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Resistance of tropical seedlings to drought is mediated by neighbourhood diversity

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Occasional periods of drought are typical of most tropical forests, but climate change is increasing drought frequency and intensity in many areas across the globe, threatening the structure and function of these ecosystems. The effects of intermittent drought on tropical tree communities remain poorly understood and the potential impacts of intensified drought under future climatic conditions are even less well known. The response of forests to altered precipitation will be determined by the tolerances of different species to reduced water availability and the interactions among plants that alleviate or exacerbate the effects of drought. Here, we report the response of experimental monocultures and mixtures of tropical trees to simulated drought, which reveals a fundamental shift in the nature of interactions among species. Weaker competition for water in diverse communities allowed seedlings to maintain growth under drought while more intense competition among conspecifics inhibited growth under the same conditions. These results show that reduced competition for water among species in mixtures mediates community resistance to drought. The delayed onset of competition for water among species in more diverse neighbourhoods during drought has potential implications for the coexistence of species in tropical forests and the resilience of these systems to climate change.

Many types of tropical forest are characterized by constant temperature and humidity, typically experiencing regular rainfall that is evenly distributed throughout the year. However, rainforests often experience infrequent droughts (for example, during El Niño Southern Oscillation (ENSO) years), although the effect of these events on forest structure and functioning is poorly understood[1,2]. On the one hand, drought could increase the success of some species, putting them at an advantage, increasing dominance and potentially decreasing diversity[3]. On the other hand, drought could promote diversity by enhancing density-dependent mechanisms that favour uncommon species[4]. For example, drought may increase intraspecific competition for light, water and associated soil resources or predispose trees to pathogen infection or insect attack[5–7], both of which are density-dependent mechanisms that can influence community diversity[8–10].

Although light is usually considered the most important resource gradient driving species distributions in tropical forests[7], climate change is projected to increase the severity and frequency of drought for substantial areas of tropical forest[1,11], thereby increasing the importance of water limitation as a driver of species distributions[12]. These changes pose a potential risk to these hyper-diverse ecosystems due to negative effects on reproduction[13], recruitment[13], growth[3,14] and survival[3,15]. Species diversity may provide an insurance effect against these alterations and stability under drought conditions[16,17] because species vary in their resistance and resilience to severe climatic disturbances[3,18]. If conditions go beyond the physiological limits of even the tolerant species, large-scale mortality will occur regardless[19]. However, there is limited empirical evidence regarding the direction and magnitude of the interactions between drought and tree diversity as research has largely focused on species distribution and functional composition shifts[20,15,20].

In the present study, we tested how drought affects interactions among tropical tree seedlings in monocultures and mixtures of different species. We used rainfall-exclusion shelters to reduce soil water availability while altering tree seedling diversity by manipulating neighbourhood richness around focal individuals (Fig. 1). Ecological theory predicts that competition for limited resources is more intense when species and individuals are more similar and closely related[21,22]. Therefore, neighbourhood diversity consisted of three treatments in which a focal individual was surrounded by three individuals of either the same species or different species, as follows: (1) a focal seedling surrounded by seedlings of three species different from the focal species (mixtures), (2) monocultures of a focal seedling surrounded by three seedlings originating from a different mature tree of the same species (non-siblings) and (3) monocultures of a focal seedling surrounded by three seedlings originating from the same mature tree as the focal seedling (siblings). The third neighbourhood represented the dense aggregated seedling communities that form under mature trees after mast seed production—a common reproductive strategy in these ever-wet tropical forests[23]. We used the rainfall-exclusion shelters for two intervals lasting three and six months over a two year period to simulate drought intensity similar to supra-annual droughts in Malaysian Borneo[24] (Fig. 2). We monitored focal seedling growth and mortality and quantified the magnitude of the drought response in leaf physiology while assessing nutrient concentrations to test if drought increased competition for water and nutrients.

