Tree growth and survival are more sensitive to high rainfall than drought in an aseasonal forest in Malaysia

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Global change research has largely focused on the effects of drought on forest dynamics while the importance of excessive rainfall that can cause waterlogged soils has largely been assessed in riparian zones or seasonally flooded sites. However, increased rainfall may also cause decreased growth and survival of tree species in lowland aseasonal tropical forests due to increased risk from potentially more extensive and frequent waterlogged soils. We used a Bayesian modelling approach on a tree dynamics dataset from 2004 to 2017 to test the concomitant effects of rainfall excess and deficit and dry period length on tree growth and survival across a network of experimentally planted trees in a primary aseasonal forest in Malaysia. Growth declined in 48% of the species and survival decreased in 92% of the species during periods of high rainfall while as little as 4% of species had decreased growth or survival with drought and long dry periods. Climate change is projected to cause more frequent and severe rainfall deficit and excess, and our results suggest increased rainfall may have stronger negative effects on aseasonal tropical forests than that of severe drought.

Climate-change induced shifts in rainfall distributions across the globe are simultaneously causing periods of more severe water deficit and precipitation events with greater quantities of rainfall[1]. Rainfall deficit and severe drought have strong negative effects on growth and survival rates in forests across the globe[2,3] while the effects of excessive rainfall on forest dynamics has largely focused on areas with regular flooding[4–6]. However, as climate change alters rainfall distributions, systems with high rainfall are likely having more soil waterlogging events beyond that of flood zones due to periods of excessive rainfall, especially in lowland humid tropical forests where regular rainfall is an inherent part of the system[1,7]. Understanding the relative importance of rainfall deficits and excesses on forest dynamics is necessary for determining the long-term impacts of these contrasting drivers on forest resilience under climate change.

Water deficit and drought reduces tree growth via stomatal closure and water limitation[8,9] that, if severe and persistent, can lead to increased tree mortality[8,10,11]. Climate change alters the timing, frequency, duration and intensity of drought[12] and tree mortality associated with these altered precipitation patterns is increasingly common[13]. In tropical forests, climate-changed induced shifts in drought are manifested as increased rainfall variability[14], extended dry seasons[15] and irregular severe deficits associated with atmospheric patterns—e.g. El Niño Southern Oscillations[16]. Despite extensive experimental research on the effects of severe water deficits with extreme events and longer dry seasons[11,17], assessments on the importance of these multiple drought characteristics remain limited in tropical forest settings over long-term timelines[18].

In contrast to the extensive research on drought-induced tree mortality, the role of rainfall excess on forest dynamics is constrained to areas which experience regular flooding such as riparian zones and seasonally flooded forests[6,19,20], although recent work has assessed the effects of extreme rainfall on tree growth and survival[7]. However, waterlogging can be a strong environmental filter in forests whereby species and populations maladapted to waterlogged soils are excluded from riparian and seasonally flooded sites[4,21,22]. Periods of more excessive rainfall with climate change[23] suggests a potential for more frequent (in systems with historically high rainfall) and widespread (across sites with poorly drained or nonporous soils) soil waterlogging. An increase in waterlogging could impact species distributions, especially for those species maladapted to soil water saturation that can cause anaerobic soils, greater pathogen loads[24] and increased treefall[25,26]. In particular, the tropical forests of SE Asia are experiencing shorter return intervals between intense rainfall events and more intense rainfall days

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annually[23,27]. Therefore, more temporally and spatially extensive soil waterlogging due to excess rainfall may have drastic effects on tree growth and mortality even in humid tropical systems with historically consistent and high rainfall.

We used a 13-year dataset (2004–2017) of tree dynamics from experimentally planted trees to examine the relative importance of rainfall deficit, length of dry period and rainfall excess (Fig. 1) across a light and topographic gradient on diameter growth and survival of 25 tropical tree species (see Supplementary Table S1 in Supplementary Information for species list) in Sabah, Borneo, Malaysia. We used generalised linear mixed-effects and Bayesian multilevel models to test the simultaneous effects of these climate variables on tree diameter growth at base and survival and compared differences in species responses. We suggest that both periods of rainfall deficit and excess negatively affect growth and survival with drought likely having stronger impacts due to the humid aseasonal conditions typically found in Southeast Asia. In addition, we posit that increased deficit and excess will lead to greater differences in species fitness (e.g., growth and survival).

Results

Size standardised relative growth rate (RGR) increased significantly with increasing light (slope of RGR with light = 0.023, 95% CI: 0.02–0.026) but declined significantly with increasing rainfall excess (slope of RGR with excess = −0.1, −0.11 to −0.08; Fig. 2a) and increasing length of dry period (slope of RGR with dry days = −0.04, −0.06 to −0.02; Fig. 2c). Rainfall deficit had a small nonsignificant positive effect on growth (slope of RGR with deficit = 0.02, −0.0003–0.03; Fig. 2b). Increasing light significantly weakened the effects of rainfall excess (light × excess interaction = 0.0057, 0.005–0.006; Fig. 2a) and rainfall deficit (light × deficit interaction = −0.001, −0.002 to −0.0001; Fig. 2b) on growth, but light did not significantly alter the effect of dry period length on growth (light × dry days interaction = 0.0003, −0.001–0.0005; Fig. 2c). Therefore, high light reduced the strength of the effects on growth for rainfall excess and rainfall deficit but not dry period length (see Wald statistics in Supplementary Table S2 of Supplementary Information). Topographic position did not have a direct effect on growth, but the effect of rainfall excess and dry period length on growth (though not deficit) was significantly different across topographic positions (see Wald statistics in Supplementary Table S2 of Supplementary Information). Specifically, growth declined significantly faster with rainfall excess in upslope sites (upslope × excess interaction = −0.03, −0.05 to −0.02; Fig. 3a) and significantly slower with dry period length in upslope sites upslope × excess interaction = 0.02, 0.002–0.04; Fig. 3c) than in riparian and lowland sites.

