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RESEARCH ARTICLE

Trait variation driven by tree size more than environment and shows limited translation to species vital rates

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Abstract

1. Functional traits are expected to predict vital rates and performance outcomes because they mediate how organisms interact with the environment. However, trait-based models often have poor predictive power for tree species survival and growth. One potential reason is that traits vary substantially within species, in relation to tree size and environment, especially given multiple interacting environmental gradients, for example light, soil moisture, climate and topography.
2. We used a seedling translocation experiment and Bayesian hierarchical models to test whether a suite of nine physiological and morphological traits correspond with species survival and growth, and how within-species variation affects these trait-vital rate relationships.
3. Trait variation and trait covariation/syndromes were driven by tree size and to a lesser extent by environment. Nonetheless, economic trade-offs between acquisitive versus conservative trait values were apparent, even at the small spatial and taxonomic scales captured in this study.
4. Species wood density and specific leaf area were associated with species-level survival. In addition, within species, survival was greater for moderately droughted trees where soil waterlogging was alleviated. There were no clear trait associations with species-level growth.
5. These results demonstrate complex dynamics between tree size, environment and traits, wherein multidimensional trait variation and trait trade-offs work in concert to define seedling performance outcomes. The complexity of within-species trait variation shown here illustrates why trait-vital rate associations are often difficult to resolve.

KEYWORDS
dipterocarp, functional trait, hierarchical models, intraspecific variation, plant size

1 | INTRODUCTION

Traits are expected to affect performance (Mlambo, 2014; Violle et al., 2012) by influencing a plant's acquisition of resources in its environment (Chave et al., 2009; Freschet et al., 2018; Paine et al., 2015). Contrary to this a priori expectation, trait models commonly have low power for predicting tree survival and growth (Bongers et al., 2009; Paine et al., 2015; Yang et al., 2018). Possibly, this fault arises because environment and plant size drive substantial trait variability within species (Des Roches et al., 2018; Freschet et al., 2018; Martin & Thomas, 2013; Poorter et al., 2018) and may shift survival and growth rankings among species (Falster et al., 2018). Thus, accounting for within-species trait variability might contribute to better inference in trait-based models (Cui et al., 2025) and improve predictions of forest dynamics across heterogeneous landscapes. While several studies have examined adjacent questions, including in temperate forests (Cui et al., 2025; Jiang et al., 2021; Zhang et al., 2026), tropical forests (Rodríguez-Alarcón et al., 2024; Rowland et al., 2021) and heathland (Dun et al., 2025), our use of a seedling translocation experiment generated trait values that likely captured the potential range of trait values expressed by our set of study species in this system, enabling a fulsome evaluation of the contributions of within-species trait variation to demographic outcomes.

The use of trait-performance frameworks is an attractive tool for understanding plant function (Reich, 2014). Traits covary due to inherent trade-offs in investment, which has most popularly been conceived of as an 'economic spectrum' of life-history strategies defined at one end by low survival and fast growth (low wood density and large, nutrient-rich, acquisitive leaves) and at the other end by high survival but slow growth (Chave et al., 2009; Reich, 2014; Shipley et al., 2016). Such frameworks are convenient for broad-scale comparisons among widely distributed species (Reich, 2014), but more empirical tests are needed to evaluate their use at smaller spatial and taxonomic scales (Kraft & Ackerly, 2010). Further, the use of small sets of easily measured traits may not be sufficient to capture the influence of traits on vital rate outcomes (Yang et al., 2018), particularly when seeking to predict individual rather than mean species performance.

Species-based mean trait models rely on the assumption that within-species variation is less than interspecific variation (Shipley et al., 2016; Violle et al., 2012), though there is evidence to the contrary. For example, within-species trait variation accounts for a significant proportion of total variation in leaf economic traits, both morphological and chemical (Siefert et al., 2015). High within-species trait variation can indicate broad individual plasticity, with both genetic and environmental components (Schlichting, 1986), or that local adaptation is acting on populations within a landscape (Brousseau et al., 2013; Sheth et al., 2020). The distinction of individual plasticity versus population-level adaptation is important because the trait–trait and trait-demography patterns observed among species do not always align with observations made within species (Kichenin et al., 2013; Yang et al., 2021). Species-based mean trait models may also tend to generate poor predictions of performance (Kichenin et al., 2013; Yang et al., 2013) if the main drivers of trait variability act within species. Given some control of genetic lines in the experiment herein, we focus on the environmental component of plasticity and restrict our discussion to trait variation.

Trait interactions are highly complex and multiple dimensions of plant function can influence vital rates. First, traits can demonstrate multiple functions in response to the environment (Fricke et al., 2019) and can vary directly in response to one environmental driver, or in coordination with other traits via trade-offs, or given allometric and environmental changes related to plant size (Chen et al., 2009; Green & Harms, 2018; Jager et al., 2015; Reich, 2014). Second, it is likely that many trait combinations can optimise performance in the same environment (Li et al., 2015), diminishing the convergence of forms within any environment. Third, the degree of coupling/trade-off among particular traits can vary between species (Fajardo & Siefert, 2018), possibly because of divergent allometric and/or physiochemical trade-offs across geographic or phylogenetic scales (Anderegg, 2023; Chave et al., 2006), or differing capacities for phenotypic plasticity (Craven et al., 2012; DeWitt et al., 1998; Rozendaal, 2006). Greater characterisation of these complexities is needed to validate trait models (Falster et al., 2016, 2018) and to identify commonalities that may enable reliable predictions of fitness from traits (Westerband et al., 2021). The trait-performance frameworks originally defined for comparisons across species may stand to be enriched by incorporating within-species trait variability and examining the multiple, co-occurring drivers of trait variation.

Complex meso- and micro-scale environmental gradients in aseasonal tropical forests are expected to drive substantial within-species trait variability and are thus likely to influence interpretations of a given species sensitivity to its multi-faceted environment. While plants on the rainforest floor are typically very light-limited—influencing seedling survival and growth (Augspurger, 1984; Philipson et al., 2012, 2014)—complex vegetation structure and temporal dynamics create heterogeneous light availability at small spatial scales (Jucker et al., 2018). Similarly, waterlogging or direct flood damage in low-lying terrain can reduce seedling survival and suppress growth (Born et al., 2015; O'Brien & Escudero, 2021), while contemporaneously, water deficits on ridges or steeper terrain can accentuate survival and growth differences (Comita & Engelbrecht, 2009; O'Brien & Escudero, 2021). Targeted considerations of the multiple and co-occurring environmental drivers of trait variation are needed to inform predictive models of vital rates.