Results

We found an interaction between the drought and diversity treatments in which the strength of competition was related to seedling neighbourhood diversity under drought but not under ever-wet conditions (Fig. 3a). Specifically, in the monocultures (that is, sibling and non-sibling treatments), the relative growth rate (RGR) was significantly lower in the drought than ever-wet treatments, but seedlings in mixtures had RGRs that were statistically

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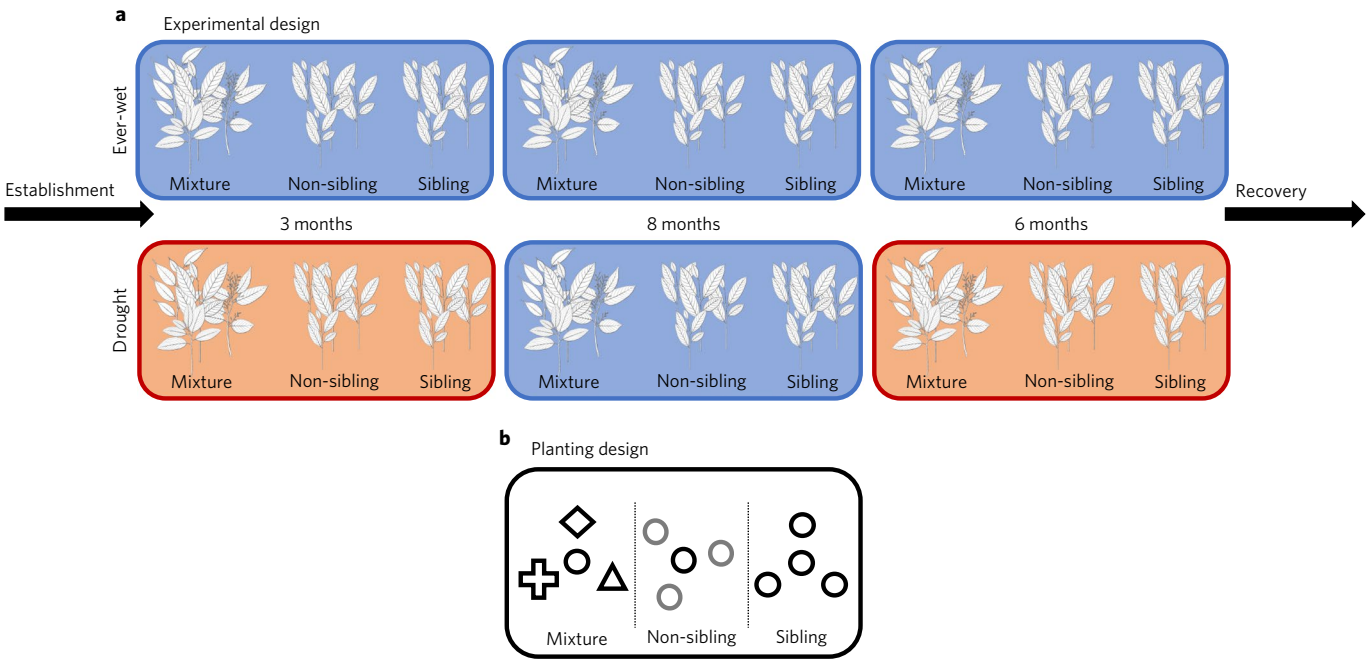

Fig. 1 | Experimental and planting design. a, The experimental design consisted of two sub-plots each with a distinct rainfall treatment: ever-wet (blue) and drought (red). **b**, Within each rainfall treatment, there were three neighbourhood treatments: (1) mixtures with three species that were different from the focal seedling; (2) non-sibling monocultures with individuals from a mature tree different from the focal seedling; and (3) sibling monocultures with individuals from the same mature tree as the focal seedling. These three conditions were replicated for each of the focal species (*D. lanceolata*, *H. sangal*, *P. malaanonan* and *S. parvifolia*) under both drought and ever-wet conditions in 20 plots. The mixture neighbourhoods were standardized for all focal species using three additional species (*H. nervosa*, *P. tomentella* and *S. argentifolia*).

indistinguishable under drought and ever-wet conditions (Fig. 3b and Supplementary Table 1). These results are consistent with reduced competition for water in species mixtures relative to monocultures. Furthermore, the average RGR for all the species under drought was higher in the mixtures than the monocultures (reduction in RGR due to non-sibling competition = -0.06 cm cm^{-1} yr^{-1}, 95% confidence interval (CI): -0.1 to -0.02; reduction in RGR due to sibling competition = -0.04 cm cm^{-1} yr^{-1}, 95% CI: -0.07 to 0.003). These results indicate that overall mixtures and monocultures were significantly different under drought (see the significant contrast × rainfall term in Supplementary Table 1), but the sibling treatment was only marginally different from the mixture treatment (see the neighbour × rainfall term in Supplementary Table 1). Although mortality was not severe (only