As with growth, probability of survival increased significantly with increasing light (slope of survival with light = 0.013, 95% CI: 0.01–0.02). However, probability of survival decreased with increasing rainfall excess (slope of survival with excess = −0.2, 95% CI: −0.25 to −0.16; Fig. 2d) and rainfall deficit (slope of survival with deficit = −0.18, 95% CI: −0.24 to −0.11; Fig. 2e) but not dry period length (slope of survival with dry period = −0.01, 95% CI: −0.07–0.05; Fig. 2f), although only excess had a significant effect (see Wald statistics in Supplementary Table S3 in Supplementary Information). Increasing light significantly weakened the effects of rainfall excess (light × excess interaction = 0.006, 95% CI: 0.004–0.009; Fig. 2d) and dry period (light × dry days interaction = 0.003,
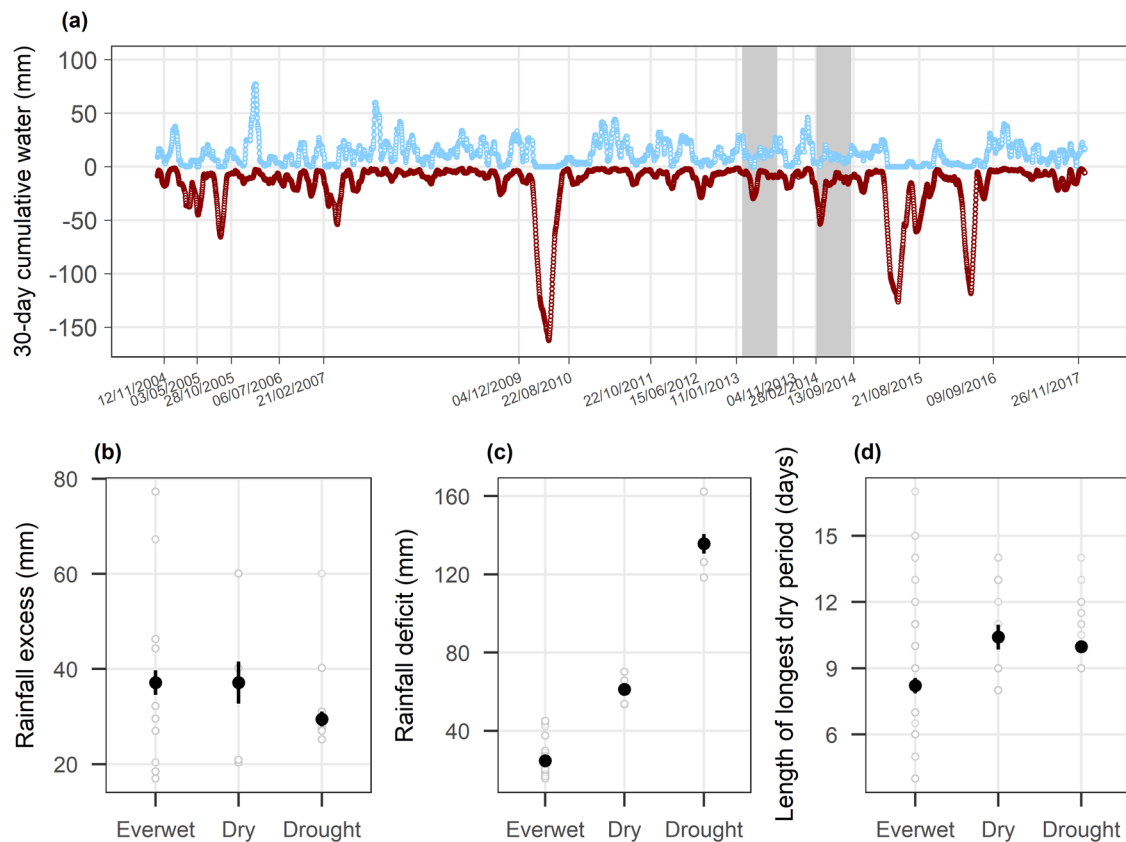