Plant size is an important mediator of trait variation (Falster et al., 2018; Fortunel et al., 2020; Wilson, 1988) and can seriously alter functional interpretations of how traits mediate organismal responses to environment (Green & Harms, 2018; Niinemets, 2006). Plant size drives trait changes via shifting allometric and allocation requirements (Gibert et al., 2016; Weiner, 2004), shifting environmental exposure and shifting demographic sensitivity to environment (Falster et al., 2018; Green & Harms, 2018). First principles about shifting allocation trade-offs across life stages suggest, for example, that WD will be negatively correlated with growth across life stages, whereas the positive association of SLA with growth will weaken across life stages (Falster et al., 2018). Both relationships are borne out by meta-analysis (Gibert et al., 2016). Some suggest the relevance and drivers of different groups of traits may differ systematically, with morphological traits shifting most in relation to life stage, and leaf chemical traits being associated more with forest habitat (and associated abiotic drivers, Fortunel et al., 2020). In a study of 17 species in temperate forest, leaf traits did not moderate size-survival or size-growth relationships, which the authors attributed primarily to large within-stage variation in some traits and dependence of traits on plant size (Cui et al., 2025). There is clearly a need to further incorporate and characterise effects of plant size in trait-demography models.

Here, we examine physiological and morphological trait variation from a seedling translocation experiment in Bornean rainforest with control of maternal genetic lines (O'Brien & Escudero, 2021). We sampled nine structural and physiological traits (selected for their expected mechanistic associations with vital rates: Table 1) across multiple environmental gradients captured by the experiment and pair these with demographic data for tree height, survival and growth. We used a suite of Bayesian hierarchical models and mixed models to: (1) identify traits associated with species survival and growth using models that capture within-species trait variation, (2) characterise the interplay of environment and tree size with trait- and vital rate responses, (3) describe trait variation and covariation (trait syndromes; Albert et al., 2011). We posited that physiological traits with clear mechanisms by which to mediate plant responses to light and soil moisture would be most strongly associated with species survival and growth outcomes and would indicate the environmental factors most limiting survival and growth, with light being most important and soil moisture becoming more important in the absence of light limitation. We also expected trait covariation to strongly reflect an economic spectrum of acquisitive versus conservative life-history strategies and for tree size to drive some variation for most traits.

2 | METHODS

2.1 | Site and experimental design

This experiment was established in Malua Forest Reserve, a logging concession in Sabah, Malaysian Borneo. Research was conducted in collaboration with the South East Asia Rainforest Research Partnership (project number 19007), with permissions from Danum Valley Management Committee, Sabah Forestry Department and the Sabah Biodiversity Council (Access and Export Licences: JKM/MBS.1000-2/2 JLD.9 (46); JKM/MBS.1000-2/2 JLD.9 (65); JKM/MBS.1000-2/2 JLD.10 (169)).

Dipterocarps are a hyper-dominant family at this site and in Southeast Asian tropical forests broadly and have been the main target of both selective harvesting and restoration efforts in the region. Sabah has an aseasonal climate punctuated by supra-annual El

TABLE 1 Functions of traits included in the present study.

Trait	Functions of trait	References
Chlorophyll	Mediates photosynthetic capacity via capacity for light harvesting.	Li et al. (2018)
Leaf nitrogen	Allocated to proteins of the Calvin cycle and thylakoids.	Evans (1989) and Onoda et al. (2017)
Intrinsic water-use efficiency	Integrated estimate of the carbon uptake per unit of water used during photosynthesis (from $\delta^{13}C$). Regulated by photosynthetic capacity (when stomata are open) and correlated with drought tolerance	Farquhar et al. (1989) and Rumman et al. (2018)
Leaf size	Reflects life-history strategy via allocation trade-offs. Larger leaves are also associated with higher evaporative demand	Niinemets (2006)
Specific leaf area	Mediated by cell wall mass fraction. Relates to leaf lifespan and photosynthetic efficiency	Onoda et al. (2017)
Osmotic potential	Cell solute potential at full hydration. Proxy for leaf turgor loss point and plant drought tolerance	Bartlett et al. (2012)
Wood density	Composite trait reflecting vessel diameter, vessel wall thickness and fibre density. Associated with growth rate and drought-induced mortality	Chave et al. (2009) and O'Brien et al. (2017)
Taproot length	Here represents rooting depth. Rooting depth is regulated by soil hydrology and improves anchorage and uprooting resistance	Fan et al. (2017) and Freschet et al. (2021)
Root mass fraction	Describes the ratio of supportive tissues to growth tissues. Increases under severe drought, decreases due to waterlogging	Poorter et al. (2012)

Niño-induced drought events. Mean daily minimum and maximum temperatures in neighbouring Danum Valley are 23.0 and 29.4°C, respectively (1985–2018; O'Brien et al., 2026), with 73% mean midday humidity and 95% mean overnight humidity. Mean annual rainfall is 2844 mm, averaging 240 mm/month.

Seeds of six dipterocarp species were collected in August 2014—see Appendix S1 in Supporting Information and (O'Brien & Escudero, 2021). These six focal species span a range of ecological strategies (Philipson et al., 2012), vary in growth capacity (Figure 1) and can be defined in terms of drought tolerance from highly susceptible (*Shorea leprosula* (SL) and *S. parvifolia* (SP)), through moderately resistant (*Parashorea malannonan* (PM) and *S. johorensis* (SJ)) to highly resistant (*Hopea nervosa* (HN) and *Dryobalanops lanceolata* (DL)). Six mature trees of each species (6 × 6 = 36 mother trees) were selected from riparian (~3 trees per species) and ridge areas (~3 trees per species) to control for maternal environment (detailed in Appendix S1). Herein we refer to the progeny of a single mother tree being of the same 'seed family'.

