

Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions

Michael J. O'Brien^{1,2}  | Adrián Escudero¹ 

¹Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Móstoles, Spain

²Southeast Asia Rainforest Research Partnership (SEARRP), Kota Kinabalu, Sabah, Malaysia

Correspondence

Michael J. O'Brien
Email: mikey.j.obrien@gmail.com

Funding information

Comunidad de Madrid, Grant/Award Number: 2018-T1/AMB-11095

Handling Editor: Emma Sayer

Abstract

1. Topography is associated with variation in soil water, biogeochemical properties and climate, which drive diversity by filtering species and promoting niche differences. However, the potential for topography to promote fitness differences and diversity among tree species and populations remains poorly tested in tropical rainforests, especially at small spatial scales in everwet climates.
2. We reciprocally transplanted tree seedlings between ridge and riparian sites and manipulated neighbour abundance and water availability to assess growth and survival differences both among species and between populations within species in response to changes in biotic interactions and soil water gradients associated with topographic heterogeneity.
3. Seedling growth rates were higher on the ridge, but probability of survival was lower on the ridge than the riparian site. Topography also altered growth and survival responses to water availability such that seedlings in the inundated soils in the riparian site had the lowest growth and survival but increased rapidly with moderate soil drying. By contrast, growth and survival on the ridge were generally unresponsive to drying, although severe drought on the ridge reinforced differences among species in growth rates and probability of survival.
4. The patterns of growth and survival within species did not provide evidence of local adaptation between seedlings from lowland and upslope origins. However, within species, topographic seed-origin determined the response of seedling growth and survival to increasing neighbour abundance, indicative of divergent selective pressures between individuals growing in different topographic environments.
5. Combined, these results suggest that topographic heterogeneity promotes tropical forest diversity both at the species level via environmental filtering due to water availability and at the population level via functional responses to the density of neighbouring vegetation.

KEYWORDS

drought responses, intraspecific variation, plant–climate interactions, plant–plant interactions, tree demography, tropical forests

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1 | INTRODUCTION

The maintenance of the hyper-diversity of tropical rainforests is commonly attributed to fitness differences maintained by environmental filtering across landscapes (Wu et al., 2016) and niche differentiation related to fine-scale heterogeneity (Born et al., 2014). Surprisingly, the role of these environmental drivers of diversity on fitness differences among populations has had limited attention in tropical ecology, despite the fact that variables such as topographic heterogeneity drive patterns of tropical forest diversity, structure and biomass (Jucker et al., 2018). These shifts in the forest community across topography are directly related to variation in soil resources (e.g. water and nutrients) that indirectly alter plant-plant interactions (Gibbons & Newbery, 2003; Jucker et al., 2018; Muscarella et al., 2020). The variation in both these abiotic and biotic variables can mediate microevolutionary processes that could promote fitness differences among populations (Cotto et al., 2017; O'Brien et al., 2021; Tito de Morais et al., 2020; Torroba-Balmori et al., 2017). Empirically testing growth and survival responses to environmental heterogeneity can provide insights into the drivers of species diversity at small spatial scales and the mechanisms of selection that help maintain the enormous diversity within tropical forests (Leibold et al., 2019; Reed & Frankham, 2003).

Soil water availability commonly decreases from lowland to upslope areas in tropical rainforests (Gibbons & Newbery, 2003; Silver et al., 1999), and to a lesser degree, nutrients also vary with topography after controlling for soil parent material (Asner & Martin, 2016; Baldeck et al., 2013; Dent et al., 2006; Takyu et al., 2002). These direct effects of topography on soil resources lead to species turnover from lowland to upslope and ridge sites (Asner & Martin, 2016) with overall lower diversity, stem density, biomass and canopy cover typically found on upslope sites (Jucker et al., 2018; Méndez-Toribio et al., 2017). Therefore, topography in tropical forests indicates a potential trade-off between competition for light and resources in the dense lowland and tolerance to reduced water availability in the dry upslope, which combine to promote diversity across the landscape (Engelbrecht et al., 2007; Jucker et al., 2018). Experimental research exploring changes in the mechanisms driving species demography across topography remains sparse in tropical forests, and direct manipulations are necessary for disentangling the relative importance of abiotic and biotic drivers for species diversity.

The importance of topography for enhancing species diversity may also function as a selection pressure on genotypes within species (e.g. local adaptation). It is reasonable to ask whether the correlation between topographically mediated water availability and the distribution of drought-tolerant species extends to selection on drought tolerance among genotypes within species (Engelbrecht et al., 2007). Elevated and upslope microsites experience frequent fluctuations in water availability and more severe drought than lowland sites (Born et al., 2014; Gibbons & Newbery, 2003; Jucker et al., 2018), which, in turn, could promote drought adapted genotypes. Adaptation to soil moisture along topographic gradients is likely functioning concurrently with selection driven by biotic interactions. For example,

lowland areas could be selecting genotypes with increased tolerance to dense vertical and horizontal vegetation—that is, increased plant abundance in lowland conditions (Russo et al., 2012). These selective pressures may lead to local adaptation—that is, genotypic selection matching traits to specific conditions along environmental gradients (Baughman et al., 2019; Kawecki & Ebert, 2004)—and in turn speciation over evolutionary time-scales, which may have contributed to the hyper-diversity found in tropical forests. Recent studies have shown evidence of the genetic structuring of neutral loci across fine spatial scales in tropical forests (Harata et al., 2012; Smith et al., 2018; Takeuchi et al., 2004; Tito de Morais et al., 2015), which suggests that environmental variables are filtering genotypes, a prerequisite for potential adaptive differences among populations to drivers of selection (Cotto et al., 2017; Kawecki & Ebert, 2004; Sedlacek et al., 2016). These observational studies in tropical forests support the hypothesis that topography triggers functional variation within species, but direct tests comparing fitness differences within species are needed to understand the mechanistic drivers that promote population diversity and richness (Brancalion et al., 2018; Chen & Schemske, 2013).

Furthermore, climate change may be altering the mechanisms and diversity patterns across these fine-scale topographic gradients in tropical forests. Everwet tropical forests are experiencing increased rainfall variability and more severe water deficits (Dai, 2013; Donat et al., 2016) in recent decades. These shifts may reinforce differences between lowland and upslope sites by increased flooding frequency in lowland areas and more severe water deficit on upslope sites (Born et al., 2014). However, the importance of drought in everwet tropical forests has received limited attention, despite observational evidence for its importance in driving mortality rates (Potts, 2003) and shade-house studies indicating a wide range of tolerance to drought (O'Brien et al., 2014). Experimental field studies exploring the interaction between drought and topography are needed to improve predictions of species responses to climate change.