Fig. 1 | 30-day rainfall, excess, deficit and dry periods over 13 years. a Mean 30-day water deficit (red) was calculated as the average rainfall minus evapotranspiration, and mean 30-day rainfall excess (blue) was calculated as the average rainfall where evapotranspiration was exceeded by rainfall. Grey areas represent the placement of rainfall exclusion shelters on some plots. The x-axis labels are the average measurement date for each census. **b** Mean rainfall deficit for each precipitation level. Everwet are census intervals with minimum deficits less than 50 mm. Dry are census intervals with minimum deficits between 50- and 100-mm. Drought are census intervals with minimum deficits greater than 100 mm. **c** Mean rainfall excess for each census at each precipitation level. **d** Maximum number of consecutive days with no rain during a census interval. Error bars are 95% confidence intervals. These three variables are not significantly correlated and the VIF values in a linear model are less than 2.
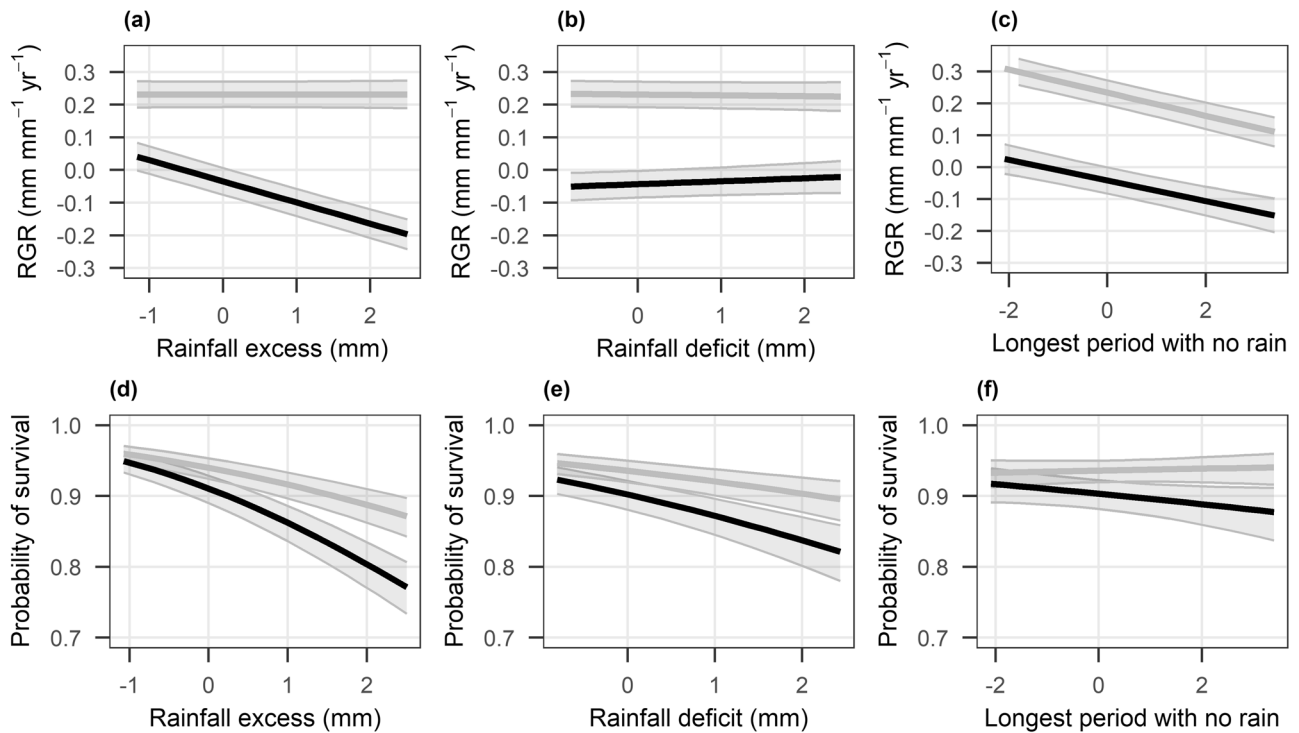
Fig. 2 | Growth and survival in response to climatic variables under different light. Basal diameter growth (**a**–**c**) and survival (**d**–**f**) as a function of rainfall excess (**a**, **d**), rainfall deficit (**b**, **e**) and dry period length (**c**, **f**) for high (grey) and low (black) light levels. Growth and survival were always higher under high light conditions (gaps). Trees tended to have decreased growth and survival with increasing climatic stress but were unaffected by rainfall deficit. Low light conditions altered the effect of climatic variables (steeper slopes under low light) of rainfall excess and deficit but had little effect on dry period length. The x-axis are z-scores for each variable. All responses are estimated with a mean diameter of 9.0 mm. Shaded areas are 95% confidence intervals.
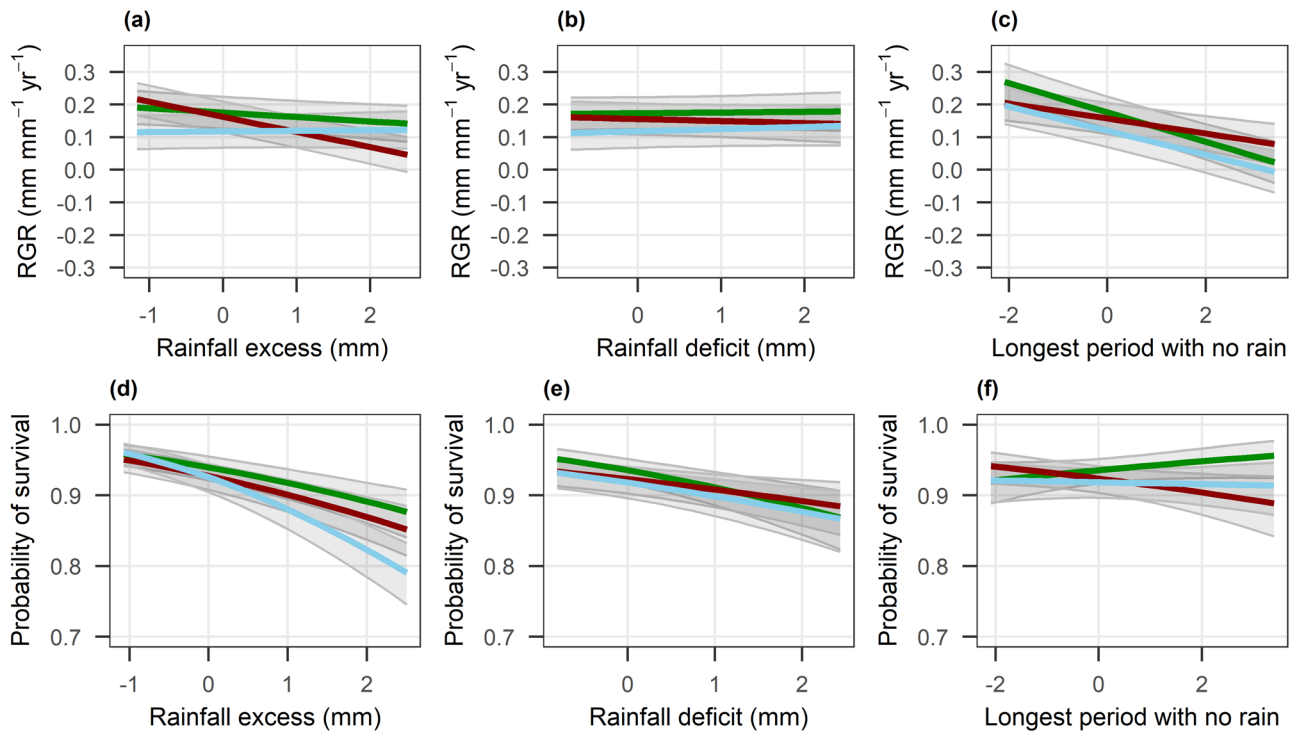
Fig. 3 | Growth and survival in response to climatic variables under different topographic positions. Basal diameter growth (**a**–**c**) and survival (**d**–**f**) as a function of rainfall excess (**a**, **d**), rainfall deficit (**b**, **e**) and dry period length (**c**, **f**) for riparian (blue), lowland (green) and upslope (red) topographic positions. Upslope sites had significantly faster declines in growth with rainfall excess and significantly slower declines in growth with longer dry periods. Survival declined faster with rainfall excess in riparian sites and with dry period length in upslope sites. All responses are estimated with a mean diameter of 9.0 mm. Shaded areas are 95% confidence intervals.

95% CI: 0.0003–0.007; Fig. 2f) on probability of survival but not for rainfall deficit (light × deficit interaction = 0.004, 95% CI: 0.000–0.007; Fig. 2e). Topographic position did not have a direct effect on survival, but the effect of rainfall excess and dry period length on survival (though not deficit) was significantly different across topographic positions (significant interaction; see Wald statistics in Supplementary Table S3 of Supplementary Information). In contrast to growth, survival declined significantly faster with rainfall excess in riparian sites (riparian × excess interaction = −0.09, −0.14 to −0.03; Fig. 3d) and with dry period length in upslope sites upslope × excess interaction = −0.09, −0.02 to −0.15; Fig. 3f) than in lowland and upslope sites. These interactions suggest survival declined with excess rainfall in riparian sites and with prolonged dry periods in upslope sites.