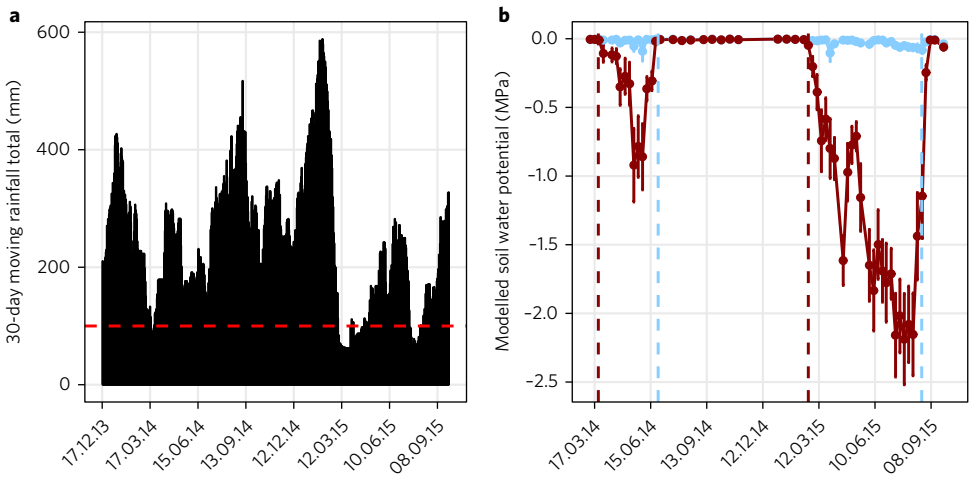

Fig. 2 | Rainfall and soil water potential during the two years of the experiment. a, Cumulative rainfall over 30 days from the first measurement of height. The red dashed line is the predicted rainfall threshold for drought. **b**, Modelled soil water potential (95% CI) during the two years of the experiment for drought (red lines and dots) and ever-wet (blue lines and dots) treatments ($n = 20$ for each rainfall treatment per sample after averaging three to five measurements per sub-plot). The vertical dashed lines represent the start (red) and end (blue) of the rainfall-exclusion shelters. The soil moisture was converted from volumetric soil moisture (%) to water potential (MPa) using the filter paper method. The soil water potential reached minimums similar to that measured during the El Niño droughts in 1997 and 1998 (ref. [24]).