We used a reciprocal transplant experiment to evaluate the differential responses of growth and survival (i.e. proxies for fitness) using seeds from lowland and upslope origins of six canopy-forming tree species widely distributed in tropical mature forests of Borneo. We manipulated the abundance of neighbours and water availability to assess the relative importance of these concomitant processes for altering growth and survival across topography. We posit that topography determines early growth and survival across species, and the patterns of response to topography depend on species life-history strategies. We extend this hypothesis to seed-origin such that we expected seedlings from upslope origins to be more tolerant of soil water deficit due to selection pressures on parental genotypes in upslope sites. By contrast, we expect seedlings from parents with a lowland origin to tolerate increased neighbour abundance due to the typically higher diversity, biomass and canopy cover in lowland sites. Overall, this experimental design allowed us to simultaneously test different drivers of selection across topographic gradients among and within species. We assumed that differential responses

of seed-origins to these environmental variables suggests evidence of population differentiation, and concurrently, a fitness advantage of local over nonlocal seed-origins supports evidence of local adaptation.

2 | MATERIALS AND METHODS

The experiment was planted in the Malua Forest Reserve (N05.09° E117.84°; 100 m a.s.l.; O'Brien, Ong, et al., 2017) in the state of Sabah, Malaysia with permissions granted by the Sabah Biodiversity Council (JKM/MBS.1000-2/2 JLD.5 136) and the Danum Valley Management Committee (YS/DVMC/2016/241). Seeds were collected across a contiguous group of forest reserves—Taliwas (N04.99° E118.08° 200 m a.s.l.), Danum Valley (N04.96° E117.80°; 180 m a.s.l.) and Ulu Segama (N04.99° E117.90°; 240 m a.s.l.). Except for Danum Valley, these forests were initially logged in the 1970s and 80s with many areas re-logged between the late 1990s and 2010 (Reynolds et al., 2011). The canopy of the primary forest in surrounding areas (e.g. Danum Valley) is dominated by the family Dipterocarpaceae (dipterocarps), which has been the main target of the logging industry (Kettle et al., 2012). The logged forests consist of fast-growing early successional species and climbing vines (e.g. lianas, bamboo and rattan; O'Brien et al., 2019). Remnant dipterocarps larger than 30 cm diameter at breast height (DBH) are still present, estimated to be approximately 18 trees per hectare (Berry et al., 2008), and the vegetation composition and structure are heterogeneous due to variability in the topography and logging history. Reproduction and recruitment in these forests occurs predominantly during supra-annual mast fruiting events defined by synchronous flowering and fruit production across species, genera and families (Appanah, 1993; Kettle et al., 2010). These events lead to dense seedling cohorts that can persist for months to years constituting relatively long-standing seedling banks. A study in the Malua Forest Reserve found seedling densities between 1 and 242 seedlings per m² up to 6 months after a mast fruiting event and between 1 and 82 seedlings per m² a year after the event (M. J. O'Brien, unpublished data).

Eastern Sabah has an aseasonal climate and an average monthly rainfall (standard error) of 240 mm (12) and an average yearly total of 2,900 mm (90), as recorded at Danum Valley Field Centre from 1986 to 2018. Severe drought events in the area (>100 mm of soil water deficit) occurred periodically since the mid-1980s (e.g. 1986–1987, 1991–1992, 1997–1998, 2005, 2010 and 2015–2016). The mean daily minimum temperature measured at the Malua Field Station during the experiment was 23.0°C and the mean daily maximum temperature was 29.4°C. The mean midday humidity was 73% and the mean night-time humidity was >95%.

2.1 | Seed collection

In August 2014, fruits were collected during a mast fruiting event in Sabah, Borneo from six different mature trees (seed-families)

for each of six dipterocarp species. The six focal species were chosen to span a range of drought tolerance from highly susceptible (*Shorea leprosula* and *S. parvifolia*) to moderate resistance (*Parashorea malaanonan* and *S. johorensis*) to resistant (*Hopea nervosa* and *Dryobalanops lanceolata*), based on functional traits such as fruit size (O'Brien et al., 2013), nonstructural carbohydrates (O'Brien et al., 2014, 2015), maximum growth rate (Philipson et al., 2014) and wood density (O'Brien et al., 2014)—that is, traits associated with drought tolerance; see previous research (O'Brien, Ong, et al., 2017; O'Brien et al., 2013, 2014, 2015; O'Brien, Reynolds, et al., 2017). Fruits from a single mother of an additional 12 dipterocarp species (selected based on availability during the 2014 mast flowering event) provided the interspecific neighbour treatment. Approximately 10 fruits without wings per mother tree were dried and weighed to estimate mean biomass (see Table S1 for mother tree list). Because fruits contain a single seed, we use the term seed hereafter.

Mature trees of the six focal species were selected from lowland (three trees per species) and upslope (three trees per species) areas. The average distance between upslope and lowland trees within a species was 11.5 km (range: 4.2–21.4). Trees were placed in these topographic categories based on their location to the nearest river or stream such that trees defined as lowland were adjacent to (within a few metres) and <8 m elevation from watercourses. The 8 m distance is a post-hoc calculation, but it is within a distance to allow trees continuous access to water (except under the most severe drought conditions) from a fairly young age based on root lengths and depths for these species (Cao, 2000; Reynolds, 2006). Upslope areas were not determined by elevation but instead defined as convex and freely draining upslope topography without a nearby water source (usually >50–100 m). Because seed production is infrequent in this system and not all trees produce seeds during flowering events (Appanah, 1993), the experiment is not perfectly balanced for species by topographic position. One species had only two trees of lowland origin and one species had only two trees of upslope origin (see Table S1 for species list). Therefore, the level of topographic origin was balanced across species (18 for each topographic position). Hereafter, we use the terms lowland and upslope to describe the seed-origin and the terms riparian and ridge to describe the topographic position of planted seedlings.