Twelve plots were established (May 2015) in each of 3 topographic positions representative of the lowland rainforest: riparian edge, lowland forest or a ridgetop 50 meters above the riparian zone (12 × 3 = 36 plots). Plots were 3 × 3 m, spaced a minimum of 3 m apart and arranged randomly within sites at each topographic position. Each plot comprised two identical subplots (a drought and 'normal rainfall' treatment), one of which was periodically droughted using wooden rainfall exclusion shelters; initially for 12 months (February 2016 until January 2017) and again for 6 months (February 2018 until August 2018) (further details in Appendix S1). Drought severity varied among plots, but all droughted subplots had reduced water availability relative to the control subplot.

Three neighbourhood treatments (high density, conspecific, low density) were established within each subplot. A full description of the planting design is in Appendix S1, but we did not include an analysis of neighbourhood density. Subplots (~1.5 × 3 m) were arranged with the high-density treatment at one end (one 4 × 6 24-point grid, 10 cm spacing, up to eight neighbours within a 15 cm radius) and the conspecific treatment at the other end (six 2 × 3-point grids; summarised in Appendix S1 but not sampled in the present study). The low-density treatment was planted at the plot margins and between grids comprising the conspecific treatment (single plants, maximum of four neighbours within 30–50 cm distance). The design was blocked such that seed families of each species were balanced among sites and was randomised such that species had unique neighbours among plots, but identical neighbours within paired subplots to reduce spatial effects between the other treatments. This design equates to 1296 focal trees planted across the experiment in the treatments relevant to this study; 738 were still alive at the time of this study.

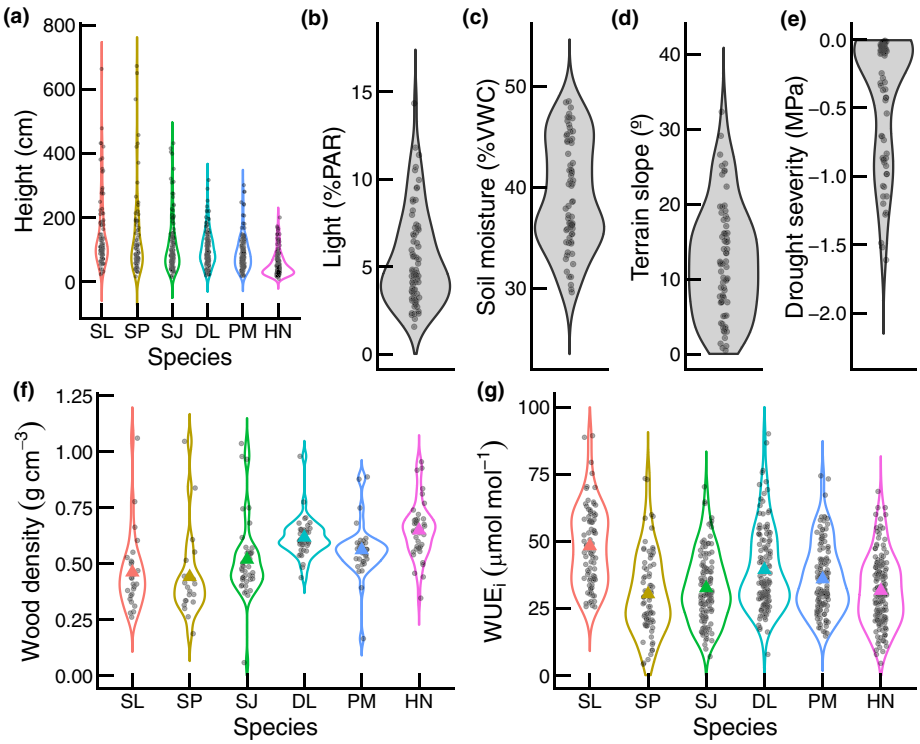

FIGURE 1 Overview of raw data used in the analyses. (a) Tree size distributions differed among the six focal species. (b–e) Trait variation was modelled in relation to four environmental gradients at the study site. (f) Wood density ($n = 373$) and (g) intrinsic water-use efficiency (WUE_i; $n = 725$) are shown here as examples of the wider trait dataset (nine traits; Table 1).

2.2 | Environmental data

Light availability was logged twice in each subplot for 24 hours using quantum sensors (QS5 sensors; Delta-T Devices, Burwell, Cambridge, UK) positioned above the planted trees (ca. 1 m). Light was logged between June–August 2015 and again between May–July 2018 (Table S1 in Supporting Information) and was normalised to simultaneous measurements taken in an open field (Appendix S2). We combined these measurements to estimate mean light for each subplot.

Soil volumetric water content (VWC) was measured every 2 weeks in each subplot from January 2016 to March 2019 (this period includes the two drought treatments) using an ML3 Theta Probe and HH2 Moisture meter (Delta-T Devices) at ~10 cm depth. We converted these VWC measurements to soil water potentials (MPa) using the filter paper method (Deka et al., 1995), because soil water potentials could better indicate the intensity of the imposed drought treatments (Appendix S2). We then calculated the mean minimum soil water potential for each subplot, as a proxy of drought severity (Table S1). Mean minimum soil water potentials were then multiplied by −1 such that greater values correspond to more intense drought (to aid interpretation). This measure summarises the severity of soil water deficit realised during the rainfall exclusion treatment.

In February 2020, we measured soil VWC (0–20 cm depth) using a HydroSense II meter (Campbell Scientific) to characterise soil moisture for all plots under normal rainfall conditions. This measure captures soil moisture levels concurrent with the trait measurements and biomass harvest, 18 months following removal of the drought treatment. Terrain slope was characterised at plot-level using inclinometer measurements at each plot corner.

2.3 | Survival and growth

Seedlings were measured (Feb-2016 to Feb-2020) for height (cm) and diameter (mm) at 5 cm above the soil surface and mortality was recorded when the tree was no longer present or when no living tissue was found. Censuses were conducted every 175 days (95% CI: 162–188 days). Individual relative height growth rates (RGR_h: $(\ln(height_1) - \ln(height_0))/(t_1 - t_0)$) were calculated for each census interval, then averaged across censuses for each tree (RGR_{mean}).

2.4 | Functional trait measurements

In early 2020, roughly 5 years after trees were originally planted, we sampled all trees in the high- and low-density treatments ($n = 738$) for a suite of traits that would indicate tree responses to light, water availability and topography (Table 1).

