

Drivers of tree species distribution across a tropical rainfall gradient

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Abstract. Understanding the factors shaping species distribution patterns along tropical rainfall gradients is necessary to predict the consequences of climate change for tropical tree communities. Direct effects of water availability exclude wet forest species from dry forests, but the exclusion of dry forest species from wet forests remains unexplained. We tested the hypothesis that high light and nutrient requirements exclude dry forest species from dark, infertile, wet forests. We transplanted seedlings of 26 woody species to six sites along a pronounced regional rainfall gradient across the Isthmus of Panama. We examined the effects of soil moisture, phosphorus and light availability, and species' drought resistance on seedling performance, and linked the results directly to known species distribution patterns. Surprisingly, seedlings of wet forest species did not exhibit a home advantage: All species survived better under moister conditions, and the effects of phosphorus availability and light on seedling performance did not differ among species from dry or wet forests. Instead, dry forest species had intrinsically slower growth rates than wet forest species, which may lead to their exclusion from wet forests at later life history stages. High phosphorus exacerbated susceptibility to drought, although the mechanism remains unknown. Overall, our results demonstrate that seedling performance across tropical rainfall gradients is determined primarily by variation in soil water availability across space and time, while variation in nutrient and light availability plays a lesser role. Future changes in rainfall patterns will therefore have direct and pervasive consequences for forest composition and ecosystem function.

Key words: climate change; growth; habitat association; Panama; population dynamics; precipitation; regeneration; soil moisture; survival; water availability.

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INTRODUCTION

Tropical forests are among the most diverse plant communities on earth. The controls of diversity and species distribution patterns in such species-rich communities remain a central question in ecology. The most prominent pattern of diversity in tropical forests is an increase in species richness (i.e., α -diversity) with increasing rainfall and decreasing dry season length (ter Steege 2003, Davidar et al. 2005). At the same time, the change

in forest composition (i.e., β -diversity) is extremely high along tropical rainfall gradients (Condit 2002) and species distribution patterns vary with rainfall (Swaine 1996, Engelbrecht et al. 2007, Condit et al. 2013). While these patterns are well documented, the underlying causes remain poorly understood. Given that pronounced changes in rainfall are projected for the tropics (Hidalgo et al. 2013, IPCC 2013), with potentially dramatic yet highly uncertain consequences for tree communities (Cook and Vizy 2008, IPCC

2013, Corlett 2016), improvements in our understanding of the mechanisms underlying changes in tropical forest composition with rainfall are urgently needed.

Drought periods have been suggested to act as a filter, excluding drought-sensitive species from drier areas and thus reducing the number of species at a site (physiological tolerance hypothesis, Currie 2004). Pronounced correlations between species' drought resistance and their distribution across tropical rainfall gradients indicate that drought directly shapes species' distribution patterns (reviewed in Comita and Engelbrecht 2013). However, the physiological tolerance hypothesis alone fails to explain a considerable part of the variation in species distribution across tropical rainfall gradients (Engelbrecht et al. 2007), particularly why dry forest species are excluded from wet forests (Condit 2002). Environmental factors that can co-vary with rainfall have been hypothesized to play an important role in shaping distribution patterns across rainfall gradients, including the availability of nutrients (ter Steege 2003, Brenes-Arguedas et al. 2008) and light (Brenes-Arguedas et al. 2011) as well as pest pressure (Baltzer and Davies 2012). The availability of phosphorus, which is considered the nutrient most limiting in tropical forests, generally decreases with increasing rainfall due to leaching (Walker and Syers 1976, Austin and Vitousek 1998). Therefore, species growing in nutrient-rich dry forests have been hypothesized to have higher nutrient requirements, and thus be excluded from nutrient-poor wet forests (ter Steege 2003, Brenes-Arguedas et al. 2008). We refer to this as the nutrient availability distribution hypothesis. A trade-off between plant shade and drought tolerance has been hypothesized (Smith and Huston 1989), and higher understory light conditions are expected in dry than in wet forests (Wright 1992, Brenes-Arguedas et al. 2011). Dry forest species, which are more drought-resistant (Engelbrecht et al. 2007) and occur in higher light environments, should therefore have higher light requirements than wet forest species, leading to the exclusion of dry forest species from wet, dark forests (light availability distribution hypothesis, Brenes-Arguedas et al. 2011). In addition, herbivore pressure has been hypothesized to influence species distribution and community composition by excluding species with low defences from wet

sites with high herbivore pressure (pest pressure gradient hypothesis, Baltzer and Davies 2012).

These long-standing hypotheses are central to pressing ecological questions, yet previous studies of the role of the various factors potentially shaping distribution and diversity patterns across tropical rainfall gradients remain inconclusive (Engelbrecht et al. 2007, Brenes-Arguedas et al. 2008, 2009, 2011, Baltzer and Davies 2012, Gaviria and Engelbrecht 2015, Spear et al. 2015, Fortunel et al. 2016). Correlations between moisture, light, and nutrients make it challenging to separate environmental factors and to test specific hypotheses (Swaine 1996, Condit et al. 2013).

While tropical trees partition local and regional nutrient gradients (John 2007, Condit et al. 2013), and nutrient addition increases plant performance in field experiments (Yavitt and Wright 2008, Wright 2011, Santiago et al. 2012), there is no conclusive evidence that nutrients shape species distributions along rainfall gradients (Brenes-Arguedas et al. 2008). The light availability distribution hypothesis has—to our knowledge—only been specifically tested in one study, which did not find support (Brenes-Arguedas et al. 2011). There is also no convincing evidence to date that wetter forests are consistently darker (Engelbrecht 1998, Harms et al. 2004), that there is a trade-off between drought and shade tolerance in tropical plants (Engelbrecht et al. 2007, Markesteijn and Poorter 2009), or that dry forest species are more light-demanding (Brenes-Arguedas et al. 2011). That pests (pathogens or herbivores) exclude dry forest species from wet forests (Brenes-Arguedas et al. 2009, Baltzer and Davies 2012, Gaviria and Engelbrecht 2015, Spear et al. 2015) has also not yet been conclusively shown. Thus, the factors excluding dry forest species from wet forests and leading to the high β -diversity of tropical forests across rainfall gradients remain unknown.