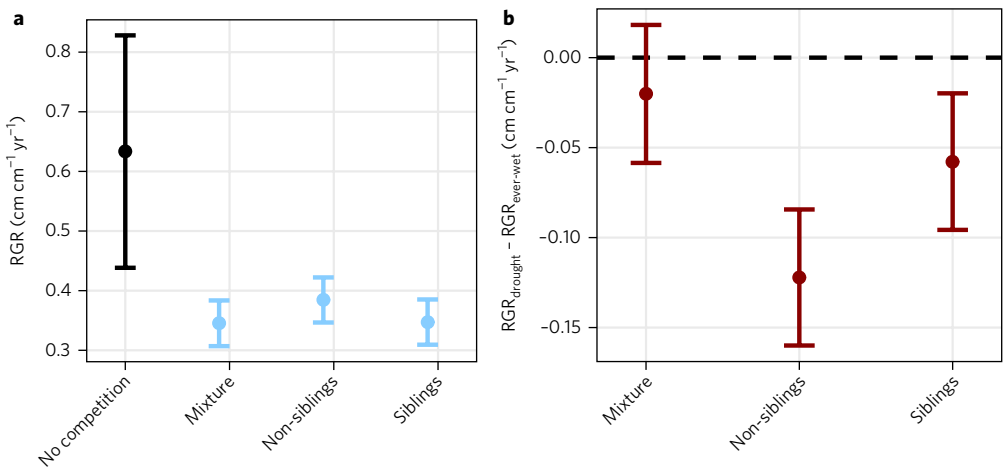

Fig. 3 | RGR for each neighbourhood and water treatment. a, RGR (95% CI) for seedlings under ever-wet (blue) conditions for mixture, non-sibling and sibling neighbourhoods ($n = 80$ for each neighbour × rainfall treatment). The black point is the estimated RGR (95% CI) without competition from a similar experiment in the Malua Forest[3]. It represents the maximum growth rate potential for seedlings of these species. **b**, The difference in the RGR (95% CI) was statistically indistinguishable between drought and ever-wet seedlings—that is, the 95% CI in the difference crossed zero (black dashed line)—for the mixture neighbourhoods (reduction in RGR due to drought = −0.02 cm cm^{-1} yr^{-1}, 95% CI: −0.06 to 0.02). However, growth was significantly reduced under drought for non-sibling (reduction in RGR due to drought = −0.12 cm cm^{-1} yr^{-1}, 95% CI: −0.16 to −0.08) and sibling neighbourhoods (reduction in RGR due to drought = −0.06 cm cm^{-1} yr^{-1}, 95% CI: −0.1 to −0.02). The RGR was calculated at a standardized average height of 50.75 cm for comparison among individuals with initial size differences. A covariate for focal seedling size relative to average neighbour size was used to account for initial height differences among competing individuals.

3% of the focal seedlings died), 80% of mortality occurred in the drought treatment.

Measurements of seedling physiology support intensified competition for water as the cause of lower growth rates in monocultures during drought. Our experimental drought caused seedlings in all neighbourhoods to close their stomata to levels of 44% conductance (95% CI: 35–55) in ever-wet conditions (Fig. 4a and Supplementary Table 2). Therefore, seedlings in all neighbourhoods were responding to drier soils—at levels similar to seedlings after approximately 70–100 days of no water in a dry-down pot experiment[25] (Supplementary Fig. 1). Despite all neighbourhoods showing reduced (but not completely inhibited) stomatal conductance, leaf water potentials were significantly different among neighbourhoods under drought. Leaf water potentials of focal seedlings were only significantly lower in the drought than the ever-wet treatment in the non-sibling (reduction in leaf water potential due to drought = −0.3 MPa, 95% CI: −0.4 to −0.2) and sibling neighbourhoods (reduction in leaf water potential due to drought = −0.2 MPa, 95% CI: −0.3 to −0.1) (Fig. 4b). Conversely, the leaf water potential of focal seedlings in mixture neighbourhoods was statistically indistinguishable in the drought and ever-wet treatments (reduction in leaf water potential due to drought = −0.03 MPa, 95% CI:

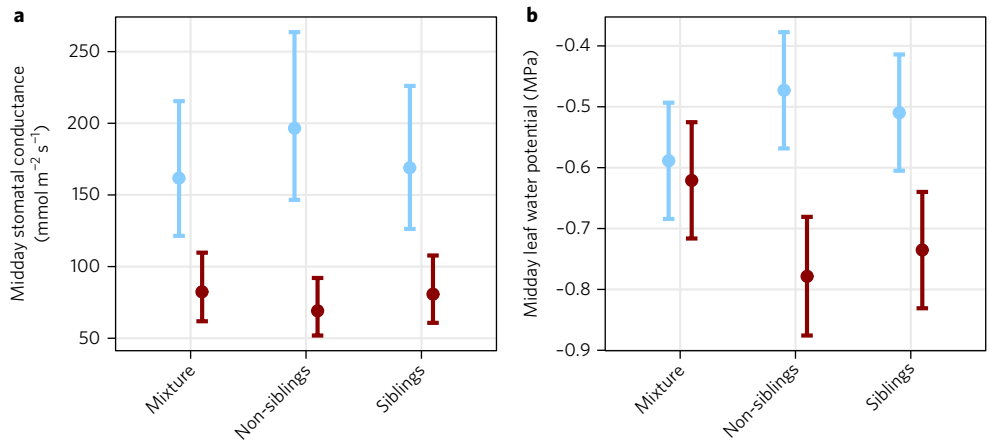

Fig. 4 | Seedling water stress under rainfall and neighbourhood treatments. Physiological response of seedlings to drought (red) and ever-wet (blue) conditions in mixture, non-sibling and sibling neighbourhoods. **a**, Midday stomatal conductance (95% CI) was significantly lower than the ever-wet treatment for all neighbourhoods in the drought treatment ($n = 32$ for each neighbourhood × rainfall treatment). Stomatal data were log transformed, but are presented on a normal scale after back transformation. **b**, Leaf water potentials (95% CI) were significantly lower under drought for non-sibling and sibling neighbourhoods ($n = 24$ for each neighbourhood × rainfall treatment), but the leaf water potential was statistically indistinguishable between the drought and ever-wet conditions for species mixtures.