We measured chlorophyll using a CCM-300 chlorophyll fluorescence meter (OptiSciences) on four fully expanded upper canopy leaves of each tree. These same leaves were sampled for leaf nitrogen and carbon isotopes ($\delta^{13}C$), which we analysed with a continuous flow stable isotope ratio mass spectrometer (CR-RRMS, Isoprime, England). We calculated intrinsic water-use efficiency (WUE_i) from $\delta^{13}C$, adjusting for decoupling of subcanopy air from the troposphere and an assumed gradient in $\delta^{13}C_{air}$ with height above the forest floor (details in Appendix S3).

At four plots per topographic position ($n = 276$ trees), we sampled two leaves per tree for osmotic potential, using one leaf to test for full leaf rehydration using a pressure bomb, and the second to sample and analyse using a PSY1 Stem Psychrometer (ICT International; details in Appendix S3). We calculated specific leaf area (SLA) with leaf area measurements from photographs using ImageJ (github.com/imagej/imagej1) and measurements of leaf dry mass (g).

At three plots per topographic position ($n = 228$, Table S4), we harvested trees by excavating a wide area around the plot to ensure the majority of root material was intact to measure wood density and biomass (e.g. dry weights for leaves, stems and roots) and dry length of the longest root (in all cases the central taproot). Harvested plant material was dried to constant mass or for a minimum of 3 months in a hot glasshouse (ca. 60°C); leaves were dried in hanging envelopes and roots/shoots were bench dried. Stems larger than 1 cm diameter were intermittently placed in a gas oven to assist dry down. Wood density was measured for a 10 cm section of basal stem using the water displacement method. We calculated root mass fraction (RMF) as root dry mass divided by total plant dry mass. Trait values beyond three *z*-scores from the mean were removed from analyses. An overview of the raw data is shown in Figure 1. Trait data are available from (Carle et al., 2025).

2.5 | Modelling and statistical analyses

Tree height and traits could only be measured on surviving trees (missingness mechanism). To address this issue for tree height, we used a linear mixed effects model with tree height as a function of species and census year (2016–2020 inclusive, centred on 2020) with varying intercepts for individual trees and plots, and extracted varying height intercepts for each tree (alive or dead) to provide a tree height proxy for all individuals. Missing trait data for dead individuals could not be addressed in this way. Instead, we assumed that traits of surviving trees were representative of related individuals that had died (Hadfield, 2008), which was consistent with a prior analysis based on seed families that found no considerable effect of differential trait expression on survival outcomes (O'Brien & Escudero, 2021).

We used Bayesian hierarchical models (package rstan) to test for associations of vital rates with traits, and Bayesian generalised linear mixed models (package brms) to assess variation in traits, survival and growth. Continuous predictor variables were mean-centred to facilitate model fitting and exploration of posterior distributions. Weakly regularising priors were set based on prior simulations to constrain posteriors to realistic values. Trait and growth models used a Gaussian distribution with an identity-link function. Survival models used a Bernoulli distribution with a logit-link function. Hierarchical models were run with four chains for 10,000 iterations,

including 5000 of warm-up. Generalised linear mixed models were run with four chains for 2000 iterations, including 1000 of warm-up. Chain mixing and model convergence was checked visually and using automated diagnostics. Parameter posterior distributions were shown in their entirety and/or summarised using the median and Highest Posterior Density Interval (HPDI) (0.90, 0.66) (package tidybayes), which is the narrowest interval that includes 90% or 66% of the probability mass. All analyses were conducted using R (version 4.5.2; http://cran.r-project.org/) and all R packages used are cited in Appendix S4.

2.6 | Drivers of survival and growth variation

We tested the drivers of within-species variation in survival and growth using Bayesian mixed models (2 models). We aimed to quantify the effects of modelled height and environment (including light, soil volumetric water content (VWC), drought severity and terrain slope). We included varying intercepts for species to control for inherent interspecific differences. Varying intercepts were included for plot but not subplot-within-plot because subplots were closely collocated; the main difference between subplots was captured by the drought measure included in the main effects, and use of a nested intercepts structure added unnecessary model complexity.

$$\begin{aligned}\text{Growth/Survival} \sim\ & \text{modelled height} + \text{light} + \text{soil VWC} + \text{drought} \\ & + \text{terrain slope} + \text{species} \times \text{light} + \text{species} \times \text{soilVWC} + \text{species} \\ & \times \text{drought} + \text{species} \times \text{slope}\end{aligned}$$

$$\text{Varying intercepts} = \text{plot} + \text{species} \quad (1)$$

In these models, survival was a binomial (1/0) response variable indicating survival at the final census in 2019. Growth was a continuous response variable for the mean relative height growth rate of an individual, across all censuses. We further checked for the relationship between survival and growth (one model: survival ~ modelled height + RGR_{mean} + species, with varying intercepts for plots). Modelled tree height was used because all trees were roughly the same age and size when planted but were at various life stages by 2020. Light and modelled height were not strongly correlated (Pearson's correlation: 0.04, $p = 0.170$). We included varying intercepts for species to control for inherent interspecific differences. Varying intercepts were included for plot but not subplot-within-plot because subplots were closely collocated; the main difference between subplots was captured by the drought measure included in the main effects, and use of a nested intercepts structure for subplots added unnecessary model complexity.

Next, we tested whether species survival and growth were associated with species trait values using Bayesian hierarchical models. These models were fit with two levels: one for the trait and a second for growth or survival (18 models: nine for survival and nine for growth). Both levels were structured as per Equation 1 but with the addition of varying slopes for species × size (modelled height). For each species, four random effects (i.e. trait intercept, growth intercept, trait × size slope and growth × size slope) were assumed to follow a 4-dimensional multivariate normal distribution with a species covariance matrix, which allowed us to estimate correlations between trait and vital rate intercepts and trait × size slopes and vital rate intercepts. These models were fit with normal priors for the fixed effects, non-centred parameterisation and folded-Cauchy priors for the random effects, with location parameter of zero and scale parameter of 0.1 for standard deviations and a Cholesky LKJ prior for the correlation matrix.