In this study, we focused on the role of drought, nutrients, and light for species regional distribution patterns across a rainfall gradient. We focused on the seedling stage, which should be especially vulnerable to environmental stressors and is a bottleneck in population dynamics (Harper 1977). We tested the physiological tolerance hypothesis, the nutrient distribution hypothesis, and the light distribution hypothesis. Each of these hypotheses can be separated into two assumptions: First that environmental conditions change, with wet forests

having higher moisture availability, lower nutrient availability, and casting deeper shade than dry forests. Second that dry and wet forest species differ in resource responses, with dry forest species being more nutrient- and light-demanding, and more drought-resistant than wet forest species. Each of these combinations of variation in environmental factors and species resource requirements could lead to a species performance advantage in their respective home range, relative to "foreign" species, and thus exclude foreign species and shape distribution patterns across rainfall gradients.

Overall, we expected an increase in species growth and survival with increasing soil moisture, phosphorus, and light availability. However, we also expected that the effect should differ between species associated with dry vs. wet forests (origin \times environmental factor interaction), leading to a home advantage. Specifically, we expected moisture to have a stronger positive effect on wet forest species, especially in the dry season when water is potentially limiting, and that any observed effects in the field would correlate with independently assessed drought resistance of the species. We further expected phosphorus and light to have a stronger positive effect on dry forest species, and this effect to be especially pronounced in the wet season, when nutrient and light availability are lowest and water is not limiting.

MATERIALS AND METHODS

Study area and forest sites

The study was conducted in lowland tropical forests in Central Panama. Annual rainfall doubles from 1600 mm/yr on the Pacific Coast to more than 3000 mm/yr on the Caribbean Coast, a distance of only 65 km; dry season length correlates negatively with annual rainfall (Engelbrecht et al. 2007, Condit et al. 2013). Soil nutrient availability varies markedly in the region, due in large part to the complex geology (Turner and Engelbrecht 2011, Condit et al. 2013).

We conducted a seedling transplant experiment at six sites spanning the full range of annual rainfall, with three sites in the wetter range and three sites in the drier range (Appendix S1: Table S1, Fig. S1). Sites were mature secondary forests or old-growth forests, ranged from semi-deciduous

to evergreen forests, and included a variety of geological formations including sedimentary and volcanic rocks and associated soils (Turner and Engelbrecht 2011). For brevity, we refer to drier sites as "dry" and the wetter ones as "wet," although all are considered moist tropical forests in the Holdridge system.

Species and plant material

We studied 26 focal woody species from 25 genera in 19 families, including shrubs, small and large trees (Appendix S1: Table S2). Species were chosen based on the following criteria: (1) a wide range of drought resistance, (2) a wide range of distribution patterns with respect to rainfall, and (3) capability to regenerate in the forest understory (i.e., excluding strict pioneers), since shade-tolerant species represent the majority of the species in these forests (Bongers et al. 2005). Based on these criteria, seeds were opportunistically collected in the Panama Canal Watershed, mainly in the Barro Colorado Nature Monument (Appendix S1: Fig. S1), from at least three mother trees per species. Preliminary and ongoing studies indicate that intraspecific variation across populations in the area is minimal compared to interspecific variation (B. M. J. Engelbrecht, F. A. Jones, E. Manzané, and L. S. Comita, *unpublished data*). We included only those species for which we were able to collect enough seeds and germinate sufficient healthy seedlings.

Drought resistance of the species (see Appendix S1: Table S2) was quantified from previous irrigation experiments (Engelbrecht and Kursar 2003, Engelbrecht et al. 2007) as the percent seedling survival in dry relative to irrigated conditions in the forest understory. It thus represents the direct effects of moisture on species performance, with higher values indicating greater drought resistance. Drought resistance of the focal species covered the full range from 0% to 98%. Distribution (referred to as origin in the analyses) was quantified based on occurrence (presence/absence) of the species at 122 inventory sites across the rainfall gradient (Appendix S1: Table S2) following Engelbrecht et al. (2007), with higher (more positive) index values indicating a higher association of the species with dry sites. The distribution index reflects all factors influencing the actual distribution of the species (i.e., abiotic and biotic, deterministic and stochastic, present and

past). Distribution indices ranged from -4 to $+6$ and covered most of the range of common species in the area. We used the distribution index from Engelbrecht et al. (2007), because it covered a broader range from “dry”- to “wet”-origin species for our focal species than other distribution indices (e.g., Condit et al. 2013). The different indices gave qualitatively identical results.

Seeds were collected from May to October 2006 (i.e., rainy season) and germinated in a greenhouse under moderately low light conditions (about 7%) in mixed forest soil. Seedlings were maintained with regular watering until they were transplanted to the forest sites 6–8 weeks before the onset of the dry season (October/November 2006). Species age (1–7 months) and size (4–25 cm height) at the start of the experiment were thus equivalent to those in the natural forest environment. Of initially 3900 seedlings, >85% survived until the first census in December 2006. All mortality prior to the first census was considered a transplanting effect, and those seedlings were excluded from the analyses.

Experimental design

We established 25 seedling plots in each of the six 1-ha forest sites, with one seedling plot located in the center of each 20×20 m grid. Plots were 1.20×1.20 m, with seedlings planted in a 20×20 cm grid. No canopy gaps were present when establishing the plots. One seedling of each species was planted in each plot (i.e., in total 150 seedlings per species), with species assigned randomly to positions, and seedlings assigned randomly to the plots (within species). Bare root seedlings (carefully extracted from the pots onsite) were directly transplanted into the soil. Disturbance of the leaf litter during transplanting was minimized to ensure natural microhabitat conditions.

Monitoring of seedling performance

Seedling performance in terms of growth (based on leaf area) and survival was assessed over one year. Seedling total leaf area and survival were monitored every three weeks from December 2006 to June 2007, and again at the end of the experiment in December 2007.

To assess seedling leaf area, the length and width of every living leaf (or leaflet) was measured. The species-specific relation between leaf length \times width, and leaf area measured with a

leaf area meter (LI-COR 3100, LI-COR Biosciences, Lincoln, Nebraska, USA), determined for at least 15 leaves per species, was used to calculate the total area of each leaf (all $R^2 > 0.83$, see Appendix S1: Table S3). The amount of damage to the leaf area (absent or dead) was estimated in 10% categories for each leaf, and subtracted. For each seedling, we calculated the sum of all single leaves/leaflets for the total seedling leaf area. Survival was assessed by stem color and elasticity. Dead seedlings were maintained in the census, and their status retrospectively changed in the rare cases that any signs of resprouting were detected.