−0.1 to 0.1). In addition, under drought, seedlings in monoculture neighbourhoods had significantly lower leaf water potential than seedlings in mixtures (reduction in leaf water potential due to non-siblings = −0.2 MPa, 95% CI: −0.3 to −0.1; reduction in leaf water potential due to siblings = −0.1 MPa, 95% CI: −0.2 to −0.02). These results indicate that competition for water was more intense between individuals of the same species than among seedlings of different species, which may be due to different rooting strategies or water use efficiencies, which produce complementarity in mixtures[26].

Discussion

Two pathways to reduced plant growth under drought have been suggested: carbon limitation due to stomatal closure[27] and sink limitation (that is, limited water or nutrient availability) that inhibits plant function and decouples growth and photosynthesis[28,29]. Previous research indicates that dipterocarps continue to photosynthesize during drought, leading to accumulated non-structural carbohydrates but eventually hydraulic failure[25,30–32]. Our results support the hypothesis that the mechanism limiting growth during drought—and eventually leading to mortality with increased drought severity—is water limitation that inhibits cell expansion or division and not carbon limitation due to stomatal closure[28–30]. Furthermore, although drought could also affect the availability or uptake of other soil resources, the leaf nitrogen and phosphorus concentrations and nitrogen-to-phosphorus ratios[33] were statistically indistinguishable among all levels of competition and water availability (Supplementary Fig. 2 and Supplementary Table 3), which indicates that competition for nutrients was similar among all neighbourhoods. The incomplete closure of stomata, reduced leaf water potentials in monocultures and lack of differences in leaf nutrients suggest that focal seedlings in diverse mixtures had delayed water limitation during drought (and not a limitation of carbon or nutrients), enabling them to maintain higher RGRs. In contrast, seedling growth in monocultures became more quickly limited by water during drought.

Surprisingly, under ever-wet conditions, the growth of the focal seedlings was statistically indistinguishable among the three levels of diversity (Fig. 3a). A comparison of these growth rates with those of seedlings grown for two years at low density without competition in a nearby experiment[3] showed that the RGR was reduced by about 38% (Fig. 3a). Competition for resources other than water appears to have had strong negative effects on seedling growth in general, but the effect was independent of diversity under ever-wet conditions, consistent with small differences among species at the seedling stage in an ever-wet climate[34]. More unexpectedly, our results suggest that intermittent drought induces competition for water among conspecifics, which raises the possibility that ENSO events may promote coexistence. The role of differences in species' tolerance of drought—usually inferred through differences in drought-induced mortality—in determining their spatial distribution in tropical forests[12] and shifts in functional composition in response to drought were investigated in a previous study[20]. However, our results lead us to hypothesize a potential stabilizing role of competition for water during intermittent drought—a type of hydrological realized niche—which may act as another driver of species distributions, in conjunction, and interacting with, heterogeneity in light and nutrients[7,35].

Non-sibling and sibling neighbourhoods had similar effects on focal seedling growth. We did not observe competitive differences at the genotypic level (that is, the contrast of mixtures versus monocultures explained the most variation among neighbourhoods). Instead, responses were mainly at the species level (Supplementary Fig. 3) and between mixtures and monocultures (see the significant species × contrast × rainfall term in Supplementary Table 1). Our diversity treatment was designed to vary the genetic similarity of seedlings in a three-level gradient from most similar (siblings) to intermediate (non-siblings) to most dissimilar (mixtures), but the lack of effect between the sibling and non-sibling treatments may be explained by insufficient genetic dissimilarity among seed sources. For example, a high degree of out-crossing and long-distance pollen dispersal among mature trees would reduce variability among seed sources[36].

