 1). Dry and wet sites were defined as the 10th percentile driest and wettest site along the soil water potential gradient respectively. Asterisks identify significant performance differences ($p < 0.05$). Tables 1 and 2 present results for the 25%, 33%, and 50% of driest and wettest distributed species.

(Figure 4a). In addition, species that were more abundant at wet sites grew faster “at home” (Figure 5a) and had a “home advantage” over dry distributed species (Figure 5b). Seedlings of species with such a growth advantage become taller than seedlings of species with slower growth. As we found that mortality rates declined rapidly with seedling height for all species (Green, Harms, & Connell, 2014; Rose & Poorter, 2003), a growth advantage allows seedlings to escape the vulnerable small seedling stage more rapidly (Kitajima & Fenner, 2000) than seedlings of other species. Experiments have documented species-specific responses of seedling growth to water availability (Ashton et al., 1995; Baltzer & Davies, 2012; Born et al., 2015; Bunker & Carson, 2005; O’Brien, Ong, & Reynolds, 2017; O’Brien, Philipson, Tay, & Hector, 2013; Yavitt & Wright, 2008). Our study is the first to show that differential growth responses of naturally regenerating seedlings contribute to local species distributions along a gradient of soil water availability.

The significant relationship between the growth responses of species to SWP and their distributional centres along the SWP gradient emerged from mostly non-significant growth responses to soil moisture at the within-species level. Just four of 53 species showed significant growth responses to SWP. There are several possible

reasons for the lack of significant within-species responses. First, spatial differences in SWP among sites are likely subtle compared with other tropical forests due to the rather homogeneous topography of the BCI 50-ha plot (Brown et al., 2013; John et al., 2007). Second, seed dispersal limits seedling occurrence across the SWP gradient (Hubbell et al., 1999; Muller-Landau, Wright, Calderón, Condit, & Hubbell, 2008). For example, few seeds disperse to dry sites for species whose reproductive adults are restricted to wet sites. Dispersal limitation limits our ability to assess performance “away from home.” Third, many species had relatively small overall sample sizes, which further increased uncertainty in SWP responses (Supporting Information Figure S1.7) and decreased the likelihood of detecting statistically significant responses (Supporting Information Figure S1.8). Nonetheless, the fitted slopes of the relationship between growth and SWP represent the best estimates of the magnitude of species’ growth response to SWP (i.e., effect sizes, Nakagawa & Cuthill, 2007). These responses were significantly related to species distributions along the SWP gradient.

Surprisingly, three of the four species with significant growth responses to SWP grew slower at wetter sites. At wetter sites, higher pathogen pressure, anoxic conditions due to waterlogging in the wet

TABLE 1 Test of the “best at home” hypothesis. Shown are fitted growth or mortality rates of dry and wet distributed species at dry vs. wet sites. Bold values indicate significantly different mean performance ($p < 0.05$), and the italic value indicates marginally significantly different mean performance ($0.05 \leq p < 0.10$).

	Classification dry/wet species ^a	Dry sites ^b	Wet sites ^b	<i>t</i>	<i>df</i>	<i>p</i>
		Mean (SD)	Mean (SD)			
Growth						
Dry distributed species	50%	0.209 (0.077)	0.195 (0.059)	0.933	27	0.359
	33%	0.209 (0.087)	0.185 (0.056)	1.327	18	0.201
	25%	0.215 (0.093)	0.181 (0.048)	1.603	15	0.130
Wet distributed species	50%	0.209 (0.062)	0.228 (0.059)	-3.427	24	0.002
	33%	0.208 (0.071)	0.231 (0.068)	-2.915	16	0.010
	25%	0.203 (0.077)	0.237 (0.077)	-3.187	11	0.009
Mortality						
Dry distributed species	50%	0.478 (0.159)	0.494 (0.158)	-0.880	20	0.389
	33%	0.478 (0.172)	0.519 (0.172)	-1.724	13	0.108
	25%	0.492 (0.183)	0.534 (0.182)	-1.661	11	0.125
Wet distributed species	50%	0.544 (0.165)	0.498 (0.182)	1.800	21	0.086
	33%	0.577 (0.167)	0.536 (0.190)	1.396	14	0.184
	25%	0.611 (0.166)	0.578 (0.175)	0.897	11	0.389

^aEach analysis was repeated contrasting the 25%, 33%, or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Figure 1). ^bDry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient respectively.

TABLE 2 Test of the “home advantage” hypothesis. Shown are fitted growth or mortality rates of dry vs. wet distributed species at dry and wet sites. Bold values indicate significantly different mean performance ($p < 0.05$), and the italic value indicates marginally significantly different mean performance ($0.05 \leq p < 0.10$).