2.7 | Drivers of within-species trait variation

We tested the drivers of within-species trait variation using Bayesian mixed models (9 models) including modelled height, environment and maternal environment (riparian or upslope). We also assessed how size mediates the effect of environment on traits with two-way size-by-environment interactions between modelled height and each environmental variable.

$$\begin{aligned}\text{Trait} \sim\ & \text{modelled height} + \text{light} + \text{soil VWC} + \text{drought} \\ & + \text{terrain slope} + \text{maternal environment} + \text{modelled height} \\ & \times \text{light} + \text{modelled height} \times \text{VWC} + \text{modelled height} \\ & \times \text{drought} + \text{modelled height} \times \text{slope}\end{aligned}$$

$$\text{Varying intercepts} = \text{plot} + \text{species} \quad (2)$$

We further tested for trait *covariation* using a principal components analysis (package factoextra; $n = 168$) and used a post hoc permutation MANOVA (function adonis2 in package vegan) to test whether tree size and/or environmental heterogeneity drive that trait covariation. For this post hoc test, we used the Euclidean method with marginal effects, which generates a single p-value for each predictor variable.

3 | RESULTS

Average subcanopy light levels were low (5.5% PAR), ranging from 1.6% to 14.3% PAR (Table S1). Soil moisture was generally high (29.6% to 48.5% VWC), especially in riparian plots where the terrain is flat (Table S2). Droughted subplots had significantly lower average soil water potentials over the course of the study (Table S2). Terrain slope ranged from 1 to 33° (Table S1). Trait data are summarised in Table S3 in Supporting Information.

3.1 | Drivers of survival and growth outcomes

Our main aim was to test whether species trait values were associated with species survival and growth, accounting for within-species variation due to tree size and environment. Species-level growth was not correlated with any of the traits tested. Species-level

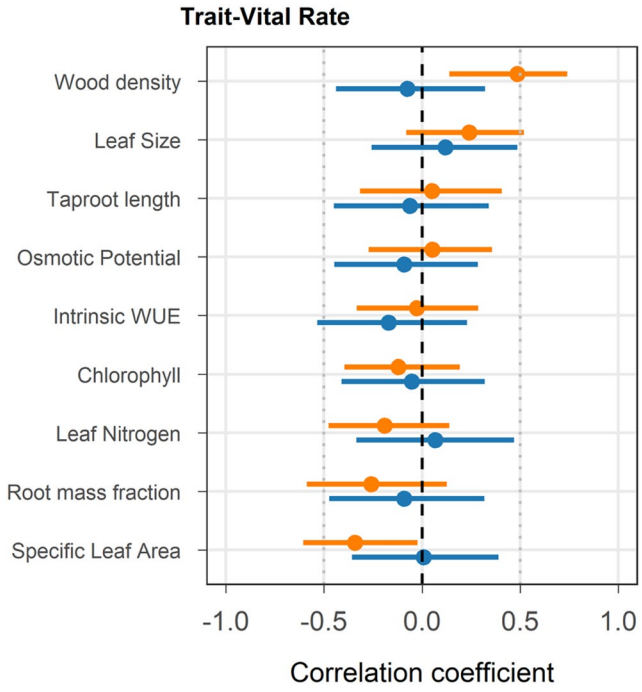

FIGURE 2 Correlation of species survival (orange) and growth (blue) with species traits. Posterior draws from Bayesian hierarchical models are summarised with median HDPI at 0.66.

survival was correlated (at 0.66 HDPI) with higher WD and lower SLA (Figure 2). Trait changes with size were not correlated with any survival/growth intercepts, and survival/growth slopes with size were not correlated with any trait intercepts (Figure S2).

Trees that were moderately droughted had improved survival (Figure 3). Trees also tended (at HDPI 0.66) to have greater survival and growth in higher light and lower survival on steeper terrain (Figure 3). At mean modelled tree height, faster growth was associated with higher survival (0.29, 0.95 HDPI of 0.15–0.44). Both survival (0.32, 0.95 HDPI of 0.18–0.47) and growth (0.06, 0.95 HDPI of 0.05–0.07) were greater for taller trees.

3.2 | Drivers of trait variation

We used Bayesian mixed models to characterise within-species trait variation in relation to tree height and environment (light, soil moisture, terrain slope, drought history). All traits, except for osmotic potential, varied with tree height, while five of nine traits varied in response to at least one environmental variable (Figure 4). Taller trees had bigger, thicker leaves with more chlorophyll and leaf nitrogen, and greater WUE_i as compared with smaller trees (Figure 4). Taller trees also had lower WD and longer taproots but allocated relatively less to roots than shoots as compared to smaller trees (Figure 4).

Trees in higher light had lower WUE_i (at HDPI 0.95) and tended to have larger leaves with less chlorophyll and nitrogen, as well as longer taproots and lower WD than trees in lower light (at HDPI 0.66: Figure 4). Higher soil VWC led to lower nitrogen content (at HDPI 0.95) and a tendency towards smaller leaves with lower WUE_i, longer taproots and lower WD than trees in less saturated soils (at HDPI 0.66: Figure 4). Trees on steeper terrain had more chlorophyll and higher WUE_i (at HDPI 0.95) than trees on shallower terrain and tended to have leaves with higher SLA and leaf chlorophyll, as well as longer taproots and greater overall allocation to roots—RMF (at HDPI 0.66 Figure 4). Trees with a drought history had less chlorophyll, greater RMF and higher wood density (at HDPI 0.95) than non-droughted trees (Figure 4). Droughted trees also tended to have smaller leaves, lower leaf osmotic potentials and shorter taproots than non-droughted trees (at HDPI 0.66: Figure 4). All traits differed among species (Figure S1) but only minorly in relation to maternal environment (Figure 4).