We analyzed seedling performance separately for three time periods: dry season, wet season, and the whole year (see *Analyses* for more details). We defined the dry season as the period between the first strong and consistent decrease in soil moisture until the first census in which a >10% increase in soil moisture was observed followed by another interval of soil moisture increase (Appendix S1: Fig. S2). The wet season lasted from that date to the end of the experiment. Dry and wet season length thus varied among sites, with the dry season lasting between 87 and 129 d and the wet season lasting between 238 and 280 d.

For each time period analyzed (dry season, wet season, annual), relative growth rate based on leaf area (RGR_{LA}) was calculated. Relative growth rate was then calculated as $RGR_{LA} = (LA_{end} - LA_{start}) \times LA_{start}^{-1}$, with LA_{start} and LA_{end} being total leaf area at the beginning and the end of the period. Survival data (0/1) for each time period were directly implemented in the models (see *Analyses*). For comparability with other studies, monthly growth rates were additionally calculated, by dividing through the actual duration of the seasons (compare Appendix S1: Fig. S2). Similarly, we calculated total survival rates and monthly mortality rates for each time period.

Monitoring of environmental conditions

Gravimetric soil water content, light availability in terms of canopy openness, and soil phosphorus concentration were assessed in each seedling plot. Gravimetric soil water content was monitored with every seedling census, canopy openness was determined once at the height of the dry season (March 2007) and once during the wet season (July 2007), and soil phosphorus concentration once in the wet season (August 2007).

Gravimetric soil water and phosphorus contents were determined for the upper 10 cm of mineral soil in a random location in each plot. Fresh weight (FW) and dry weight (DW, after drying to constant weight at 105°C) of the soil samples were determined, and gravimetric soil water content (GW) calculated as $GW = (FW - DW) \times DW^{-1} \times 100$.

Plant available phosphorus was extracted using Mehlich-3 solution (Mehlich 1984), and inorganic phosphate was determined by automated molybdate colorimetry on a Lachat Quik-chem 8500 (Hach Ltd, Loveland, Colorado, USA). Soil phosphorus concentrations of individual plots varied more than 100-fold from 0.1 to 11.4 mg P/kg (Appendix S1: Fig. S3).

Canopy openness (in percent) was assessed with hemispherical photographs (Engelbrecht and Herz 2001). Photographs were taken over the center of each plot at 90 cm height during uniformly cloudy conditions using a Nikon Coolpix P5000 camera with a 183° Fisheye Converter (FC-E8 Fish-Eye Converter Lens; Nikon, Tokyo, Japan). Photographs were analyzed with the program Gap Light Analyzer v2 (Frazer et al. 1999) after manual threshold selection. Overall, canopy openness ranged from 1.8% to 19.4% (Appendix S1: Fig. S3). In the forests of the study area, 2 mol m⁻²/d photosynthetic active radiation, the typical whole-plant light compensation point in shade-tolerant tropical saplings (Baltzer and Thomas 2007), corresponds to about 5% canopy openness (calculated from Brenes-Arguedas et al. 2011). Forty-one percent of our canopy openness values were at or below 5%.

Analyses

The effects of environmental parameters on seedling growth and survival were analyzed both for the entire year, and separately for the dry and the wet season, and related to drought resistance and origin of the species. We based analyses on seasonal as well as annual growth and survival, since we were interested in the overall outcome of processes during the dry season and the wet season or the whole year, and their influence on species distributions.

We initially assessed correlations among the explanatory variables soil moisture, phosphorus, and light availability for each time period, as well as rainfall (Appendix S1: Table S4), origin, and drought resistance. Correlations were weak,

with all $|r| < 0.7$ (Appendix S1: Table S4). Values of $|r| < 0.7$ are typically low enough to prevent collinearity from affecting model estimations (Dormann 2013). We were therefore able to address the seedling performance responses to variation in all three resources (moisture, phosphorus, and light) independently.

One model per performance parameter (survival and RGR_{LA}) and time period (over the dry season, the wet season, and annual) was set up, accounting for the different length of the dry and wet season in each site. Probability of survival was analyzed with generalized linear mixed-effect models (GLMM) using binomial distribution, and growth with linear mixed-effect models (LMM). Random effects were site, plot, and species, with plot nested in site. To account for size dependence of growth rates, we included log initial leaf area as a covariate in the LMM. The explanatory variables (fixed effects) used in every model were soil moisture, soil phosphorus content, canopy openness, species origin, and drought resistance. A main aim of this study was to test for differences in responses to environmental parameters with species origin (see hypotheses); we therefore included the interaction terms origin \times soil moisture, origin \times soil phosphorus, and origin \times canopy openness in every model. We additionally included the interaction soil moisture \times drought resistance, to test whether species drought resistance reduced negative effects of drought. Preliminary analyses showed a strong negative effect of soil phosphorus on species growth and survival. To test whether this pattern is influenced by soil moisture availability, we also included the interaction soil moisture \times soil phosphorus. Addition of this interaction did not qualitatively change the remaining results.

For each respective period, we used the soil moisture parameter most relevant for seedling performance: For dry season soil moisture, we used the minimum values observed in each site (Appendix S1: Fig. S2); for the wet season, we used the average of the wettest wet season months, when soil moisture reached a plateau (December 2006, June 2007, and December 2007, see Appendix S1: Fig. S2); and for the annual analysis, the whole-year average of soil moisture. For canopy openness, we used the respective value for each season, or the average for the annual analysis. Soil moisture and canopy openness measures

Table 1. Effects of soil moisture, soil phosphorus, light (canopy openness), origin, drought resistance of the species, and the logarithm of seedling initial leaf area, as well as their interactions, on seedling survival and growth (RGR_{LA}) for the dry season (a), the wet season (b), and the whole year (c).