	Classification dry/wet species ^a	Dry distributed species	Wet distributed species	<i>t</i>	<i>df</i>	<i>p</i>
		Mean (SD)	Mean (SD)			
Growth						
Dry sites ^b	50%	0.209 (0.077)	0.209 (0.062)	-0.715	48.332	0.478
	33%	0.209 (0.087)	0.208 (0.071)	-0.676	29.170	0.504
	25%	0.215 (0.093)	0.203 (0.077)	-0.405	18.421	0.690
Wet sites ^b	50%	0.195 (0.059)	0.228 (0.059)	-2.106	49.759	0.040
	33%	0.185 (0.056)	0.231 (0.068)	-2.086	28.687	0.046
	25%	0.181 (0.048)	0.237 (0.077)	-1.805	16.468	0.089
Mortality						
Dry sites	50%	0.478 (0.159)	0.544 (0.165)	-1.358	40.665	0.182
	33%	0.478 (0.172)	0.577 (0.167)	-1.639	26.971	0.113
	25%	0.492 (0.183)	0.611 (0.166)	-1.607	21.999	0.122
Wet sites	50%	0.494 (0.158)	0.498 (0.182)	-0.202	39.462	0.841
	33%	0.519 (0.172)	0.536 (0.190)	-0.361	26.532	0.721
	25%	0.534 (0.182)	0.578 (0.175)	-0.836	21.924	0.412

^aEach analysis was repeated contrasting the 25%, 33%, or 50% of species with the most extreme distributions based on their distributional centres on the soil water potential (SWP) gradient (see Figure 1). ^bDry and wet sites were defined as the 10th percentile driest and wettest site along the SWP gradient respectively.

season, or lower light conditions may limit growth (Brenes-Arguedas, Roddy, Coley, & Kursar, 2011; Gaviria et al., 2017; Lopez & Kursar, 2003; Spear, Coley, & Kursar, 2015). Indeed, sites with higher SWP

were more shaded ($r = 0.27$, $p < 0.001$; Supporting Information Table S1.3, shade data from Condit, 2018). Thus, low light availability likely limited growth in wetter sites. Wetter sites also had lower

Mg ($r = -0.16$, $p = 0.03$) and N ($r = -0.25$, $p < 0.001$; Supporting Information Table S1.3, nutrient data from Wolf, Hubbell, Fricker, & Turner, 2015). However, a fertilization experiment near BCI showed that Mg did not limit seedling growth and that N only limited growth in combination with P (Santiago et al., 2012), suggesting that it is unlikely that lower Mg and N availability caused negative growth responses to higher SWP in the 50-ha plot.

Comita and Engelbrecht (2009) compared performance and distributions of larger seedlings (20–50 cm tall) for slopes (wet) and plateaus (dry) in the BCI 50-ha plot and found no evidence for the “best at home” and “home advantage” hypotheses for growth. We improved on their dichotomy of wet vs. dry sites. We used the most appropriate measure of soil water availability for plants (SWP) and resolved variation in soil water availability within plateaus and slopes (see Supporting Information Figure S1.1). This highlights the importance of small-scale soil moisture gradients in structuring plant communities (Araya et al., 2011).

Growth responses to water availability may also affect regional distributions of species along a rainfall gradient from the drier Pacific to wetter Caribbean coasts of central Panama. Although species common to dry forests in Southeast Asia and Amazonia often occur in wet forests as well (Baltzer et al., 2007; Esquivel-Muelbert et al., 2017), species turnover in Panama is strong, that is, dry forest species are often absent from wet forests (Condit et al., 2013; Jones et al., 2013; Pyke, Condit, Aguilar, & Lao, 2001). Reciprocal transplant experiments suggest that inherently slower growth rates may prevent dry forest species from colonizing wet forests in Panama (Brenes-Arguedas et al., 2009; Gaviria & Engelbrecht, 2015; Gaviria et al., 2017). Thus, wet forest species may have a “home advantage” in terms of growth over dry forest species at the regional scale.

4.2 | The role of mortality in shaping species distributions

Unexpectedly, the distributions of species along the SWP gradient were not related to first-year mortality responses to SWP (Figure 4b). We also found little evidence for species having lower mortality rates “at home” (Table 1) and we found no evidence for a “home advantage” (Table 2). These results indicate that the role of first-year mortality responses to SWP in shaping species distributions was relatively minor, even though experiments suggest that first-year mortality influences distributions with respect to variation in water, nutrient, and light availability (Baltzer & Davies, 2012; Engelbrecht & Kursar, 2003; Engelbrecht, Kursar, & Tyree, 2005; Lucas, Bruna, & Nascimento, 2013). Contrasting with our results, larger seedlings (20–50 cm tall) of dry-associated species had lower mortality than wet-associated species in the same 50-ha plot, particularly on the dry plateau (i.e., “home advantage”) in a severe dry season (Comita & Engelbrecht, 2009).