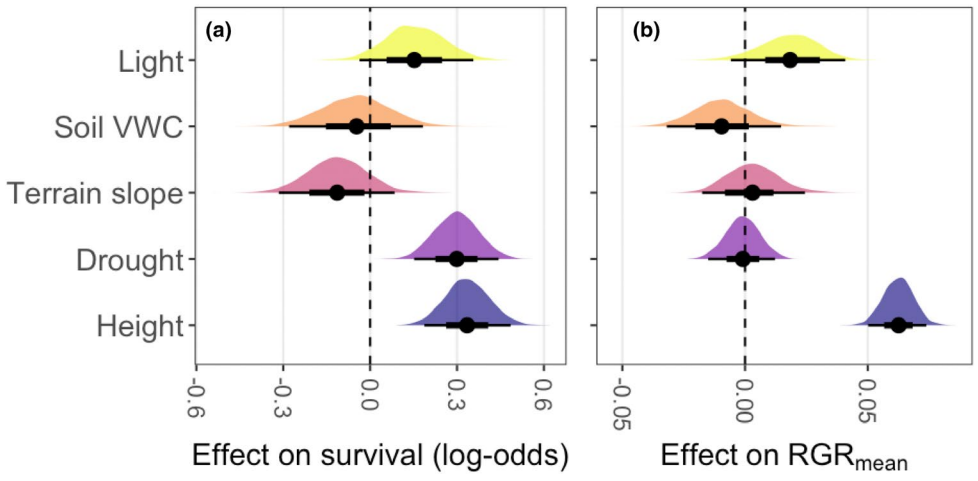

FIGURE 3 Intraspecific survival and growth (mean relative growth rate: RGR_{mean}) responses to environment and tree height. Environmental gradients: Light, as photosynthetically active radiation (PAR, %); soil volumetric water content (VWC, %); terrain slope (°); drought (mean minimum soil water potential: MPa). For drought, larger positive values reflect more severe water deficit. Posterior draws are summarised with median HDPI at 0.66 and 0.95.

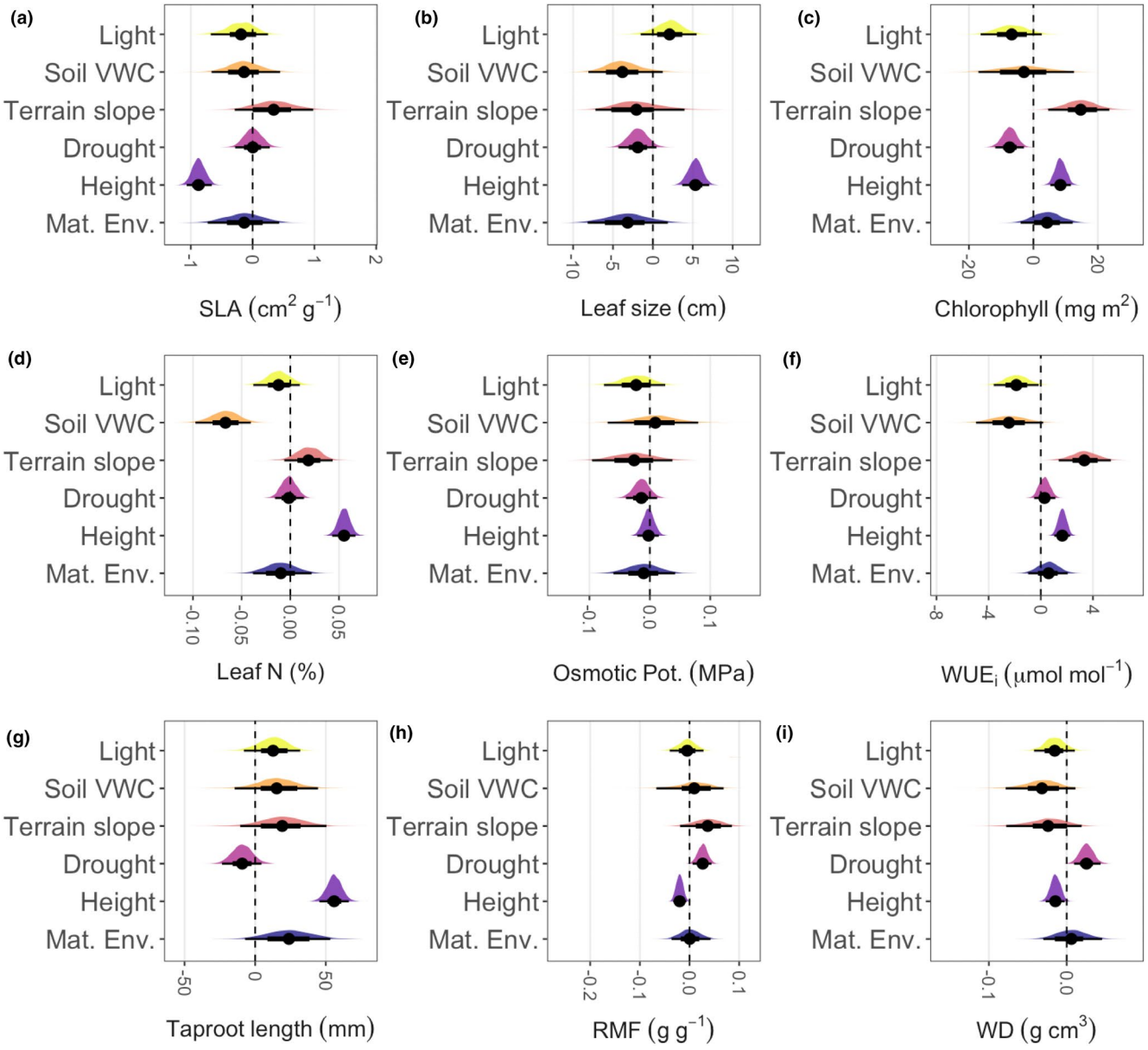

FIGURE 4 Intraspecific trait variation due to environment, plant size and maternal environment. Environmental gradients: Light, as photosynthetically active radiation (PAR, %); soil volumetric water content (VWC, %); terrain slope (°); drought (mean minimum soil water potential: MPa). For drought, larger positive values reflect more severe drought. Maternal environment compares trait values of plants grown from mother trees in the riparian zone to those from upslope areas. Posterior draws are summarised with median HDPI at 0.66 and 0.95.

Our tests of interactions between tree size and environment in driving trait values showed many trait-environmental relationships were mediated by size. Smaller trees had unique trait values between low- and high-light conditions: trees in lower light had lower leaf chlorophyll, SLA, WUE_i and greater leaf size than trees in higher light (Figure 5). These differences were lost in larger trees. For leaf area and SLA this was due to increased trait variation of individuals in high light; for chlorophyll and WUE_i this was due to increased trait variation of individuals in low light (Figure 5). Size-environment interactions were more mixed with respect to soil moisture and terrain slope. Larger trees had lower WD in wetter soils (high VWC versus lower VWC) and on steeper terrain (versus flatter terrain) but did not vary among smaller trees in relation to these environmental factors (Figure 5). Smaller trees had longer taproots in wetter soils (high VWC versus lower VWC) but larger trees did not. However, larger trees did have longer taproots on steeper terrain (versus shallow terrain) while smaller trees did not (Figure 5). WUE_i was lower in wetter soil (high soil VWC versus lower VWC) for larger trees while no difference was evident among smaller trees (Figure 5). Smaller trees had smaller leaves on steeper terrain (versus flatter terrain), but larger trees did not (Figure 5). Six other size-environment interactions were statistically significant but their posterior predictions at these levels were not, indicating that the interactions were small.