2.2 | Reciprocal transplant

Seeds were germinated in a nursery and grown in polyethylene pots under 5% light until planting in May 2015. Plots were placed along the Malua river in an area with a nearby ridge, approximately 50 m above the riparian area. The riparian plots were placed along a stretch of approximately 150 m of river edge, and the ridge plots followed a contour around the terminal of the ridge (before the ridge descends towards the river below). The riparian and ridge topographic positions were selected with low presence of dipterocarp overstorey, although a couple of *P. malaanonan* and *D. lanceolata* were present in the surrounding area of both topographic

positions. Plots were between 5 and 100 m apart within topographic position. In each topographic position (riparian and ridge), 12 plots were established with each comprised of two subplots (a drought and everwet treatment). We refer to each topographic position as a site in the analysis and results. Prior to planting, competing understory vegetation within the plot area was removed to ground level and was removed regularly during the first 12–18 months of the experiment. Three neighbourhood treatments (intraspecific, interspecific and no neighbours) were established within each subplot to assess the effects of seedling neighbour relatedness. Seedlings were planted at 10 cm spacing within intraspecific and interspecific treatments with approximately 35 cm between neighbourhood groups (Figure S1). For the no neighbour treatment, individual seedlings of each species were planted around the other two treatments to allow seedlings to grow in the absence of direct interactions with other seedlings (>25 cm distance to their nearest neighbour).

Within each intraspecific treatment, a seed-family (defined as seedlings from the same mature tree) was randomly assigned to a planting point in a 2 × 3 grid for each species. Every seed-family for each species was in a centre planting point in four plots at each site. Within each interspecific treatment, an individual from each seed-family that was planted in the centre of the intraspecific treatment of that plot (two individuals from two different seed-families of each of the six species) was randomly assigned to a planting point in a 4 × 6 grid. The additional 12 planting points in the interspecific treatment were filled with one individual of each of the non-focal species. Each seed-family of each species was planted with no neighbours in approximately two plots per site. The design was randomized for every plot, but the two subplots within a plot were identical to reduce spatial variation in neighbourhoods between the subplots within plots. Therefore, among plots, species had unique neighbours but within plots neighbours were identical between subplots (see Figure S1). This design led to a planting density from 1 to 225 seedlings per m² calculated based on a 20 × 20 cm square around each seedling. For example, a centre seedling in the interspecific treatment equated to nine seedlings in a 20 × 20 cm square, which extrapolates to a density of 225 seedlings per m². These densities were high relative to observed cohorts of naturally established seedlings (although still within post-masting densities for the area) to induce interactions among neighbours.

In summary, one individual of each seed-family per species was planted in every subplot with intraspecific neighbours (2 subplots × 12 plots × 2 sites = 48 individuals per seed-family). One individual of each seed-family per species was planted in both subplots of four plots with interspecific neighbours (2 subplots × 4 plots × 2 sites = 16 individuals per seed-family). One individual of each seed-family per species was planted in both subplots of two plots with no neighbours (2 subplots × 2 plots × 2 sites = 8 individuals per seed-family). Therefore, each seed-family per species had 72 seedlings (72 individuals × 6 seed-families × 6 species = 2,592 seedlings with an additional 576 non-focal seedlings in the interspecific treatment).

Analysis was performed at the level of maternal environment (lowland vs. upslope origin, which is balanced with $n = 18$ for both environments) and not at the level of seed-family. Because of the edge effects in the planting neighbourhoods, the impact of neighbours was analysed as the mean immediate neighbour abundance (<15 cm) over the experimental period. This metric ranged from a maximum of eight neighbours in the centre of the interspecific groups with no mortality to a minimum of zero for individuals planted with no immediate neighbours.

2.3 | Growth, survival and drought

Seedlings established in the field for 8 months before the onset of the experiment during which time any seedlings that died were replanted to avoid including mortality due to planting stress in the experiment. After 3 months of stable survival (February 2016), seedlings were measured for height (cm) above the soil surface, and seedling mortality was recorded (0 = dead and 1 = alive). Censuses were subsequently conducted approximately every 179 days (range = 140–215) with nine measurements in total. Rainfall exclusion shelters (approximately 1.5 × 2 m, allowing a 30 cm exclusion buffer around subplots) were constructed from clear polyethylene sheeting and placed above one subplot within each plot from February 2016 to January 2017, removed from January 2017 to January 2018 and placed again from February 2018 to August 2018. Shelters were checked every 2 weeks and repaired if damaged. Seedlings were measured every 6 months and directly before the placement of rainfall exclusion shelters and immediately after their removal. Supplemental watering (approximately 3–5 L of water per subplot) during dry periods (>3 days with no rain) was used to maintain water availability in plots and subplots where exclusion shelters were not present and continued every 3–4 days until the end of a dry spell.

2.4 | Environmental conditions

Sand, silt and clay content and total N and P were measured in four plots at each site with 30 cm deep soil cores. The content was similar between the ridge (sand = 49%, SD: 10, silt = 15%, SD: 2; and clay = 36%, SD: 9) and the riparian (sand = 52%, SD: 8; silt = 22%, SD: 5; and clay = 26%, SD: 4) sites, although the ridge had higher clay content. Total N was not significantly different ($F_{1,6} = 3.8$, $p = 0.1$) between the ridge (N = 0.158 mg/g, 95% CI: 0.14–0.18) and riparian (N = 0.128 mg/g, 95% CI: 0.11–0.15) soils, despite the ridge being higher on average than the riparian. Total P was also not significantly different ($F_{1,6} = 4.48$, $p = 0.08$) between the ridge (P = 2.1 mg/g, 95% CI: 1.0–3.2) and the riparian (P = 3.2 mg/g, 95% CI: 1.6–4.7) soils, despite the riparian being higher on average than the ridge.

Photosynthetically active radiation was measured using a quantum sensor (QS5 sensors; Delta-T Devices) in the centre of each subplot

for 24 hr from June to August 2015 and again from May to July 2018. These measurements were compared to simultaneous measurements of direct sunlight at the Malua Field Station to calculate per cent direct sunlight and compare light differences among plots and between subplots within a plot. On average, light was statistically indistinguishable between subplots and between sites (see Table S2 and Figure S2), but among plots, light ranged from 3.3% to 23.0%. Basal area for the riparian and the ridge areas was estimated from mapped overstorey tree data (trees ≥ 10 cm DBH mapped in three 10×50 m plots on a ridge and six 10×25 m plots in the riparian, which extended 25 m each side of the river) in a nearby plot of the Sabah Biodiversity Experiment (~ 200 m upstream from the experiment). The riparian area was $20.2 \text{ m}^2/\text{ha}$ ($SD: 11.2 \text{ m}^2/\text{ha}$), and the ridge area was $15.0 \text{ m}^2/\text{ha}$ ($SD: 8.2 \text{ m}^2/\text{ha}$).