Our results are based on seedling responses under experimental conditions and require comparison with existing and future data from natural droughts. To impose competition, our experiment required relatively high seedling densities, although these were within the range of seedling densities four years after a mast fruiting event (that is, 3–75 seedlings m^{-2}). We used midday leaf water potential as an indicator of water limitation. The use of pre-dawn leaf water potential or loss of hydraulic conductivity may have provided more direct means of assessing water limitations on growth since midday water limitation can be overcome with diurnal refilling (although it might be expected that the recovery of water potential during the day would require greater refilling than in the pre-dawn period). Supra-annual ENSO droughts in our study system normally lasted for between one and three months[37]. In our experiment, rainfall-exclusion shelters were maintained for as long as six months to induce soil drying during natural tropical rainfall, which caused water movement through the soil and higher cloud cover and humidity than there would be during an ENSO event. However, this application achieved soil water potentials similar to and slightly greater than an ENSO drought[24].

Seedling dynamics and recruitment into the sapling stage are important processes that influence the future structure and composition of a forest[3,38,39] and drought is likely to play a more prominent role in mediating those dynamics under climate change scenarios. Although these results at the seedling level have implications for future forest canopies, they may not directly relate to interactions among adult trees. In addition, tropical forest diversity is far greater than the number of species used in this experimental manipulation. However, the species were selected to encompass the range of functional traits found in the natural forest (Supplementary Fig. 4), and these species showed highly variable responses to both water availability and neighbourhood diversity that could not be solely explained by traits[40]. Further research on the drought responses of adult trees and more diverse tropical forest communities in general are needed to improve our understanding of the implications of a changing climate for this important ecosystem.

Our results have implications for two related areas of ecology. Our experimental demonstration of reduced competition for water among seedlings in diverse neighbourhoods suggests that intermittent drought may be a process that promotes and maintains diversity in these tropical rainforests, as has been shown to be the case in a prairie grassland[4]. At the same time, our findings of differential responses of species to drought and of complementarity (reduced competition) among species in mixtures are consistent with the idea that diversity can also increase the resistance and stability of ecosystem functioning to extreme climatic events[3]. Interestingly, this suggests that intermittent drought may promote tree diversity in tropical forests, which in turn increases the resilience of the system to these drier conditions.

Methods

Site description. We established the experiment in Malua Forest near to the Malua Field Station (N 05° 05' 20" E 117° 38' 32"; 102 metres above sea level). This forest is located ≈22 km north of the Danum Valley Field Centre in Sabah, Malaysia. Eastern Sabah has historically had an aseasonal climate and, for the last 25 years, an average monthly rainfall ± standard error of 240 ± 33 mm and an average yearly total of 2,900 ± 90 mm, as recorded at the Danum Valley Field Centre. The mean temperature during the experiment was 25.6 °C with an average daily low of 22.6 °C and a high of 31.5 °C.

Experimental design. In May 2013, seedlings of four dipterocarp species (*Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan* and *Shorea parvifolia*) were planted into 20 plots randomly distributed across a small

topographic gradient from 100 to 130 metres above sea level. The species were selected to represent a range of different functional traits and growth and allocation strategies (see Supplementary Fig. 4 for trait differences among species). Seeds of the four species were collected in August and September 2010 and seedlings were grown in a standard nursery environment with 5% sunlight for the two years before they were planted in the forest. Seeds were collected from three different mature trees for every species except *H. sangal*, which only had two mature trees. Each plot consisted of two sub-plots. Within each sub-plot, we planted three focal seedlings of each species (20 plots × 2 sub-plots × 4 species × 3 seedlings = 480 focal seedlings). For each species within each plot, the focal seedlings originated from the same mature tree and seedlings from each mature tree were planted as focal seedlings in 8–12 plots (depending on seedling quantities). Seedlings that died in the first five months were replanted (all plants were alive and healthy at the first measurement in December 2013).