Variables	(a) Dry season		(b) Wet season		(c) Annual	
	Survival	RGR_{LA}	Survival	RGR_{LA}	Survival	RGR_{LA}
Moisture	0.040***	0.013**	0.019***	2.4e-3	0.035**	5.2e-3
Phosphorus	-0.433***	-0.103**	-0.086	8.8e-3	-0.449**	-0.195*
Light	-0.111**	-0.023†	0.039	0.073***	-0.128*	2.1e-3
Drought resistance	0.020***	4.7e-3***	0.013***	-6.6e-5	0.032***	-1.3e-3
Origin	0.083**	-0.069***	-0.064†	0.022*	0.014	-0.090*
Log initial leaf area		-0.054***		-5.3e-3		-0.159***
Interactions						
Origin × moisture	-5.3e-4	1.4e-3**	0.001	3.3e-4	0.001	1.8e-3*
Origin × phosphorus	-0.015	1.8e-3	0.010	-3.5e-3	0.009	2.4e-4
Origin × light	0.020	3.4e-3	0.002	6.5e-3	0.024	0.014
Moisture × phosphorus	0.015**	4.3e-3**	0.2e-3	6.5e-4	0.008†	5.5e-3**
Moisture × drought resistance	-6.6e-5	-1.0e-4**	-0.1e-3	-2.2e-5	-0.2e-3*	-8.5e-5

Notes: Given are the slopes of the relations and their significance; bold values are significant at the 0.05 level. The results are based on one model per time period and performance parameter (generalized linear mixed-effect models for survival, linear mixed-effect models for growth) totaling seven models. For non-significant variables that were removed during the model selection process, the slope for their last occurrence in the model is given.

Levels of significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.1$.

were highly correlated between the different time periods (Appendix S1: Table S4).

We checked the normality of the residuals and homogeneity of variances by visual inspection and all tests for over-dispersion passed. Single-term deletion was used to sequentially remove non-significant factors from the model, resulting in a minimum adequate model (Crawley 2007). The results presented in Table 1 are the ones for the minimum model; slopes of non-significant variables show the values of their last occurrence in the model.

All analyses were performed with R version 3.0.2 (R Development Core Team 2013) and the package lme4 1.0-5 (Bates et al. 2013). For the LMM, we assessed P -values using the package lmerTest 2.0-6 (Kuznetsova et al. 2014). Graphs were created with the package LMERConvenienceFunctions 2.5 (Tremblay et al. 2013). For clarity, origin and soil phosphorus content were categorized in the figures, rather than presented as continuous variables.

RESULTS

Environmental conditions

With increasing rainfall, soil moisture increased, while soil phosphorus and canopy openness decreased (Appendix S1: Fig. S3). The increase in

soil moisture with rainfall was strong and significant in both seasons and over the year (all $r > 0.55$, Appendix S1: Fig. S3, Table S4). Soil moisture was significantly higher in the wet than in the dry season in all plots (Appendix S1: Fig. S3) although the dry season during the experimental year was relatively weak and shorter than normal, with more than twice as much rainfall in March, April, and May compared to the long-term average (ESP 2015). The relation with soil phosphorus and canopy openness was much weaker ($r = -0.36$ and r from -0.02 to -0.19 , respectively, Appendix S1: Fig. S3, Table S4), and in the case of phosphorus, mainly driven by two of the sites (P9 and P2, Appendix S1: Fig. S3). The decrease in canopy openness with rainfall was only significant in the wet season (Appendix S1: Table S4), and in four of the sites, canopy openness was significantly lower in the wet than in the dry season (Appendix S1: Fig. S3).

Overall survival and growth rates

Survival and growth varied significantly among species (all $P < 0.001$). In total, 54% (1879/3374) of the seedlings survived until the end of the experiment after one year. Survival throughout the dry and wet season was overall similar, although marginally significantly higher in the wet season (69% and 78%, respectively, $P = 0.047$,

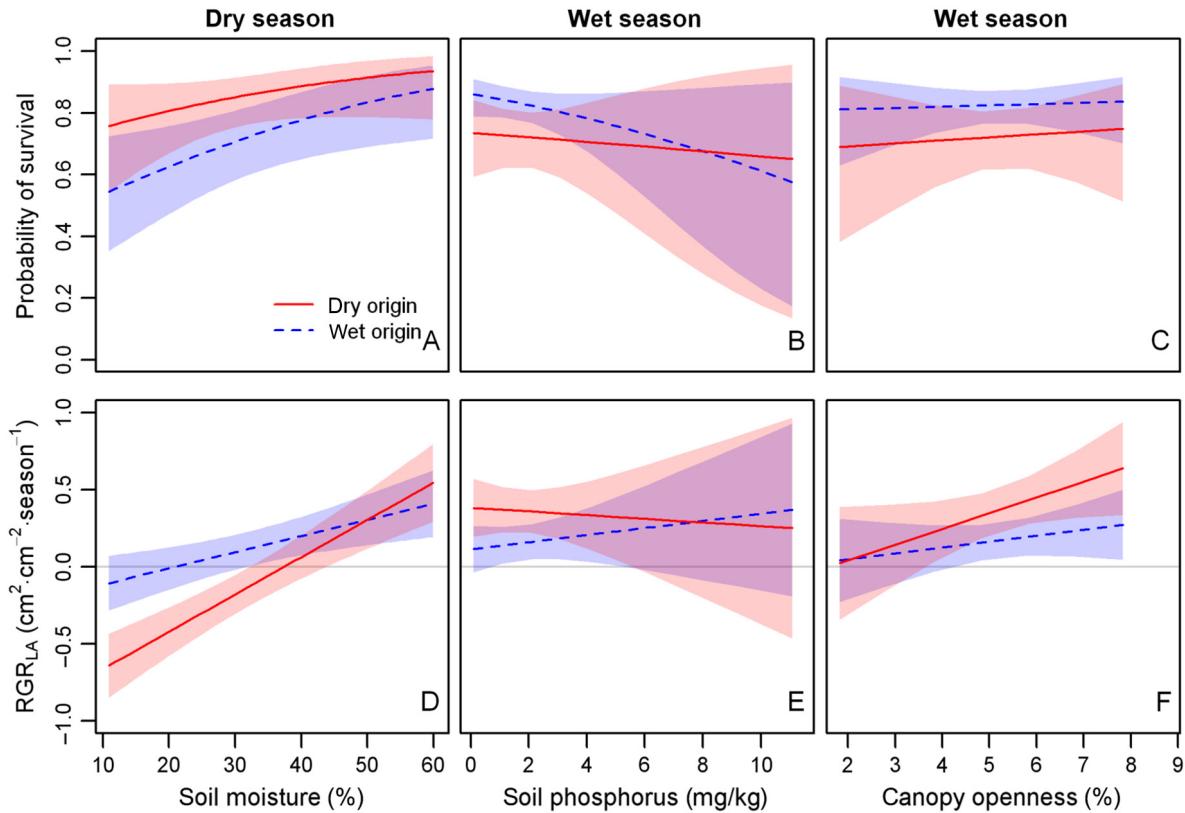


Fig. 1. Relation of seedling performance of wet- and dry-origin species to moisture, phosphorus, and light, in the respective season where they are expected to be most limiting: moisture in the dry season (A, D), and phosphorus (B, E) and light (canopy openness, C, F) in the wet season. Performance is given with respect to survival (A, B, C) and growth (RGR_{LA} , D, E, F). For clarity, origin is represented as a discrete factor (dry: red/wet: blue) instead of continuous variable, as analyzed (Table 1). Shaded bands show the 95% confidence intervals. For significance of the main effects and interactions, see Table 1.