Volumetric soil moisture content was measured in the top 10 cm of the soil every 2 weeks from January 2016 to November 2019 at three locations in each subplot using a ML3 Theta Probe and HH2 moisture metre (Delta-T Devices). These measurements were converted to MPa by collecting 63 samples from a gradient of 4%–45% volumetric soil moisture, measuring their gravimetric moisture content with the filter paper method and then converting to MPa using the equations from Deka et al. (1995). These data were used to parameterize models of MPa as a function of volumetric soil moisture (O'Brien, Reynolds, et al., 2017).

At the end of the second exclusion period, we measured the predawn leaf water potential (measured with a Scholander Pressure Chamber; model 670, PMS Instruments) of every seedling of each focal species that had a minimum of four leaves in the everwet and drought treatment in three plots at each site to test if seedlings were responding to reduced soil water availability. This sampling measured ~ 22 seedlings per species per water treatment per site and ~ 4 seedlings per species per water treatment per neighbourhood treatment per site. We could not remove leaves during the first drought period because most seedlings were small and likely sensitive to leaf removal. Seedlings showed a decrease in predawn leaf water potentials in the drought treatment (see Figure S3 and Table S3), which indicates that treatments affected both the soil water availability and seedling water status.

Rainfall showed typical aseasonal patterns throughout the experiment. There were droughts in the first and third years of the experiment (see Figure S4a) that caused soil water deficit > 80 mm (calculated as the cumulative deficit of rainfall after accounting for 4 mm of daily evapotranspiration). The rainfall exclusion shelters reduced soil water potential in both sites to levels similar to an El Niño-induced drought (see Figure S4b,c) while the everwet treatment was maintained at high water availability. The riparian site was buffered against more severe and prolonged drought relative to the ridge due to regular water inundation from the river (Figure S4c). The rainfall exclusion treatments did not significantly affect relative humidity (midday humidity = 96%, 95% CI: 95–97) or temperature (midday temperature = 26.3°C , 95% CI: 25.9–26.9) relative to everwet treatments (midday humidity = 97%, 95% CI: 96–98 and temperature = 26.0°C , 95% CI: 25.7–26.4).

2.5 | Statistical analysis

Relative growth rate (RGR) of height was calculated as the slope of the natural log transformed height of each individual as a function of time in years (days divided by 365.25; see Wald Statistics in Table S4 and slopes in Figure S5). Relative growth rate was analysed as a linear mixed effects model with a Gaussian distribution, and final survival (1 = alive and 0 = dead) was analysed as a generalized linear mixed effects model with a binomial distribution. These response variables were both analysed as a function of site (a factor with two levels: riparian and ridge), mean immediate neighbour abundance (a continuous variable ranging from 0 to 8), neighbour relatedness (a factor with three levels: interspecific, intraspecific and no neighbour), drought severity (a log-transformed continuous variable of the mean minimum MPa of a subplot), species (a factor with six levels), seed-origin (a factor with two levels: lowland and upslope) and an origin by planting site term to test local adaptation (a factor with two levels: local and foreign and referred to as local|foreign throughout). The neighbour abundance term represents a relative, continuous and simple estimate of neighbour interaction. It ranges from nearly no interactions for individuals planted more than 20 cm from any neighbour (0 neighbour abundance) to intense interactions for individuals having eight neighbours within 15 cm for the entirety of the experiment and potentially 21 neighbours within 30 cm (eight neighbour abundance). Similarly, the drought severity term was calculated as the average minimum soil matric potential for each subplot between each census (see Figure S4 for MPa data) over the duration of the experiment (range of average minimum soil water potential from -1.29 to -0.009 MPa). This term represents the level of drought severity for each subplot during the experiment.

Two-way interactions between planting site (ridge and riparian) and species, drought severity and neighbour abundance tested for differential effects of these variables on growth and survival at each site. Species \times seed-origin and species \times local|foreign interaction terms were included to test whether the role of seed-origin and local adaptation varied among species. The response to drought severity and neighbour abundance by species, seed-origin and the local adaptation term was assessed with two-way interactions (i.e. species \times drought, seed \times drought, local|foreign \times drought, species \times neighbours, seed \times neighbours and local|foreign \times neighbours). These terms tested for differential responses of these biological variables to drought and neighbour abundance.

A covariate for average height accounted for size differences among individuals, and a covariate for light in each subplot was included to account for differences among plots that affect growth and survival. Random factors for planting group in each subplot within each plot (864 levels) and seed-family (36 levels) were included in both the survival and growth model (see Wald Statistics in Tables S5 and S6). Model predictions and figures were made with covariates set to their average values (height = 45 cm and direct sunlight = 9.9%). All analyses were done with the ASREML-R package

(ASReml 4; VSN International, UK) in the R statistical software (version 4.1.0; <http://r-project.org>). The predict.asreml function was used to calculate 95% CIs, and the significance of variables was determined using Wald tests using the test.asreml function in the PASCAL package.

3 | RESULTS

After controlling for height and light differences, average RGR across species differed significantly between the ridge ($0.21 \text{ cm cm}^{-1} \text{ year}^{-1}$, 95% CI: 0.20–0.23) and the riparian ($0.18 \text{ cm cm}^{-1} \text{ year}^{-1}$, 95% CI: 0.17–0.19) sites. Topography also significantly influenced the

magnitude of the effect of drought severity on RGR (Figure 1; significant site \times drought term Table S5). On average across species, seedling growth in the riparian site increased significantly with increasing drought (slope of RGR to drought severity = 0.014, 95% CI: 0.002–0.025) while seedling growth was unresponsive to drought severity on the ridge (slope of RGR to drought severity = -0.003 , 95% CI: -0.014 – 0.009).