Neighbourhood treatments. Each focal seedling was randomly assigned one of three neighbourhoods: (1) seedlings of different species (mixture), (2) seedlings of the same species but from a different mature tree (non-siblings) and (3) seedlings of the same species and from the same mature tree (siblings). To standardize the interspecific competition for all focal species, three dipterocarp species that were not used as focal seedlings (*Hopea nervosa*, *Parashorea tomentella* and *Shorea argentifolia*) were planted as the neighbourhood seedlings. These species were selected because they spanned a similar spectrum of growth strategies to those of the focal species. The neighbourhoods consisted of three seedlings planted in a triangle pattern approximately 15 cm from the focal seedling (480 focal seedlings × 3 neighbours = 1,440 neighbourhood seedlings). Sub-plots contained a total of 48 seedlings in an area of 1.5 m × 2 m for an overall density of 16 seedlings m^{-2}, but concentrated densities around focal seedlings (based on planting distance) could be estimated at 42 seedlings m^{-2}. However, these values fall within the natural densities (mean = 22 seedlings m^{-2}; range = 3–75 seedlings m^{-2}) monitored for four years after a mast fruiting event in 81 plots at the Malua Forest Reserve.

Rainfall-exclusion treatment. From 23 March 2014 to 27 June 2014 and from 23 February 2015 to 24 August 2015, rainfall-exclusion shelters were built over one sub-plot in every plot. The rainfall-exclusion shelters were made of clear polyethylene sheeting draped over the plots (covering an area of approximately 1.8 m × 2.3 m) at a height of approximately 3 m. The rainfall-exclusion shelters were designed to remove 100% of rainfall within the sub-plot. Small aluminium barriers (10 cm high and buried 5 cm in the soil) were placed upslope from every drought sub-plot to prevent overland flow into the rainfall-exclusion shelter during heavy rain events. Sub-plots without rainfall-exclusion shelters were watered by hand if a period of three days of no rain occurred naturally. This watering was also done for both sub-plots when rainfall-exclusion shelters were absent, in an effort to limit the drought treatment to only the periods when rainfall-exclusion shelters were present. Because the shelters prevented leaves and woody debris from falling into the sub-plot, we added surrounding litter on a weekly basis to maintain litter levels approximately equal to those of the sub-plots without an exclusion shelter (that is, a constant layer of litter with no bare soil).

Environmental conditions. The volumetric soil moisture content was measured weekly at a depth of approximately 10–15 cm (equivalent to approximately half of the rooting depth of the seedling based on a root growth experiment) during the drought at three to five locations in each sub-plot with an ML3 Theta Probe and HH2 moisture meter (Delta-T Devices). The frequency of these measurements was decreased to biweekly when the rainfall-exclusion shelters were removed and monthly during the rainiest period from November to February. The relationship between soil water potential and volumetric soil moisture content was determined using the filter paper method[41,42]. A single batch of Whatman Grade 42 filter papers was used to measure the gravimetric water content, which enabled calculation of the soil matric potential using the equations from Deka et al.[41]. Soils were dried to volumetric soil moisture levels of between 2 and 50% and used to calculate a drying curve relating volumetric soil moisture and soil matric potential. Two equations were defined (above and below 25% volumetric soil moisture) because soil matric potential declined at a faster rate below this threshold.

Photosynthetically active radiation was measured using quantum sensors (Delta-T Devices) in each sub-plot for 24 h and compared with simultaneous measurements of direct sunlight at the Malua Field Station to assess the light differences among plots and between sub-plots within a plot. Light was statistically indistinguishable between sub-plots (difference between sub-plots with and without rainfall-exclusion shelters = 0.9%, 95% CI: −0.8 to 2.5) and ranged from 1 to 10% among plots. The temperature was measured simultaneously with light and was statistically different between the sub-plots (difference between sub-plots with and without rainfall-exclusion shelters = 0.2 °C, 95% CI: 0.0 to 0.4), but this difference was probably biologically unimportant in this climate with persistent high temperatures and humidity.

Seedling measurements. Beginning in December 2013 (after mortality from planting shock had subsided), we measured all seedlings for height and base diameter (1 cm above the soil) and counted all the leaves. Seedling deaths were recorded for both the focal and neighbourhood seedlings. These measurements were done approximately every 80 days between December 2013 and October 2015.