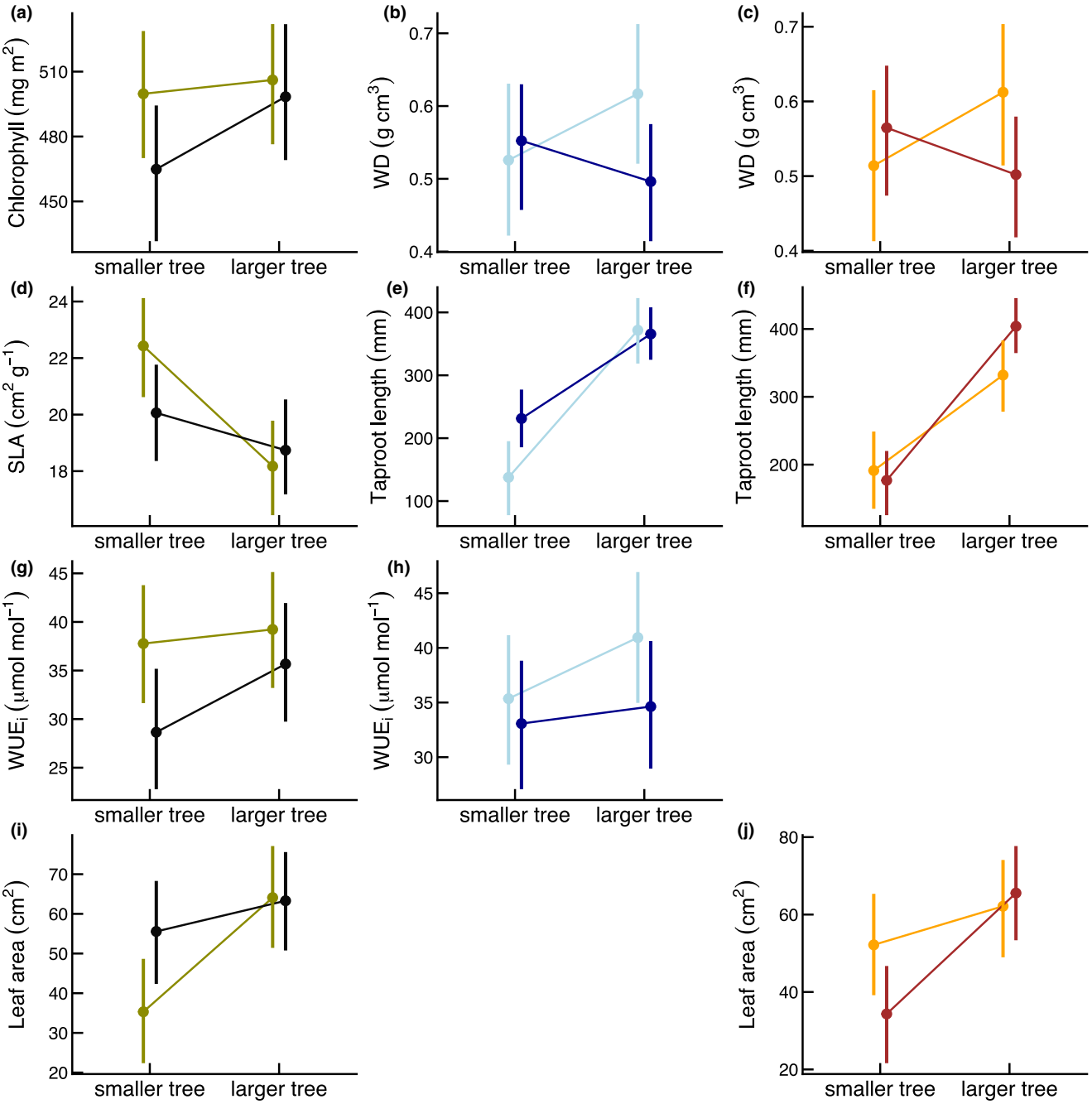

FIGURE 5 Plant size mediates a subset of trait-environment interactions. Trait responses to light (% PAR), soil volumetric water content (VWC, %) and terrain slope (°) differed between smaller versus larger trees for several of the traits recorded (a-j). Posterior predictions were generated for tree height quantiles 0.1 and 0.9 (smaller tree: 29 cm; larger tree: 197 cm), *z*-scores of −1.3 and 2 for light (lower light: 2%; higher light: 11% PAR) and *z*-scores of −1 and 1 for soil volumetric water content (lower VWC: 34%; higher VWC: 45%) and terrain slope (shallow slope: 5°; steeper slope: 19°). These prediction values are ecologically representative for each predictor. Posterior predictions are summarised with median HDPI at 0.90.

3.3 | Coordination of multiple traits

The PCA of trait *covariation* explained 68% of total variance in the first four dimensions (Figure 5; Table S5). The first dimension (22% of var.) was defined by morphometric traits. The second di-mension (18% of var.) was defined by the inverse relationship be-tween wood density and SLA and leaf nitrogen. The third dimension (15%) was defined by root mass fraction and WUE_i, varying against SLA and leaf nitrogen. The fourth dimension (13%) was defined by chlorophyll and osmotic potential.