Growth differed significantly among species and within species between seedlings of different seed-origins (Figure 2a), but there was no evidence of topographic position directly promoting an advantage of local seed-origins over foreign seed-origins (i.e. no pattern of local adaptation; local|foreign term was not significant at any level; Table S5). After controlling for height and light differences with no neighbours,

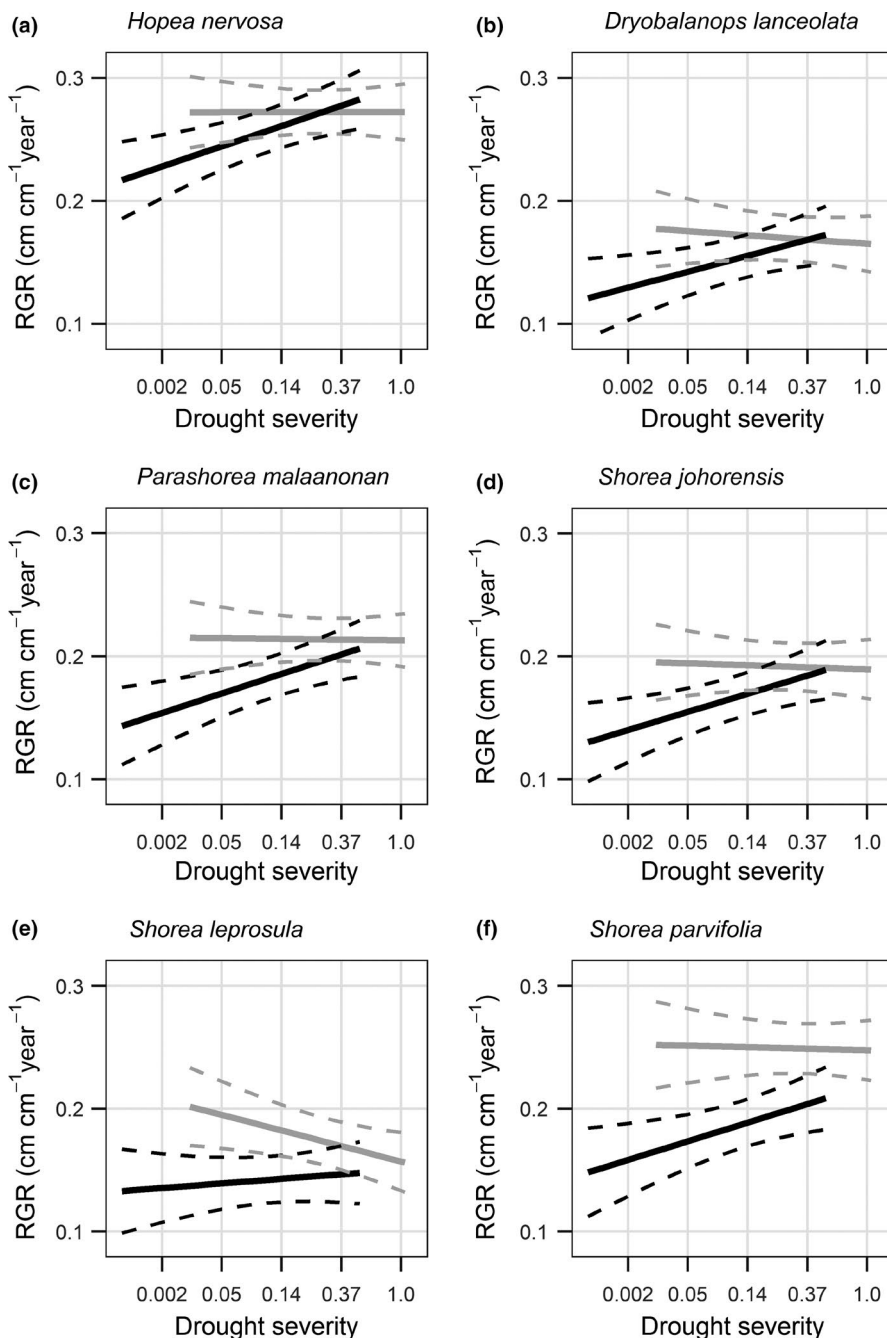


FIGURE 1 Relative growth rate (RGR) in response to drought severity. Relative growth rate (95% CI) of seedlings planted at the ridge (grey) and riparian (black) sites for seedlings of each species (a–f) growing with increasing drought severity during the experiment. Drought severity is the mean minimum soil MPa (average of the minimum MPa between each census in each subplot). Increasing values equal greater drought as the data were transformed by taking the log of the absolute value. The x-axis label provides the untransformed values for interpretation (i.e. 1.0 is a -1.0 MPa). Predictions were generated with average height and light to control for variation among plots and species

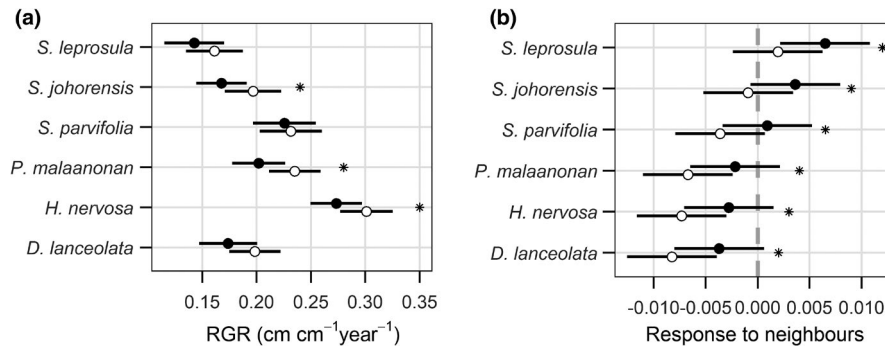


FIGURE 2 Growth between seed-origins within species with no neighbours and in response to neighbours. (a) Relative growth rate (95% CI) of seedlings originating from upslope (○) and lowland (●) sites for seedlings growing with no neighbours (y-intercept at zero neighbours with average height and light conditions). (b) The response of growth to increasing neighbour abundance for seedlings from upslope and lowland origins (neighbour abundance parameter for each seed-origin). Lowland seed-origins never showed a significantly negative response to increasing neighbour abundance. Asterisks represent significant differences between seed-origins for a species, and species are sorted from least (top) to most (bottom) responsive to increasing neighbour abundance. Figure S6 shows the full response of relative growth rates across neighbour abundance

S. leprosula had the lowest RGR followed by *D. lanceolata* and *S. johorensis*, then *P. malaanonan* and *S. parvifolia*, while *H. nervosa* had the highest RGR (Figure 2a). In addition to growth differences among species, RGR between seed-origins differed significantly whereby upslope origins grew significantly faster than lowland origins on average (difference = $0.03 \text{ cm cm}^{-1} \text{ year}^{-1}$, 95% CI: 0.001–0.05; Figure 2a; significant seed-origin term Table S5). This difference was greatest for *H. nervosa*, *P. malaanonan* and *S. johorensis* (Figure 2a).