There are several possible explanations for why we did not find a clear link between mortality responses to SWP and species distributions. First, our study spanned 21 years including many years with mild dry seasons, during which differences in mortality rates

between dry and wet distributed species are likely less pronounced (Comita & Engelbrecht, 2014) than in years with severe dry seasons (Comita & Engelbrecht, 2009; Condit, Hubbell, & Foster, 1995). Accordingly, the population of drought-sensitive species may have recovered after droughts (Condit, Pérez, Lao, Aguilar, & Hubbell, 2017) at drier sites. Second, small seedlings are more vulnerable than tall seedlings to various causes of mortality besides resource availability, such as falling debris or herbivory (Rose & Poorter, 2003) and negative distance or frequency dependence (Green et al., 2014; Murphy, Wiegand, & Comita, 2017), which may have diluted the effect of water availability on mortality of the first-year seedlings in our study. Third, the annual censuses did not allow us to distinguish between dry and wet season mortality, which probably also diluted the signal of drought-induced mortality that is concentrated in the dry season (Comita & Engelbrecht, 2014).

4.3 | Implications for niche differentiation

We found evidence for spatial niche differentiation along the SWP gradient within the BCI 50-ha plot, as indicated by significant associations of distributional centres with the dry and wet end of the SWP gradient (Figure 1) and by the larger number of species with restricted rather than widespread distributions along the SWP gradient (Supporting Information Figure S1.6). However, in null models that took spatial clustering within and among sites into account, the number of significant distributional associations declined considerably. This indicates that dispersal limitation, often responsible for aggregation of individuals (Detto & Muller-Landau, 2013), caused seedlings of many species to occur in clumps that were not associated with the moisture gradient. Dispersal limitation, therefore, also played an important role in shaping the seedling distributions (Hubbell et al., 1999; Muller-Landau et al., 2008).

Seedling distributions along the SWP gradient were correlated with the distributions of larger seedlings and saplings and trees across wet slope vs. dry plateau habitats in the 50-ha plot (Figure 2), indicating that species associations to soil water availability arise early and hold across life stages. In contrast, previous studies found that habitat associations vary strongly between early and late life stages (Comita et al., 2007; Webb & Peart, 2000). However, these studies focused on significant topographic habitat associations of species (across life stages), whereas we compared relative positions on a soil water gradient (SWP and wet vs. dry habitats) among species. This allowed us to identify a consistent distributional signature of hydrological niche differentiation across life stages.

We speculate that a “home advantage” is a more important demographic signature of niche differentiation than “best at home” performance, because niche differentiation takes place when a species is superior to competitors at a specific location on a niche axis (Kawecki & Ebert, 2004; Silvertown, 2004). As we found a “home advantage” for growth but not mortality, this further suggests that growth responses to water availability shape species distributions along the SWP gradient.

5 | CONCLUSIONS

By quantifying a detailed gradient of SWP, we found that subtle interspecific differences in growth responses to SWP influenced species distributions across a naturally regenerating seedling community. Our findings emphasize the value of measuring small-scale spatial differences in SWP for studying the mechanisms driving hydrological niche differentiation. Future studies may test which traits that determine drought sensitivity, such as leaf water potential at turgor loss and embolism resistance (Anderegg et al., 2016; Bartlett, Scoffoni, & Sack, 2012), drive demographic responses to SWP. Such studies will improve predictions of compositional changes in tropical forests due to shifting rainfall patterns caused by climate change (Choat et al., 2018; IPCC, 2014).

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AUTHORS' CONTRIBUTIONS

S.J.K., N.R., B.M.J.E., S.J.W., and C.W. conceived the study. S.J.W. and A.H. designed and performed the seedling censuses. S.J.K. conducted the soil water potential measurements, analysed the data, and wrote the manuscript with input from N.R., B.M.J.E., S.J.W., and C.W.

DATA ACCESSIBILITY

Soil moisture data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1023m1d> (Kupers et al., 2018). Seedling data are available via ForestGEO (<https://forestgeo.si.edu/research-programs/flowers-seeds-and-seedlings-initiative>, ForestGEO, 2018). Hydrological and meteorological monitoring data are available from http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado (STRI, 2018).

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SUPPORTING INFORMATION

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