In June 2015 during the second drought period, one mature leaf was removed from every focal seedling, weighed wet, photographed to calculate the leaf area and then dried at 64 °C for one week and weighed again. The specific leaf area was calculated from each leaf measurement for each focal seedling. Leaves were selected based on three criteria: (1) young but fully developed, (2) in direct sunlight and (3) without herbivory. However, in plots where these criteria could not be met, leaves in similar conditions across the rainfall and neighbourhood treatments were selected to allow comparisons. Furthermore, a subset of 192 focal seedlings from 8 plots were measured for midday (between the hours of 11:00 and 13:00) stomatal conductance using a porometer (model SC-1; Decagon Devices) and 120 of those seedlings were also measured for midday leaf water potential using a Scholander pressure chamber (model 670, PMS Instruments). An analysis of the nitrogen and phosphorus content in the leaves was performed for each species in each neighbourhood and each rainfall treatment to test the effect of neighbourhood and drought on nutrient uptake. For this analysis, plots were pooled (based on similar light conditions) into five groups so that there was enough leaf biomass per sample (4 species × 3 neighbourhoods × 3 rainfall treatments × 5 groups = 120 nutrient analysis samples).

Statistical analysis. To estimate the RGR for each seedling, height was log transformed and analysed as a function of time (a continuous variable in years; days since the first measurement divided by 365.25) in a mixed-effects model with random intercepts and slopes for individuals (a random factor with 480 levels). These RGR values were then analysed as a function of species (a fixed factor with four levels: *D. lanceolata*, *H. sangal*, *P. malaanonan* and *S. parvifolia*), neighbourhood treatment (a fixed factor with three levels: siblings, non-siblings and mixture), rainfall treatment (a fixed factor with two levels: ever-wet and drought), all two-way interactions and a neighbourhood × rainfall × species interaction. Covariates for initial seedling height (a continuous variable in cm) to account for initial height differences among focal seedlings and relative size (a continuous variable; seedling height relative to average neighbour height) to account for initial differences between focal seedlings and their neighbourhood were used to control for differential size effects. We also used an a priori contrast to test whether mixture and monoculture neighbourhoods accounted for most of the variation in neighbourhood treatments at every interaction level. Random effects were used for plot (a random term with 20 levels), sub-plot nested in plot (a random term with 40 levels), species nested in sub-plot nested in plot (a random term with 160 levels) and neighbourhood treatment nested in sub-plot nested in plot (a random term with 120 levels). See Supplementary Table 1 for the analysis of variance table and variance components. We also performed this analysis separately for each year of the drought to validate that the results were consistent across years and not solely a cumulative effect (see Supplementary Fig. 5 for this validation).

Midday leaf water potential and stomatal conductance were analysed as a function of species (a fixed factor with four levels: *D. lanceolata*, *H. sangal*, *P. malaanonan* and *S. parvifolia*), neighbourhood treatment (a fixed factor with three levels: siblings, non-siblings and mixture), rainfall treatment (a fixed factor with two levels: ever-wet and drought) and the interaction between neighbourhood and rainfall treatments. Random effects were used for plot (a random term with 20 levels), sub-plot nested in plot (a random term with 40 levels), species nested in plot (a random term with 80 levels) and neighbourhood treatment nested in sub-plot nested in plot (a random term with 120 levels). The stomatal conductance data were log transformed to meet assumptions of linearity.

Leaf nitrogen concentration and leaf phosphorus concentration were analysed the same way as midday leaf water potential, but with a modified random error structure because the plots were pooled. Random effects were used for group (a random term with 5 levels), sub-plot nested in group (a random term with 10 levels), species nested in group (a random term with 20 levels), neighbourhood nested in group (a random term with 15 levels) and neighbourhood treatment nested in sub-plot nested in plot (a random term with 30 levels). All analyses were performed with the asreml-R package (ASReml 3; VSN International) in the R statistical software (version 3.3.2; http://r-project.org).

Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request and are publicly available on www.searrp.org.

Code availability. All R script is available in the Supplementary Information.

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Author contributions

M.J.O.B. came up with the concept, designed and carried out the experiment, analysed the data and wrote the manuscript. G.R. and R.O. contributed to the logistics and implementation of the experiment in Sabah. A.H. contributed to the design, analysis and writing.

Competing interests

The authors declare no competing financial interests.

Additional information

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