By contrast, neighbour abundance and relatedness had no direct effects on growth, although the effect of neighbour abundance on RGR differed significantly among species and between seed-origins within species. Among species, the growth of the more conservative species (*H. nervosa*, *D. lanceolata* and *P. malaanonan*) was on average negatively affected by increasing neighbour abundance while the growth of the more acquisitive species (*S. johorensis*, *S. leprosula* and *S. parvifolia*) had a neutral to positive response to increasing neighbour abundance (Figure 2b). Within species, growth of the seedlings from upslope seed-origins was more negatively affected by increasing neighbour abundance than growth of the seedlings from lowland seed-origins (Figure 2b; significant seed-origin \times neighbour abundance term Table S5).

Topography promoted differences in seedling survival whereby seedlings on the ridge had a significantly lower probability of survival (58%, 95% CI: 52–63) than seedlings in the riparian (71%, 95% CI: 66–76). Probability of survival increased with drought severity (Figure 3; significant drought severity term in Table S6), but as with growth, the increase was significant in the riparian site (slope of drought severity = 0.42, 95% CI: 0.12–0.72) but not on the ridge site (slope of drought severity = 0.17, 95% CI: –0.12–0.45).

Species showed significant differences in their probability of survival, which was enhanced by drought severity, but, in general, inundated soils led to lower survival for all species (Figure 4). Under severe drought (i.e. when drought severity reached -1.29 MPa), the probability of survival differed significantly among species (except between *S. johorensis* and the two other *Shorea* spp.; Figure 4).

However, the probability of survival among species was more statistically similar with saturated soils (i.e. when drought severity did not decline below -0.009 MPa ; Figure 4) leading to more grouped survival probabilities across species. This led to a clumped pattern with *Shorea parvifolia* and *S. leprosula* having low probability of survival, *S. johorensis*, *P. malaanonan* and *D. lanceolata* having a moderate probability of survival and *H. nervosa* having a high probability of survival.

Local seed-origins did not have a survival advantage over foreign seed-origins (local|foreign term was not significant at any level; Table S6), and probability of survival did not differ between seed-origins (Figure 5a; seed-origin term was not significant in Table S6). However, probability of survival of individuals from lowland seed-origins all significantly increased in response to neighbour abundance (Figure 5b and Figure S7). This interaction between seed-origin and neighbour abundance led to lower probability of survival of lowland seed-origins relative to upslope seed-origins with no neighbours (average difference in probability of survival of -7.4% over 5 years, 95% CI: -1.6 to -13.2) and higher probability of survival of lowland seed-origins relative to upslope seed-origins with eight immediate neighbours (average difference in probability of survival of 12.3% over 5 years, 95% CI: 3.9 – 20.8).

4 | DISCUSSION

Our experimental manipulation of neighbour abundance, water availability and topographic position with six tree species and two different topographic origins within species reinforces topography as a driver of fitness differences among species via water availability. In addition, the results provide novel evidence that seedlings within species from upslope and lowland origins respond differently to neighbour density. Despite a lack of direct evidence for local adaptation, topographic origin promotes differential growth and survival responses to increasing neighbour abundance, shifting fitness differences in relation to seed-origins. In general, both