Appendix S1: Table S5). The contrast in monthly mortality rates was much more pronounced—almost three times higher during the dry than during the wet season (8% and 3% per month, respectively; $P < 0.001$, Appendix S1: Table S5).

Average relative leaf area change (RGR_{LA}) throughout the season and monthly rates in the dry season were only about 0.15% and 10% of those in the wet season, respectively ($P < 0.001$, Appendix S1: Table S5). On average, RGR_{LA} in the dry season was close to zero with a wide variation among species from negative to positive values (Appendix S1: Table S5), because leaf area for some species was reduced either through leaf shedding or through damage, while others developed new leaves. In the wet season, RGR_{LA} was overall positive in all species, but variation

among species was even higher. Over the entire year, species' RGR_{LA} ranged from slightly negative to positive values. RGR_{LA} was negatively influenced by the initial leaf area of the seedlings during the dry season and over the whole year, but not during the wet season (Table 1).

Effect of environmental factors on performance and relations to species distribution

Moisture.—Soil moisture had an overall positive effect on performance. The increase in survival with soil moisture was especially pronounced in the dry season (Table 1a, Fig. 1A) when water availability is potentially limiting, underlining the importance of spatial variation in water availability during the dry season. Even in the wet season, survival was significantly positively influenced

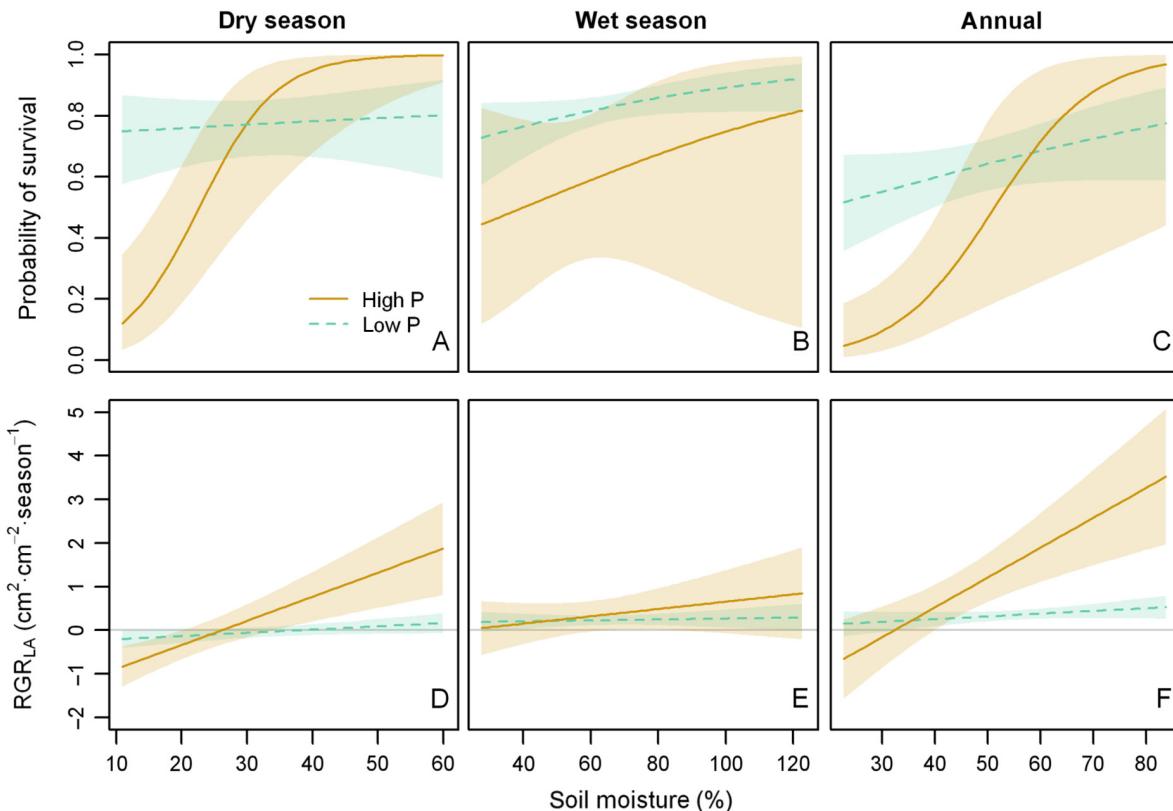


Fig. 2. Relation of seedling performance to soil moisture under high vs. low phosphorus conditions. Survival (A, B, C) and growth (RGR_{LA}, D, E, F) are given over the dry season (A, D), the wet season (B, E), and the entire year (C, F). For clarity, soil phosphorus content is represented as a discrete factor (high: brown/low: light blue) instead of continuous variable, as analyzed (Table 1). Shaded bands show the 95% confidence intervals. For significance of the main effects and interactions, see Table 1.

by soil moisture (Table 1b, Fig. 1B), resulting in an overall positive effect throughout the year (Table 1). The effect of spatial variation of soil moisture on growth was much weaker than on survival (Table 1). There was a significant positive effect in the dry season, but not in the wet season, or over the whole year (Table 1b, c). The increase in survival with moisture did not vary with origin (i.e., no origin × moisture interaction, Table 1). For growth, there was a significant interaction between origin and soil moisture in dry season and over the whole year (Table 1). However, it was opposite to what we expected: Dry-origin species benefited more from higher water availability than wet-origin species.