The model examining species level responses showed that growth of all species had a significant positive response to light (Fig. 4a). Growth of twelve species had a significant negative response to rainfall excess (average effect size across species = −0.03, 95% CI: −0.4 to −0.1; Fig. 4b), and only two species had a significant positive response to rainfall excess. Growth of most species had a neutral response to rainfall deficit (average effect size across species = 0.002; 95% CI: −0.01 – 0.01) with one species showing a significant

negative response (*Shorea oleosa*) and one species showing a significant positive response (*Shorea argentifolia*; Fig. 4c). Dry period length showed a significant negative growth response for twelve species (average effect size across species = −0.04, 95% CI: −0.05 to −0.03; Fig. 4d).

All but one species showed a positive survival response to light (Fig. 5a). By contrast, survival of all but two species (*Hopea sangal* and *Shorea superba*) had a significant decrease with greater rainfall excess (average effect size across species = −0.18, 95% CI: −0.21 to −0.15; Fig. 5b). Survival of nine species showed a significant negative response to rainfall deficit (average effect size across species = −0.1, 95% CI: −0.13 to −0.07; Fig. 5c) while survival of only two species responded negatively to dry period length (average effect size across species = −0.01, 95% CI: −0.04 – 0.02) but survival of one species responded positively to dry period length (*Shorea argentifolia*; Fig. 5d).