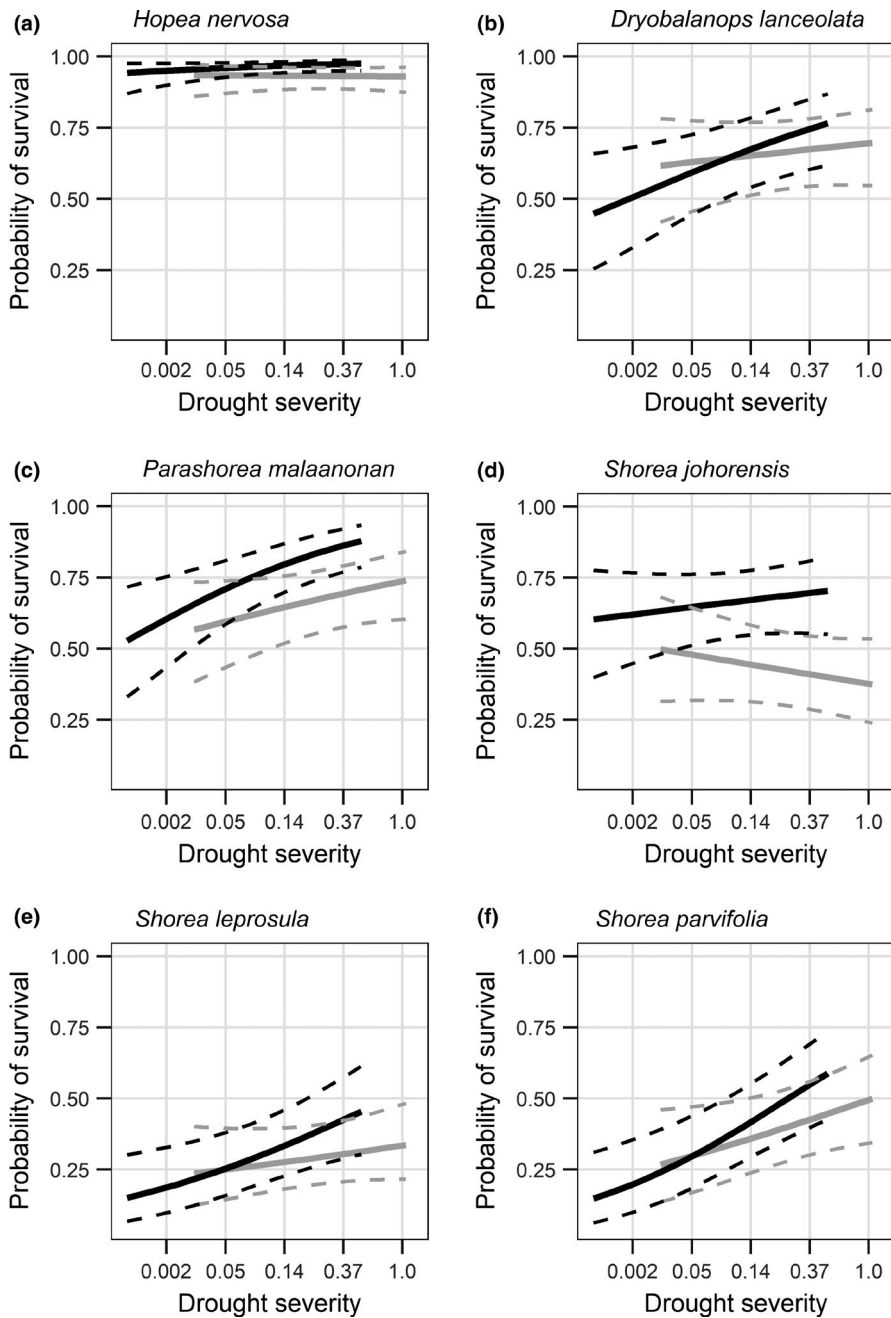


FIGURE 3 Probability of survival in response to drought severity. Probability of survival (95% CI) of seedlings planted at the ridge (grey) and riparian (black) sites for seedlings of each species (a–f) with increasing drought severity during the experiment. Drought severity is the mean minimum soil MPa (average of the minimum MPa between each census in each subplot). Increasing values equal greater drought as the data were transformed by taking the log of the absolute value. The x-axis label provides the untransformed values for interpretation (i.e. 1.0 is a -1.0 MPa). Predictions were generated with average height and light to control for variation among plots and species

among and within species, topography directly influenced growth and survival in this experimental setting, which provides empirical evidence to illuminate mechanisms driving the diversity, structural and abiotic patterns found in observational studies across tropical landscapes (Jucker et al., 2018; Muscarella et al., 2020).

4.1 | Response to water availability across species

The improved growth on the ridge was likely due to a combination of the slightly lower basal area of the surrounding forest and improved water dynamics compared to the riparian site—that is, more freely draining, less saturated and rarely inundated during everwet periods (Figure S4). Saturated soils and inundation events lead to

anaerobic soil conditions that can inhibit growth (Born et al., 2014; Ferreira et al., 2007; Parolin, 2001) while extreme floods along rivers are also turbulent and cause physical damage to seedlings via stem damage and leaf loss (Kramer et al., 2008). The results suggest the former mechanism has substantial influence on seedling growth as minor decreases in soil water in the riparian site caused large increases in growth rates. By contrast, growth on the ridge was largely insensitive to reduced soil water availability (except for the most drought sensitive species). From an evolutionary perspective, palaeoclimate and geological evidence suggests that dipterocarps evolved in a more seasonally dry climate relative to the current conditions (Bird et al., 2005; Kurten et al., 2017; Ng et al., 2021) and occupied a larger geographic range at the last glacial maximum (Cannon et al., 2009). The improved growth in

the drier ridge conditions, despite significant water deficit during drought, may be a legacy from these more seasonal climates (Bird et al., 2005; Cannon et al., 2009). In addition, dipterocarps often show reduced growth to droughts, but overcompensate with faster growth after droughts leading to overall faster growth than continuous water availability over the same period (O'Brien, Ong, et al., 2017). This mechanism may maintain growth rates over multiple years, despite slowed growth during more severe drought in some years.

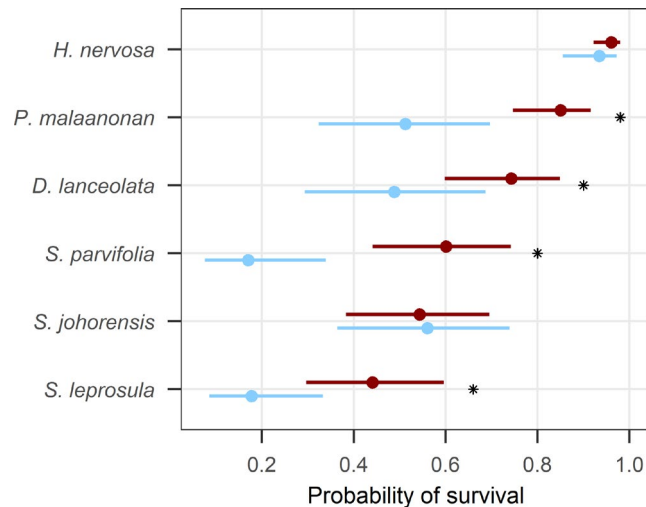


FIGURE 4 Distribution of probability of survival across species. Probability of survival (95% CI) was significantly different among species under severe drought (red) while species show a more clumped distribution of probability of survival under high soil water availability (blue). Within species, inundated soils typically had lower survival. Asterisks indicate significant differences within species between seedlings planted in sites with inundated versus severe drought during the experiment. Soil saturation led to greater mortality, but species partitioned more distinctly in their response to severe drought. Species are sorted by survival from top (highest) to bottom (lowest) under severe drought

Topographic position had less of a role on survival but highlighted differences in stress tolerances among species mainly in their response to saturated soils typical of riparian sites. Dipterocarp species vary in their tolerance to abiotic conditions (nutrient cycling, light and soil water availability) and biotic interactions (competition, herbivores and fungal mutualisms) that change along topographic gradients (Méndez-Toribio et al., 2017; Peay et al., 2015; Takyu et al., 2002; Werner & Homeier, 2015). This study reinforces fitness differences among species but suggests tolerance to saturated and often inundated soils is a strong environmental filter in everwet tropical forests (Silver et al., 1999). In addition to topography, the response of species to water deficit led to the partitioning of survival among species analogous to their known drought tolerances (O'Brien et al., 2015; O'Brien, Ong, et al., 2017), suggesting that drought, independent of topography, promotes species filtering and fine-scale distribution patterns.