Phosphorus.—Growth and survival were overall negatively influenced by soil phosphorus availability in the dry season and over the whole

year (Table 1a, c), but were not affected by phosphorus in the wet season (Table 1b, Fig. 1B, E). The negative effect of high phosphorus occurred in the dry season in the driest sites, while in the wet sites, higher phosphorus strongly enhanced performance (moisture × phosphorus interaction, see Table 1a, Fig. 2A, D). In contrast, there was no interaction between moisture and phosphorus in the wet season (Table 1b, Fig. 2B, E). The negative effect of phosphorus in the dry season was directly reflected in annual survival and growth (Table 1c, Fig. 2C, F). In contrast to our expectations, dry-origin species did not show a stronger response to nutrients than wet-origin species (no origin × soil phosphorus interaction).

Light.—The influence of light availability on species performance depended on the season: During the wet season, higher light conditions

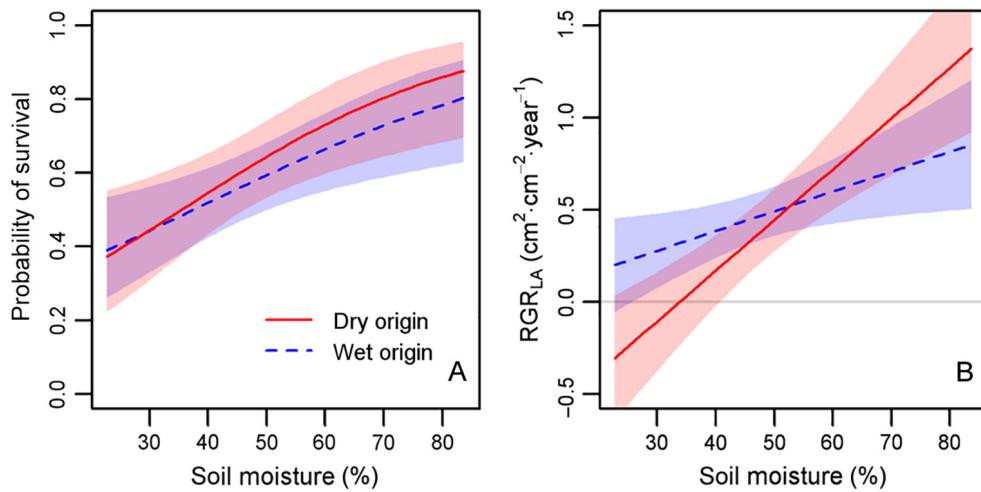


Fig. 3. Relation of annual survival (A) and growth (RGR_{LA} , B) of seedling of dry- and wet-origin species to soil moisture. For clarity, origin is represented as a discrete factor (dry/wet) instead of continuous variable, as analyzed (Table 1). Colors follow Fig. 1; shaded bands show the 95% confidence intervals. For significance of the main effects and interactions, see Table 1.

significantly increased growth, but not survival (Table 1b, Fig. 1C, D). In contrast, during the dry season, light had a negative effect on growth and survival (Table 1a). Over the whole year, light availability had a significant negative effect on survival, and a positive, though non-significant, effect on growth (Table 1c). In contrast to our expectations, light did not affect dry-origin more than wet-origin species (no origin \times canopy openness interaction, Table 1).

Effects of drought resistance and origin on seedling performance

Drought resistance.—There was a significant positive relation between species origin, indicative of the strength of dry forest association based on occurrence in 122 inventory sites, and independently experimentally assessed seedling drought resistance (Engelbrecht and Kursar 2003, Engelbrecht et al. 2007) of the species ($r_{pearson} = 0.4$). Both survival and growth increased with species drought resistance in the dry season (Table 1a), while in the wet season and over the whole year, only survival was positively related to drought resistance (Table 1b, c). As expected, drought-resistant species tended to be less affected by lower water availability in the experiment than drought-sensitive species, as indicated by the negative slope of the interaction between soil

moisture and drought resistance for all parameters and seasons (Table 1). However, the interaction was only significant for dry season growth and annual survival (Table 1a, c).

Origin.—After one year, neither dry- nor wet-origin species had a home advantage with regard to survival, as indicated by a non-significant origin \times moisture interaction (Table 1c and Fig. 3A). Instead, all species, regardless of their origin, survived better under moister conditions (see Table 1). The corresponding origin \times environmental factor interactions were not significant in either the dry or wet season. Species also did not have a home advantage in terms of growth: In contrast to our expectation, annual growth was significantly greater with higher moisture for dry-origin species compared to wet-origin species (origin \times moisture interaction, Table 1c and Fig. 3B).

DISCUSSION

By analyzing the effects of environmental factors on performance of first-year seedlings with contrasting origins, we aimed to understand which factors exclude dry-origin species from wet forests and vice versa. While drought has received strong support as the main factor excluding wet-origin species from dry sites (reviewed in Comita

and Engelbrecht 2013), previous studies have not explained the mechanisms that exclude dry-origin species from wet sites. We used six sites spanning a rainfall gradient, which allowed us to assess effects of spatial environmental variation more rigorously than previous studies that compared two or three sites (Brenes-Arguedas et al. 2009, 2011, Baltzer and Davies 2012, Gaviria and Engelbrecht 2015, Spear et al. 2015). Any ecologically relevant differences in whole-plant resource requirements that shape species distributions should manifest themselves under the range and complex combinations of factors (known and unknown) that the plants are exposed to in their habitat. “Inherent” differences in whole-plant resource requirements, observable under controlled experimental conditions, may or may not play out in the habitat (e.g., Comita and Engelbrecht 2009). By using a transplant experiment across natural gradients of environmental conditions in the habitat, we ensured that we considered the range, variability, and combinations of environmental factors that seedlings actually face in their natural setting.

Species responses to variation in moisture, phosphorus, and light

Moisture.—Across sites, survival and growth in the dry season, and survival in the wet season, were greater at wetter sites (Table 1a, b; Appendix S1: Table S4). It has been suggested that seedlings perform poorly in the wet season due to lower light conditions, higher herbivore pressure, or lower nutrient availability (Wright and Van Schaik 1994). However, higher wet season survival and growth in this study clearly indicate that these factors were less limiting than the direct effects of low water availability in the dry season. Our results therefore indicate that seedling performance in moist tropical forests is directly limited by soil water availability, in agreement with previous experimental and observational studies (reviewed in Comita and Engelbrecht 2013).