Because the climatic variables were all standardised (z-scores), a direct comparison of the average effect size suggests rainfall excess and dry period length had similar negative effects on growth while growth was largely unaffected by rainfall deficit. By contrast, the average effect size suggests rainfall excess had significantly greater negative effects on survival than
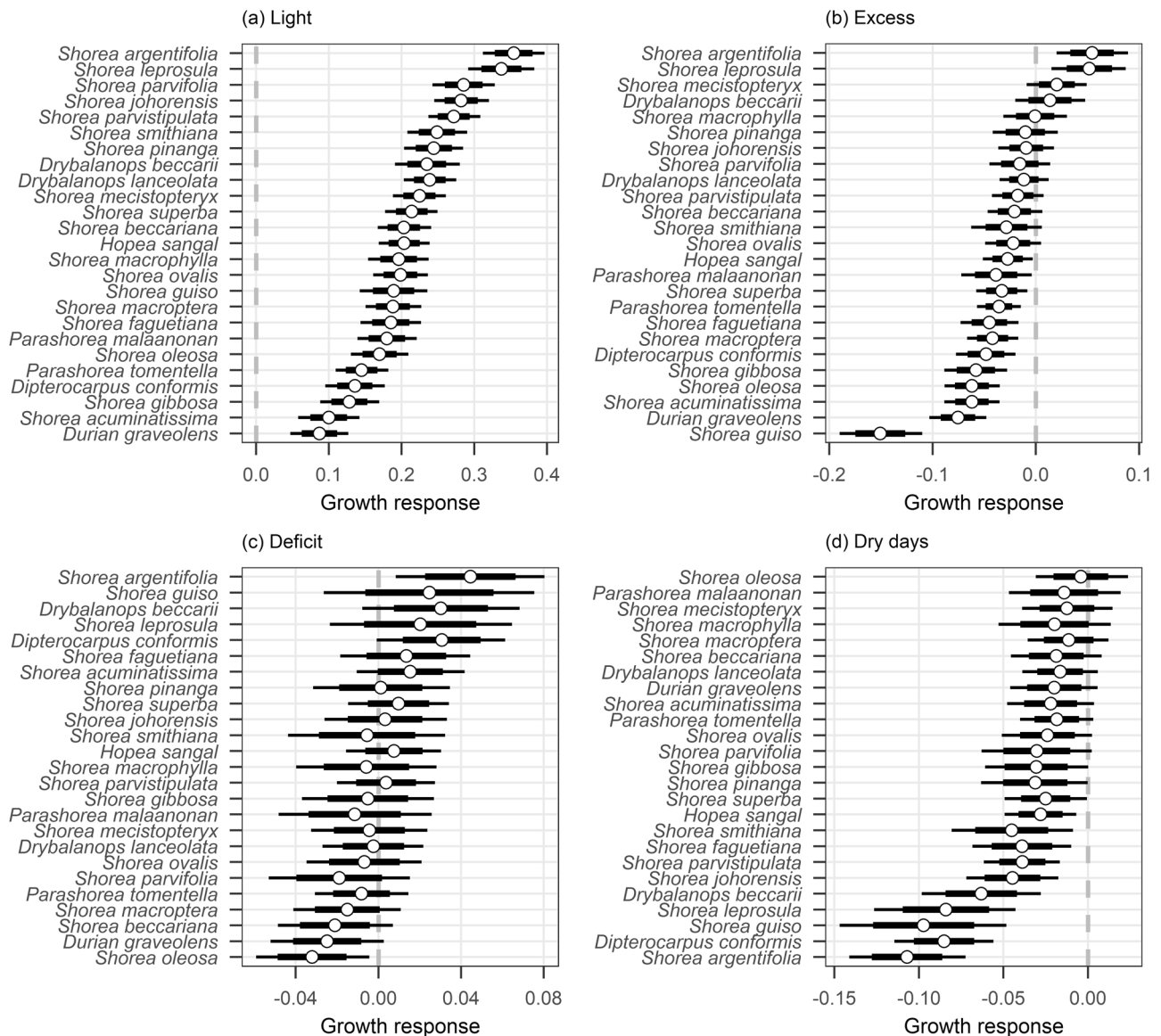
Fig. 4 | Growth response to light and climate variables for each species. Basal diameter growth response (parameter estimates for each species) to **a** light, **b** rainfall excess, **c** rainfall deficit and **d** dry period length for each species. Error bars are 90% credible intervals with one standard deviation in bold. All responses are estimated with a mean diameter of 9.0 mm.
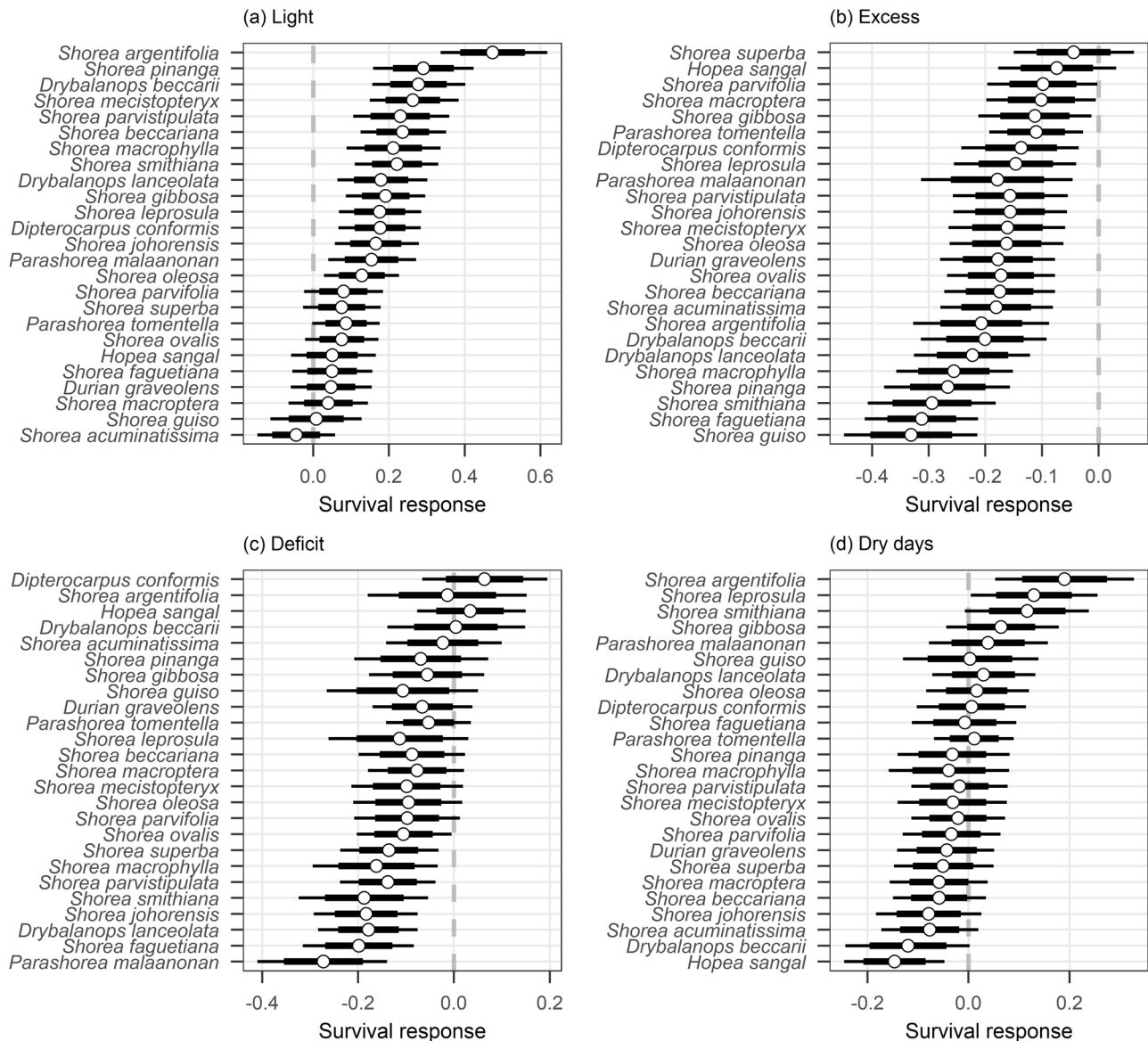
Fig. 5 | Survival response to light and climate variables for each species. Survival response (parameter estimates for each species) to **a** light, **b** rainfall excess, **c** rainfall deficit and **d** dry period length for each species. Error bars are 90% credible intervals with one standard deviation in bold. All responses are estimated with a mean diameter of 9.0 mm.
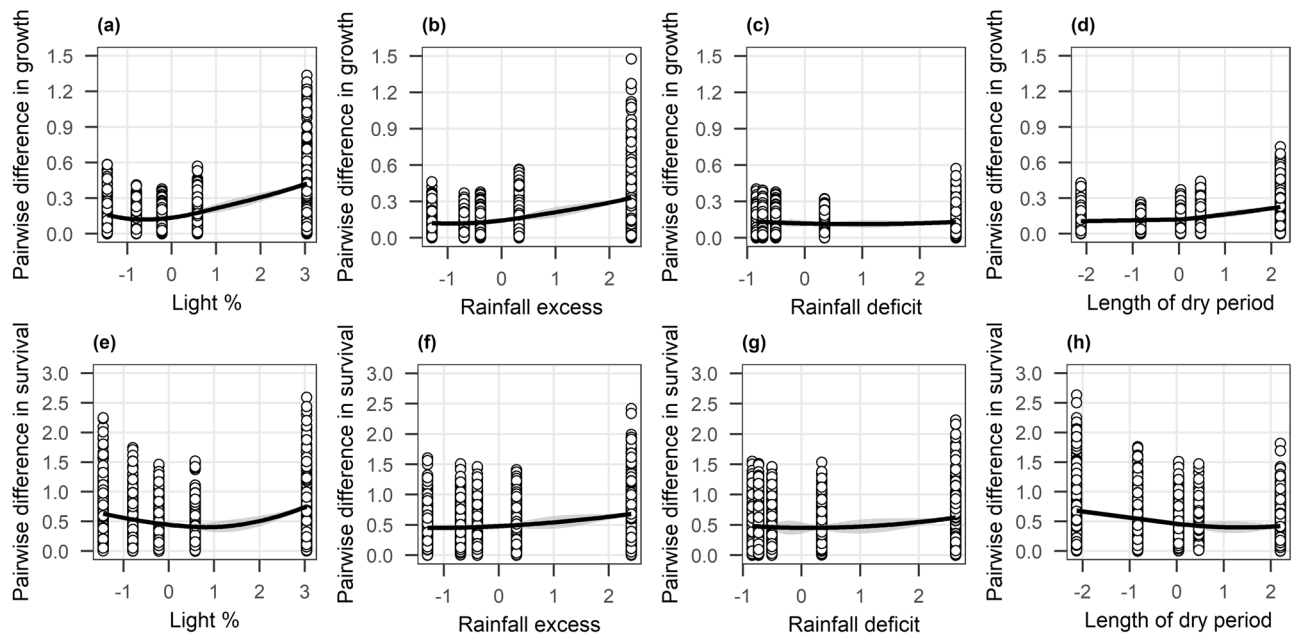
rainfall deficit and dry period length. Therefore, rainfall excess had the greatest negative impact on both the number of species significantly affected (growth of 48% of the species and survival of 92% of the species) and the magnitude of that effect while most species showed a neutral (non-significant) response to rainfall deficit (growth) or dry period length (survival).