4.2 | Neighbour interactions driven by seed-origin

The variation of species fitness differences in response to topography and water availability appears to function in parallel with biotic interactions, which strongly influenced growth and survival within species. Seedlings derived from a lowland origin consistently responded better to increasing neighbour density than their conspecifics originating from upslope origins. The typically higher nutrient and water availability in lowland sites are likely correlated with increased tree abundance and diversity (Jucker et al., 2018). Species turnover along topographic gradients is common in tropical forests (Jucker et al., 2018; Méndez-Toribio et al., 2017; Takyu et al., 2002), and the same processes influencing composition may alter genetic structure among populations within species. Interactions with neighbours led to consistently neutral (growth) or positive (survival) effects on seedlings of lowland seed-origins, and relative to upslope seed-origins, lowland seed-origins were

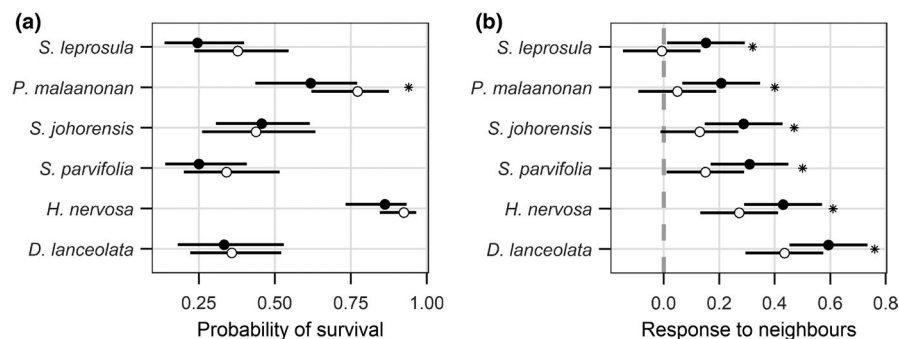


FIGURE 5 Probability of survival within species between seed-origins with no neighbours and in response to neighbours. (a) Probability of survival (95% CI) of seedlings originating from upslope (O) and lowland (●) sites for seedlings with no neighbours with average height and light conditions. (b) The response of survival to increasing neighbour abundance for seedlings originating upslope and lowland positions (neighbour abundance parameter for each seed-origin). Lowland seed-origins always responded positively to increasing neighbour abundance. Asterisks represent significant differences between seed-origins for a species, and species are sorted from least (top) to most (bottom) responsive to increasing neighbour abundance. Figure S7 shows the full response of probability of survival across neighbour abundance

less sensitive to neighbours. In terms of growth, these patterns indicate two important results for the coexistence of individuals from these seed-origins. (a) Upslope individuals grow better in the absence of neighbours, and with minimal plant-plant interactions, seedlings from this seed-origin will be favoured. (b) Interactions with neighbours neutralize these fitness differences between seed-origins to maintain the persistence of these different populations. The patterns of survival indicate the inverse such that fitness differences are lowest with no neighbours and increase due to plant interactions that favour lowland seed-origins. Taken together, our results suggest that under current conditions, populations with different seed-origins show distinct responses to neighbour density that balance fitness differences between origins and indicate unique selection pressures across topography.

These fitness differences among seed-origins may be facilitated by the reproductive biology of the studied species. First, this masting system produces high seed numbers over short intervals that cause dense patches of recruiting seedlings. Second, Dipterocarpaceae is a predominantly insect pollinated family in SE Asia and pollen dispersal is restricted spatially (Kettle et al., 2011). Third, these species typically have limited seed dispersal (Smith et al., 2015). Therefore, migration of genotypes between sites may be limited due to seed dispersal (Smith et al., 2018; Tito de Moraes et al., 2015) and pollen spread (Fukue et al., 2007; Kettle et al., 2011), enhancing selection of genotypes between lowland and upslope individuals. The extrapolation of the patterns found here to other species throughout the tropics should be taken cautiously and will likely depend on the reproductive biology of the plants.

4.3 | Neutral to positive density dependence

Three of the six species showed density-independent growth and four of the six species showed positive density-dependent survival, which contrasts commonly assumed negative density-dependent patterns commonly found in Neotropical systems (Comita et al., 2014; Queenborough et al., 2007; Swamy & Terborgh, 2010). Furthermore, neighbour relatedness was unimportant in explaining variation in growth and survival, although theoretical and empirical studies suggest stronger impacts of conspecific, relative to heterospecific, neighbours (Comita et al., 2014; Queenborough et al., 2007). However, there is increasing evidence that dipterocarps are weakly affected by conspecific density (Song et al., 2021), which may in part be due to their formation of ectomycorrhizal mutualisms (Segnitz et al., 2020). Ectomycorrhizal fungi often mediate positive plant-soil feedbacks (Bennet et al., 2017; Segnitz et al., 2020), nutrient exchange via common mycorrhizal networks (Liang et al., 2020) and defence from soil pathogens (Cannon et al., 2020) all of which would favour positive density dependence and promote local monodominance (Liang et al., 2020). Therefore, the largely neutral to positive density dependence shown here are likely due, in part, to these tree species forming ectomycorrhizal associations.

5 | CONCLUSIONS

Overall, these results offer further support for topography maintaining species level diversity in these aseasonal tropical systems and extends the role of topography to a potential driver of population level diversity. Surprisingly, topographic variation in soil moisture did not contribute to within species differences in growth and survival, suggesting fitness differences among populations to water availability is not directly linked to topography or may only function under severe drought. Regardless, the environmental and biological heterogeneity associated with topography contributes to the maintenance of the hyper-diversity of aseasonal tropical forests via environmental filtering of species and selective pressures on populations.

ACKNOWLEDGEMENTS

We appreciate the support from Dr. Glen Reynolds the Director of the South East Asia Rainforest Research Partnership, field assistance from Remmy Murus the manager of the Sabah Biodiversity Experiment and logistical support from Dr. Robert Ong in Sabah. The field work was supported by the University Research Priority Program Global Change and Biodiversity of the University of Zurich, and the experiment was funded by Atracción de Talento Investigador Modalidad I Fellowship from the Comunidad de Madrid (2018-T1/AMB-11095). Thanks to Christian Schöb and Andy Hector for comments on earlier versions and the thorough revisions by two anonymous reviewers. This publication is number 23 from the Malua Research Team associated with the Sabah Biodiversity Experiment.

CONFLICT OF INTEREST

The authors have no conflict of interest to disclose.

AUTHORS' CONTRIBUTIONS

M.J.O.B. designed and implemented the experiment, analysed the data and wrote the manuscript; A.E. contributed to writing and revisions.

DATA AVAILABILITY STATEMENT

The data are available via the Dryad Digital Repository at <https://doi.org/10.5061/dryad.kkwh70s5m> (O'Brien, 2021).

ORCID

Michael J. O'Brien  <https://orcid.org/0000-0003-0943-8423>

Adrián Escudero  <https://orcid.org/0000-0002-1427-5465>

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How to cite this article: O'Brien, M. J., & Escudero, A. (2021). Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions. *Functional Ecology*, 00, 1–13. <https://doi.org/10.1111/1365-2435.13977>