A growing body of literature shows that woody species in wetter forests or habitats are less drought-resistant than species in drier sites and that drought acts as a filter excluding wet forest species from dry sites (Bunker and Carson 2005, Daws et al. 2005, Engelbrecht et al. 2007, Brenes-Arguedas et al. 2009, Comita and Engelbrecht 2009, 2013, Baltzer and Davies 2012, Amissah et al.

2014, Muelbert et al. 2016). Our results are overall consistent with these studies: The drought resistance of species, independently quantified in previous drought/irrigation experiments, decreased with species association with wet sites, and more drought-resistant species had higher annual survival in drier sites (Table 1c). Nevertheless, such effects were not strong enough to manifest themselves in an explicit home advantage of dry forest species over the course of this study.

A home advantage of dry forest species in terms of survival across moisture gradients has been shown previously in several experiments (Comita and Engelbrecht 2009, Baltzer and Davies 2012), but not in others (Brenes-Arguedas et al. 2011, Gaviria and Engelbrecht 2015, Spear et al. 2015). The effect of drought varies considerably across years with different dry season intensity, with effects being most pronounced in extremely dry years (Comita and Engelbrecht 2013). The relatively weak dry season during the experimental year may have precluded the manifestation of a survival advantage of drought-resistant dry-origin species in their home range, and underlines the importance of pronounced and extreme dry season events for excluding wet-origin species from dry forests.

Dry-origin species also did not have a home advantage in terms of growth. Instead, their annual leaf area increase was even lower compared to wet-origin species in the driest places (Table 1c, Fig. 3B), reflecting higher dry season leaf area loss (negative RGR_{LA}) of dry forest species (Table 1a and Fig. 1D). This is likely due to facultative leaf shedding in response to drought, which has been shown even for species whose adults are not dry season deciduous (Engelbrecht and Kursar 2003). Leaf shedding might improve survival under dry conditions (Poorter and Markestijn 2008, but see Engelbrecht and Kursar 2003 and Comita and Engelbrecht 2013) and therefore confer dry-origin species an advantage in terms of survival in drier years.

Thus, despite the weak dry season that dampened the negative effects of drought and precluded the explicit manifestation of a home advantage of dry-origin species in dry sites, our results are overall consistent with the physiological tolerance hypothesis, and add to the increasing amount of studies that support the direct role of drought for the exclusion of wet-origin species

from dry forests, with dry years being especially important (Engelbrecht et al. 2007, Brenes-Arguedas et al. 2009, Comita and Engelbrecht 2009, 2013, Kursar et al. 2009, Baltzer and Davies 2012). However, the factors that exclude dry-origin species from wet forests remain unresolved. In this study, we explicitly addressed the role of nutrients and light.

Phosphorus.—In contrast to our expectations, overall seedling performance did not increase with increasing soil phosphorus concentrations (Table 1). Fertilization studies under high light conditions in the greenhouse or in common gardens often lead to increased growth and survival in tropical seedlings (e.g., Yavitt and Wright 2008, Zalamea et al. 2016). However, results are much less clear in the forest understory, and depend on the nutrient considered as well as other factors like herbivory (Andersen et al. 2010, Santiago et al. 2012). Lack of immediate and pronounced responses to fertilization in the forest understory in previous studies and a lack of response to the large (100×) spatial variation in soil phosphorus in our study indicate that other factors are more limiting for seedling performance in the field, and that nutrient effects are complex. Indeed, survival and growth even decreased with increasing phosphorus, due to high phosphorus exacerbating the negative effects of drought (Table 1a, Fig. 2A, D). It is unlikely that the latter effect was due to phosphorus toxicity, since phosphorus concentrations in our plots were relatively low—both in the region (Condit et al. 2013) and compared to fertilization experiments in tropical seedlings that showed performance increases (e.g., Yavitt and Wright 2008, Zalamea et al. 2016). Most species are able to efficiently down-regulate their phosphorus uptake (Hawkesford et al. 2012), and toxicity only appears to occur in sensitive species such as the Proteaceae (Lambers et al. 2010). Instead, indirect effects of phosphorus on below-ground allocation to roots and/or interactions with mycorrhizas may have rendered the plants in phosphorus-rich sites more susceptible to drought. Specifically, under high phosphorus conditions, a shift of biomass allocation toward aboveground parts at the expense of roots (Poorer et al. 2012), and/or reduced investment into mycorrhizal fungi (Treseder 2004), might have left the plants unable to acquire sufficient moisture under drought (Read 1991), leading to reduced

dry season growth and survival under high soil phosphorus.

We found no indication that dry-origin species are more nutrient-demanding than wet forest species, as required for the nutrient availability distribution hypothesis. Specifically, dry forest species did not show stronger response to increasing phosphorus availability, and they did not have lower performance at low phosphorus availability, when that factor might become most limiting (Fig. 1). A greenhouse study in the area similarly did not support that dry forest species have higher nutrient requirements than wet forests (Brenes-Arguedas et al. 2008). Furthermore, the strong species turnover across the rainfall gradient in the area (Condit 2002) occurs without a corresponding pronounced correlation of phosphorus or other nutrients with rainfall (Engelbrecht et al. 2007, Turner and Engelbrecht 2011, Condit et al. 2013). Thus, while nutrients are important for shaping species distributions across local and regional nutrient gradients in tropical forests in Panama and other tropical areas (Fine et al. 2004, John 2007, Condit et al. 2013, Zalamea et al. 2016), ours and previous results do not support that nutrients are a main factor excluding dry forest species from wet forests.

Light.—We expected higher light availability to increase seedling performance, congruent with the general notion that low light availability is limiting in the understory of tropical forests. Species partitioning along light gradients has been shown even within the forest understory (Montgomery and Chazdon 2002). However, in our study, annual seedling growth and survival did not increase with light (Table 1c), indicating that light was not a main factor limiting seedling regeneration in the forest understory. While growth was weakly light-limited in the wet season (Table 1b), in the dry season light even had negative effects on both survival and growth (Table 1a). This may be a consequence of the negative correlation we found between soil moisture and canopy openness (Appendix S1: Table S4), showing that negative effects of drought were exacerbated by light in the dry season. Similar effects have been found in other studies in tropical forests (McLaren and McDonald 2003, Brenes-Arguedas et al. 2011), and may be due to increased temperature and evaporation under higher light conditions.