Pairwise differences in growth and survival showed a unimodal response to light with low and high conditions increasing differences among species (Fig. 6a, e). Excessive rainfall led to the greatest change in pairwise differences among species for growth (slope of 0.06 across the rainfall excess gradient; Fig. 6b) and survival (slope of 0.07 across the rainfall excess gradient; Fig. 6f). Rainfall deficit had no effect on pairwise difference for growth but caused increases in survival differences at the most severe deficits (slope of 0.03 across the gradient of dry period length; Fig. 6c, g). Dry period length led to an increase in pairwise differences for growth (slope of 0.03 across the gradient of dry period length; Fig. 6d) and a decrease in pairwise species differences for survival (slope of −0.06 across the gradient of dry period length; Fig. 6h).

Discussion
Our assessment of 13-years of tree growth and survival data show that rainfall excess has greater negative effects (in both magnitude and frequency) on growth and survival relative to rainfall deficit and length of dry periods in this aseasonal humid tropical forest. These results suggest tolerance to drought may be common among species in this ecosystem, potentially due to legacy effects from a historically drier environment[28,29]. By contrast, periods of excessive rainfall seems limited to a small portion of species that have likely adapted to prolonged high quantity rainfall and potentially the soil conditions (both physical and chemical) associated with such events. Overall, the projected increased rainfall by climate change models in many humid tropical forests[30,31] may lead to higher mortality rates than those expected under more severe drought, as evidenced by our results from this aseasonal tropical forest[2].

Water availability is typically associated with topographic gradients in tropical forests such that water availability decreases with increasing elevation, which defines structure, composition and functional traits[32–34]. The patterns found in this study that riparian and ridge sites alter tree survival

Fig. 6 | Fitness differences among species in growth and survival in response to light and climate variables. Increasing **a** light, **b** rainfall excess, **c** rainfall deficit and **d** dry period length altered differences in growth among species whereby light, rainfall excess and dry period length increased fitness differences and rainfall deficit decreased fitness differences. Increasing light had the strongest effect on differences in growth. Increasing **e** light, **f** rainfall excess, **g** rainfall deficit and **h** dry period length altered differences in survival among species whereby light, rainfall excess and rainfall deficit increased fitness differences and dry period length decreased fitness differences. Increasing rainfall excess had the strongest effect on differences in survival followed closely by dry period length. Points are pairwise differences among species at each light or climate variable value, and the lines are loess curves showing the trends in the data. The x-axis values are the quantiles of z-scores for light and climate variables. Species values were calculated at mean the size (9.0 mm) with the other environmental variables fixed to their means. Shaded areas are 95% confidence intervals.

such that rainfall excess increases mortality in riparian sites and prolonged rainless periods in upslope sites. Therefore, the topographic extremes may drive similar species compositions whereby waterlogging at riparian sites and drought at upslope sites may explain the persistence of species with conservative growth strategies in both extremes[34–36]. Tolerance to anaerobic conditions and inhibited photosynthesis along with increased storage of nonstructural carbohydrates are physiological traits associated with resistance to waterlogged soils[37], which are the characteristics of conservative species that may facilitate their presence at riparian sites. Waterlogging at riparian sites may promote species with conservative traits just as water deficit promotes species with conservative traits at upslope sites, and increasing excessive rainfall may increase the frequency and spatial breadth of this filter in aseasonal tropical forests[7].

The higher tolerance to rainfall deficit and dry period length than to rainfall excess was unexpected given the homogeneous conditions (i.e., low environmental variation and aseasonal rainfall) of these aseasonal tropical forests over the last 20,000 year[38,39]. However, paleoclimate and geological evidence over longer timelines suggests that the family Dipterocarpaceae evolved in a more seasonally dry climate than the conditions of the last 20,000 years[28,29,38] and occupied a larger spatial area at the last glacial maximum[40]. The tolerance to water deficit may be a legacy from these more seasonal climates that have been topographically maintained as the forest reorganised during the more historically recent aseasonal conditions[38,40]. Our results support previous research from these aseasonal forests that suggest many species are well adapted to drought conditions[41,42].

Furthermore, these species tend to show an anisohydric response to drought, and often continue to maintain stomatal conductance and growth throughout dry conditions until a severe soil moisture threshold is reached[43]. The maintenance of growth during rainfall deficit is further supported by increased sunlight from reduced cloud cover[44]—these variables are highly correlated in Danum Valley based on rainfall and sunshine data over 10 years. Alternatively, many species showed a negative growth response to dry period length. Long periods with no rain (>10 days in this system) cause an abrupt and rapid soil moisture decline, especially as these periods often coincide with limited cloud cover, reduced afternoon humidity and increased afternoon temperatures whereas water deficit may occur slowly over months, with intermittent rainfall events. Therefore, species maintain growth with rainfall deficit but not long dry periods. By contrast, survival was more sensitive to deficit than dry period length suggesting that as species continue to grow during severe deficit, they become susceptible to mortality via desiccation and hydraulic failure while intense dry periods may affect growth but rarely reach the threshold to cause mortality.

Our metric of rainfall excess accounts for continuous high rainfall quantities and not single flood events thereby assessing regular and prolonged water addition to the soil but not necessarily actual inundation. Although our data are not long enough to indicate climate change trends, if climate change (as suggested by projections) leads to an increased frequency and severity of excessive rainfall[1,23], these altered rainfall patterns may suggest that waterlogged soils could become more common both temporally and spatially as areas that previously escaped waterlogging may now experience it under prolonged periods of high rainfall. Species adapted to small topographically raised microsites within a lowland matrix[45] and lower slope positions[36] may be particularly vulnerable to this increased soil waterlogging. Excessive rainfall could lead to widespread mortality if it impacts lowland sites that are often dominated by acquisitive species[34,35]. Based on these results, many of the common species that dominate the primary forest canopy of Borneo may be highly susceptible to rainfall excess.