We found no support for the hypothesis that higher light requirements of dry- than wet-origin species are relevant for their exclusion from wet forests: Dry-origin species did not show a more pronounced increase in performance with light than wet-origin species (no light \times origin interaction), and under conditions below typical whole-plant light compensation points of tropical saplings, when performance differences should become most apparent (about 5%), dry- and wet-origin species were indistinguishable (Fig. 1). Brenes-Arguedas et al. (2011) similarly found no difference in light requirements among origins in a separate species set in a transplant experiment to two sites in the area (five species overlap), lending further support to our result. There is also no convincing evidence for the hypothesized underlying trade-off between drought and shade tolerance in tropical seedlings (Engelbrecht et al. 2007, Markesteijn and Poorter 2009), and a comprehensive study in a dry forest in Bolivia even showed convergence between drought and shade tolerance, and between the underlying traits (Markesteijn et al. 2011).

In addition, in this study across six sites, we found only a very weak decrease in light availability with increasing rainfall (Appendix S1: Table S4), which was significant only in the dry season. Indeed, the highest light availability was measured in the wettest site (Appendix S1: Fig. S3). Studies that reported lower light conditions in wetter forests either compared single forest pairs (Santiago et al. 2004, Brenes-Arguedas et al. 2011), or were not designed for direct comparisons with standardized methods (Parker et al. 2005, Peña-Claros 2012). Our study adds to others that did not find lower light availabilities with increasing rainfall (Engelbrecht 1998, Harms et al. 2004), and underlines that processes shaping forest structure—and through that understory light conditions—of tropical lowland forests are complex (Toledo et al. 2011). These results challenge the assumption that light availability in the understory of tropical forests generally decreases with rainfall (Smith and Huston 1989), which is the basis for the light availability distribution hypothesis. In summary, there is no evidence that higher light requirements of seedlings of dry forest species are excluding them from darker wet forests.

What excludes dry forest species from wet forests?

Wet forest species did not exhibit a home advantage (Fig. 3A), as we had expected: All species survived better under moister conditions. In addition, the lack of a difference between species origins in light and phosphorus responses in the habitat implies that requirements for these resources do not differ in a way that is relevant for performance and distribution across the rainfall gradient (Table 1a, b and Fig. 1B, C, E, F), consistent with previous studies (Brenes-Arguedas et al. 2008, 2011). It has also been suggested that herbivores and pathogens (summarized as pests) are important because they exclude poorly defended dry forest species from wet forests, with high pest pressure (pest pressure gradient hypothesis, Baltzer and Davies 2012). If these processes are important, the outcome should again be a home advantage of wet forest species, especially in the wet season when pests are most abundant (Wolda 1978). Thus, the lack of a moisture \times origin interaction in our study (Table 1b) implies that effects of pest pressure on seedling performance do not drive the exclusion of dry forest species from wet forests. None of the studies that specifically tested the pest pressure gradient hypothesis provide convincing evidence for a home advantage of seedlings of wet forest species due to a combination of higher defenses (or lower susceptibility) and increased pest pressure (Brenes-Arguedas et al. 2009, Baltzer and Davies 2012, Gaviria and Engelbrecht 2015, Spear et al. 2015). Together, these results indicate that effects of phosphorus or light availability, or pest pressure, on the performance of young seedlings do not exclude dry forest species from wet forests and thus do not drive the high β -diversity across rainfall gradients.

Our study, as well as several others, focused on the performance of first-year seedlings (Brenes-Arguedas et al. 2008, 2009, 2011, Baltzer and Davies 2012, Gaviria and Engelbrecht 2015, Fortunel et al. 2016), because early regeneration stages are considered the most vulnerable to environmental stressors and are a bottleneck in population dynamics (Harper 1977). However, neither ours nor previous studies find that the seedling stage, or the seed–seedling transition, is crucial for excluding species associated with dry sites from wet sites (i.e., seedlings of wet forest

species did not have a home advantage, see Brenes-Arguedas et al. 2011, Gaviria and Engelbrecht 2015, Spear et al. 2015). This suggests that later life stages and longer time periods are important for excluding dry forest species from wet forests. The importance of later life stages is supported by local-scale studies: If habitat associations of adults are shaped within the first year, older juveniles and adults should exhibit the same habitat associations. However, most species have different associations as seedling and adults (Comita et al. 2007). On the other hand, by the time they reach 1 cm diameter at breast height as saplings, tropical trees have developed the distribution patterns they exhibit as adults (Baldeck 2013). This supports that older juvenile life stages may be more important for excluding dry forest species from wetter forests. Later life stages have been shown to respond differentially to all three environmental factors (nutrients, light, and pest pressure, see Lusk et al. 2008, Barton and Korcheva 2010, Bertrand et al. 2011), and thus, processes excluding dry forest species from wetter forests may act at later life stages.

In addition, higher growth rates in wet- compared to dry-origin species were found in these (Brenes-Arguedas et al. 2008, 2009, Gaviria and Engelbrecht 2015) and other tropical forests (Baltzer and Davies 2012), suggesting that it is a widespread pattern. These results are consistent with a drought tolerance–growth trade-off (Smith and Huston 1989), conferred by traits that improve drought resistance (e.g., deep roots, dense wood, cavitation-resistant xylem, high non-structural carbohydrate levels) but are also related to low growth rates (Poorter et al. 2010). Nevertheless, direct experimental evidence for this trade-off at the whole-plant performance level remains scarce and contradictory (Fernandez and Reynolds 2000, Polley et al. 2002, Wikberg and Ogren 2004). Higher growth rates of wet- than dry-origin species (Table 1c) may over longer periods lead to a home advantage of wet forest species, and contribute to excluding dry-origin species from wet forests.

CONCLUSIONS

Our results from an extensive multi-species and multi-site seedling transplant experiment indicate that effects of phosphorus or light availability, or pest pressure, on the performance of

young seedlings do not exclude dry forest species from wet forests and thus do not drive the high β -diversity across rainfall gradients. Instead, higher growth rates might contribute to a home advantage of wet forest species over longer time periods, and later life stages may be more important for the exclusion of dry-origin species from wet forests. On the other hand, our results are consistent with drought directly excluding wet forest seedlings from dry sites, especially during dry years. Through effects on species regeneration, changes in rainfall patterns, especially the frequency and intensity of drought events, will therefore have pervasive effects for tree distribution and consequently forest diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1712/full>