However, our results cannot distinguish the exact mechanisms behind the increased mortality during periods of rainfall excess. Though physiologically driven mortality due to waterlogging is one possible cause (e.g., lost root biomass from hypoxia), increased pathogen loads with greater soil water regardless of waterlogging may be exacerbating mortality[24]. Furthermore, many canopy and emergent species in Borneo (e.g., dipterocarps) are shallow rooted and may face increased treefall as soil stability decreases under severe and prolonged rain events resulting in mortality due to mechanical failure[25,26] and not physiological-induced mortality.

The increased mechanical failure may be exacerbated by high winds during extreme rainfall events. It is clear more research on the mechanistic causes of mortality are the next steps for understanding the trends found here. Regardless of the mortality mechanism, the results from the analysis of pairwise differences suggest that increased rainfall excess may have long-term impacts on species coexistence.

Climate change projected to lead to greater rainfall extremes in tropical regions with periods of both more intense rainfall and more severe drought[1,23]. Specifically, the tropical forests of SE Asia are having shorter return intervals between intense rainfall events and more intense rainfall days annually[23]. The results from 13-years of tree growth and survival in a humid tropical system unexpectedly suggest that the increase in rainfall may have more severe impacts on forest dynamics than drought, mainly due to a widespread tolerance of the growth and survival of species to water deficit. Slight increases to the already frequent and intense rainfall in this tropical region may have larger impacts on tree growth and survival than previously anticipated. Overall, the increased rainfall associated with climate change that is occurring in many humid tropical forests may lead to higher mortality rates than that expected by more frequent drought. Ecological forecasting and vegetation modelling of tropical forests should include increased rainfall to accurately predict forest dynamics and risk under novel climatic conditions.

Online methods
Study site
This experiment was conducted at the Danum Valley Field Centre (N04.96° E117.80°; 180 MASL), Sabah, Malaysia. The field centre is part of the Danum Valley Conservation Area (DVCA), a 43800-ha area of primary lowland forest dominated by the Family Dipterocarpaceae (dipterocarps). The conservation area has Class I status (fully protected) since the early 1980s with limited disturbance prior to that designation. On average, the field centre receives ~2900 mm (SD: 460 mm) of annual rainfall (1986–2021). The yearly rainfall is evenly distributed with average monthly rainfall above 100 mm across all months[46]. However, the site does receive irregular drought periods typically driven by El Niño Southern Oscillations that cause severe droughts and periods with consecutive days of no rain. In Southeast Asia, annual rainfall has been on the rise, although the distribution has become more variable with more days without rain and more regular extreme rainfall events[23]. At Danum Valley, this trend has resulted in more days with heavy rain (>20 mm) between 2004–2021 (855 days) than between 1986–2003 (812 days). This coincided with a greater frequency of heavy rains between 2004–2021 (mean return interval of 7.7 days, SE = 0.21) than between 1986–2003 (mean return interval of 8.8 days, SE = 0.27). Wind is also a regular disturbance causing wind throw events of large canopy trees, leading to heterogeneity in forest canopy and the understorey light environment[47].

Experimental design
The experiment was planted in November 2004 throughout the primary forest south and west from the field centre. Twenty plots were placed across a large size range (12–400 m^2) of natural canopy openings (gaps) and paired with identical plots under closed canopy (understorey). Understorey sites were placed 30 m from each tree-fall gap at a random compass bearing. The combined gap and understorey plots represent a block. Blocks were placed across the range of topography found in Danum Valley whereby 6 blocks were in lowland riparian areas, 7 blocks were in lowland areas away from rivers and 7 blocks were on upslope sites (Supplementary Fig. S1 in the Supplementary Information). The mean elevation across all plots was 249 m (range = 203–319 m) and the mean slope was 20 degrees (range = 3–56 degrees).

Within each gap and understorey plot, two identical subplots were planted with seedlings of 25 tree species at 0.75 × 0.75 m spacing for a total of four subplots per gap-understorey pair and a total of 80 subplots (20 pairs × 2 gap/understorey plots × 2 subplots = 80 subplots). Due to the infrequent seed production of tree species in lowland Borneo forests, species were selected mainly based on availability in local nurseries (see Supplementary Table S3 in Supplementary Information for species information). Twenty-four species were dipterocarps spanning five genera (Dipterocarpus, Dryobalanops, Hopea, Parashorea and Shorea) and one species of Bombaceae (*Durian graveolens*). Within each subplot, species were randomly assigned a planting point, therefore, all 80 subplots had a different planting pattern.

Environmental and seedling measurements
Six months after planting—to allow for mortality due to planting stress (which was replanted after one and three months—seedlings were measured for height and diameter at base (10 cm from soil surface). From 2004 to 2007 seedlings were measured every 6 months after which they were measured approximately yearly from 2007 to 2017. One census was not included in this analysis because it was measured only 3 months after the previous census, which led to a total of 16 censuses. These measurements of growth were used to calculate relative growth rate as the difference in log-diameter between two measurements divided by the number of days between measurements standardised to year by dividing days by 365.25. The average initial diameter at base of seedlings in 2004 was 4.5 mm (range = 1.0–16.0 mm), in 2010 it was 20.9 mm (range = 1.7–130.0 mm) and in 2017 it was 45.6 mm (range = 3.8–331.0 mm). Therefore, the analysis encompasses a wide size range from small seedlings to trees with a DBH of 301 mm.

Gap light within each subplot was estimated from hemispherical photos taken at the centre of each subplot on a tripod 80 cm from the ground with a Nikon D60 camera and a Nikon Fisheye lens (10.5 mm f/2.8 G; Nikon Corporation, Tokyo, Japan) in October 2004. Photos were taken on cloudy days, early in the morning to prevent sun washing of the canopy openings in the photos. The images were analysed with Gap Light Analyzer (v2.0; Frazer et al.[48]) to estimate light within each subplot. The mean light environment (Supplementary Fig. S2 in Supplementary Information) was 6.2% in the understorey (range 1.5–12.0%) and 19.3% in the gaps (range = 9.6–40.5%).

Rainfall was measured at 08:00 daily at the Danum Valley Field Centre during the entire experiment and was used to calculate climatic variables that affect seedling growth and survival (Fig. 1a). Daily rainfall deficit and excess were calculated by taking the sum of rainfall minus evapotranspiration[49]—assumed as 4 mm per day[50–52]. Evapotranspiration of 3.5 mm and 4.5 mm were also used in the calculations, and the global linear mixed effects models were analysed with these values to assess the sensitivity of our models to evapotranspiration. The global models showed no change in sign, significance nor magnitude of model parameters, which suggests our metric is robust within the bounds of the typical values measured in Borneo (see Supplementary Figs. S3 and S4 in Supplementary Information for model outputs with 3.5 mm and 4.5 mm evapotranspiration). Although a variable evapotranspiration rate could be employed (accounting for changes in light and rainfall), this would lead likely lead to a similar average of 4.0 mm as suggested by multiple studies from the region[50–52], and our calculation remains conservative as we use the minimums and maximums of the 30-day running average instead of daily extremes. Days with rainfall above evapotranspiration demands were defined as excess while days below were defined as deficits. The 30-day running average of these values were then calculated for each day. The minimum 30-day value per census period was defined as the magnitude of deficit and the maximum value as the magnitude of excess (Fig. 1). These metrics represent drought and rainfall severity (potentially causing prolonged waterlogging or saturated soils Supplementary Fig. S5) in a census period. In addition, the maximum number of consecutive days without rainfall within a census period was used as the length of the longest dry period. These three variables are not significantly correlated and the variance inflation factor values in a linear model were less than 1.5, suggesting they are not collinear.

To assess whether our metric of rainfall and deficit related to soil moisture, we used a generalised linear mixed effects model of soil moisture measured monthly from July 2015 to November 2019[36] as a function of

30-day average of rainfall deficit to excess (a continuous variable), the quadratic of 30-day average of rainfall deficit to excess (a continuous variable), topographic position (a factor with 3 levels: riparian, lowland and ridges) and the two way interactions between 30-day average of rainfall deficit to excess (both linear and quadratic) and topographic position. We treated 30-day average of rainfall deficit to excess as a continuous term taking the largest value of either the deficit or excess per month long census interval. Soil moisture increased significantly with 30-day average of rainfall deficit to excess (see Table S4 in the Supplementary Information). Volumetric soil moisture was as low as 31.8% (95% prediction interval = 17.7–45.7%) for riparian sites, 20.3% (95% prediction interval = 6.3–34.1%) for lowland sites and 19.1% (95% prediction interval = 5.1–33.2%) for ridge sites at rainfall deficit of 150 mm and as high as 38.8% (95% prediction interval = 24.8–52.6%) for riparian sites, 33.5% (95% prediction interval = 19.6–47.3%) for lowland sites and 34.3% (95% prediction interval = 20.3–48.2%) for ridge sites at rainfall excess of 40 mm (Supplementary Fig. S5 in Supplementary Information).

Experimental drought for two years

Between 2013 and 2014, clear polyethylene plastic sheeting was applied over one subplot within each gap for 15 of the plots and one subplot within each understorey for 5 of the plots. The imbalance was due to high mortality and slow growth in the understorey subplots, making it logistically difficult to apply the sheeting. This sheeting was first used between 10 February 2013 and 12 August 2013 and then again between 3 March 2014 and 1 September 2014 (allowing 7 months of rain between applications). It was suspended on a web of wires at approximately 1.5 m from the ground and covered a total of 25 m^2 (allowing 1 m buffer on all sides of the subplot). In addition, 20 cm aluminium barriers (10 cm within and 10 cm above the soil surface) were placed upslope from the plots to prevent overland waterflow. These treatments led to a significant decrease in volumetric moisture at the soil surface—23% (95% CI: 20–26%) with plastic versus 38% (35–41%) without plastic. However, these treatments were ignored in our multiyear analysis due to the difficulty in relating single point measurements of soil volumetric moisture under plastic sheeting to 30-day average rainfall because the plastic sheeting dries the soil even with rainfall.

Analysis

To explore the general trends of light and climate on tree growth and survival across species, we used generalised linear mixed-effects models to analyse size-standardised relative growth rate (RGR; Gaussian distribution with identity link) and survival (binomial distribution with complementary log-log link) across censuses. These vital rates were modelled as a function of initial size (diameter at the previous census in mm), light (% direct sunlight, a continuous variable), maximum rainfall deficit during the census interval (mm, a continuous variable), longest dry period during the census interval (days, a continuous variable) and maximum rainfall excess during the census interval (mm, a continuous variable). We included the topographic position of each plot recorded as riparian (low lying regularly saturated soils within 5–10 m elevation of waterways), lowland (low lying but well-drained soils more than 10 m elevation from waterways) and upslope (sloped or ridge sites with well-drained soils). We also tested the two-way interactions between light and the three climatic variables and between topography and the three climatic variables. Random terms for species (a random intercept with 25 levels) and each individual subplot (a random intercept with 80 levels) were used to account for species and spatial variation, respectively. The growth model also had a random term for individual (a random intercept with 2000 levels) to account for repeated measures. Models were fitted using the asreml-R package (ASreml 4, VSN International, UK) in R (version 4.3.1) and all predictions are provided at the standard mean size of 9.0 mm.

To assess responses to climate variables across species, we used a Bayesian modelling approach to examine the effects rainfall excess, rainfall deficit and length of dry periods along a light gradient on growth and survival (i.e., interaction between species and all four environmental variables but not between environmental variables). Predictions of survival and RGR were made at a standard diameter of 9 mm. All Bayesian models were fitted in Stan (https://mc-stan.org/) with the rstanarm package using default priors. The Gaussian family with an identity link function was used for growth analysis, and the binomial family with a complementary log-log link function was used for analysis of survival. We ran the models with 4 chains, for 2000 iterations with a warm-up of 1000 iterations, and checked mixing and convergence visually and using automated diagnostics.

Predictions from the Bayesian models were used to calculate pairwise differences between species pairs in RGR and survival. The relationship of these pairwise differences between species in RGR and survival was tested across the range of light and climate variables to assess the effect of these environmental variables on fitness differences. Smaller differences among species pairs indicates greater similarity in species fitness, which should promote coexistence[53,54].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

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Author contributions
M.O.B. carried out some of the field measurements, analysed and wrote the manuscript. A.H. provided logistical and financial support for experimental setup and data collections. R.O. provided logistical support for carrying out research in Sabah, Malaysia. C.D.P. designed the experiment and collected the data. All authors contributed to writing and revisions.

Competing interests
The authors declare no competing interests.

Ethics approval
All research was carried out with the approval of the Sabah government, the Sabah Biodiversity Council (SaBC) and the Danum Valley Management Committee (DVMC) to Christopher Philipson and Michael O'Brien. All local collaborators were invited as authors before submission of the manuscript.

Additional information
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