A post hoc PERMANOVA test including both plant size and environmental effects on the PCA trait space explained 41% of total trait covariation. This test showed that tree height was by far the greatest driver of observed trait covariation ($R2 = 0.32$, $p = 0.001$),

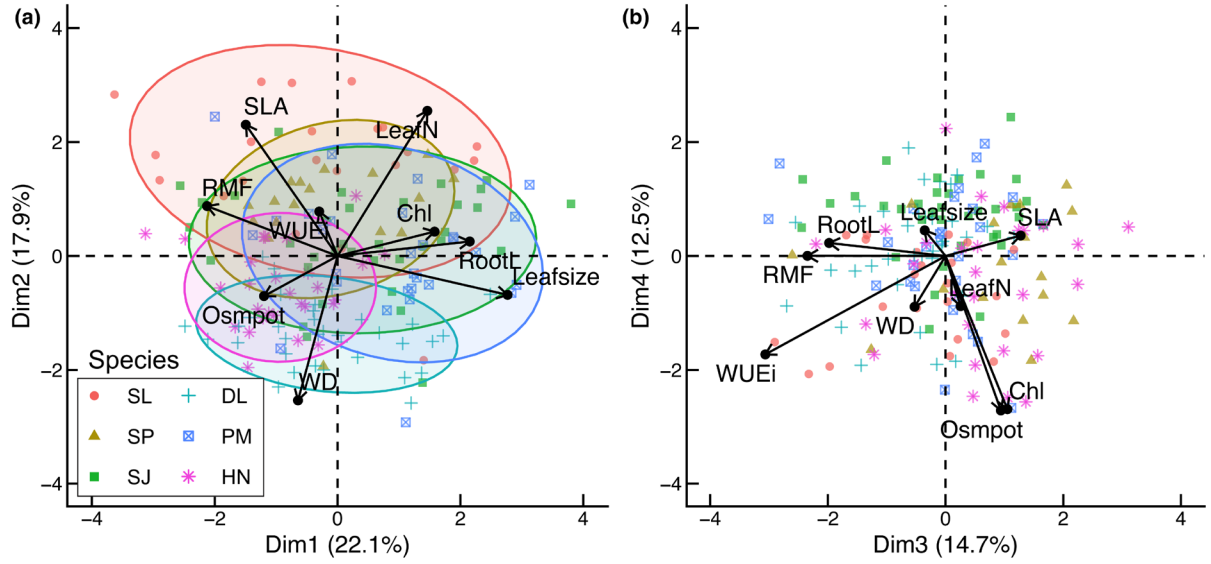

FIGURE 6 Trait covariation for six canopy-forming dipterocarp tree species. The main axes of trait covariation corresponded to (a) morphological changes with plant size (Dim1) and weak life history-related economic trade-offs (Dim2), followed by (b) trade-offs in above-belowground allocation and related physiology. Traits: Specific leaf area (SLA, $cm^2\,g^{-1}$); leaf nitrogen (LeafN, %); root mass fraction (RMF, $g\,g^{-1}$); intrinsic water-use efficiency (WUE_i, $\mu mol\,mol^{-1}$); leaf chlorophyll (Chl, $mg\,m^{-2}$); taproot length (RootL, mm); osmotic potential (Osmpot, MPa); leaf size (cm^2); wood density (WD, $g\,cm^{-3}$). Species elipses are drawn at 0.8 CI. Note change in the axis scales from panels (a) to (b).

followed by a significant but comparatively small effect of soil moisture ($R2=0.02$, $p=0.030$). Excluding tree height from the post hoc test, light became the only significant predictor of trait covariation ($R2=0.02$, $p=0.039$) but the proportion of total variation explained dropped to 9.0%.

4 | DISCUSSION

Our test of associations between species traits and survival and growth outcomes in a seedling translocation experiment confirmed that SLA and WD (traits supporting shade tolerance and persistence) are linked with survival but showed no clear associations of traits with growth. Although most traits responded to at least one environmental gradient, tree size was the predominent driver of vital rates, traits and trait covariation and some trait responses to environment were size-dependent.

Species differences explained significant variation for all nine traits but the magnitude of within-species trait variation was large and resulted in extensive 'functional overlap' among species (Figure 6), despite having selected species from across a life-history spectrum. Trait values were not clearly associated with maternal environment, consistent with prior work that found maternal environment did not strongly support local adaptation in this landscape (O'Brien & Escudero, 2021).

Overall, our results suggest that trait variation due to changes in tree size overshadows that of environmental and maternal drivers of trait variation. The multiplicities and complexities of this size- and environment-related trait variation may explain why species-level associations of traits with survival and growth are limited.

4.1 | How environment and size drive vital rates

We found that a combination of light and edaphic environment predicted vital rates. This likely reflects concomitant limitations on tree performance in a heterogeneous landscape but is contrary to a prior study on seedlings of 14 tropical tree species in China, which reported that species light-defined niches did not correlate with survival or growth but soil-defined niches did (Zhang et al., 2024).

While light tended to improve individual survival and growth, as has been shown at species-level (Augspurger, 1984; Philipson et al., 2012, 2014), survival and growth responses to the edaphic environment were more complex. Trees on ridgelines where the terrain is steeper generally had poorer survival than those in the riparian zone where the topography is flat (O'Brien & Escudero, 2021). However, the fact that moderate drought improved survival suggests that waterlogging, particularly on flat terrain, also impacts survival in this landscape (O'Brien et al., 2024). Importantly, our analyses emphasise the effects of environment across relatively stable gradients in the landscape, whereas mortality may be driven instead by extreme events (Yang et al., 2018).

Both survival and growth increased with tree size, likely as plants established larger root and leaf systems for capturing resources, thereby promoting faster growth and greater resistance to environmental fluctuations, including extremes. Alternatively, smaller seedlings may face more hazards than larger juveniles, for example falling

debris, animal damage and flooding or drought perturbations (Green & Harms, 2018).

4.2 | A lack of trait associations with survival and growth

Consistent with a growing body of literature (Bongers et al., 2009; Paine et al., 2015; Rodríguez-Alarcón et al., 2024; Rowland et al., 2021; Yang et al., 2018), we found that traits generally had poor capacity to predict survival and growth differences among species: in this case using individual trait and vital rates measurements and attempting to generalise to species-level differences in performance. Similar approaches show that only a small proportion of individual vital rate differences is explained by traits. For example, combining 17 traits and demographic measurements for 176 trees in a drought experiment in Brazil explained only 20%–30% of growth differences among individuals (Rowland et al., 2021). Evaluating predictive performance on test datasets (rather than using internal validation tests) suggests even poorer predictive capacity, in one case of less than 10% in a study of 967 trees from 263 woody species in Colombia (Rodríguez-Alarcón et al., 2024).

Nonetheless, in our study, some trait associations were evident for survival. As has now been shown in many study systems (Chave et al., 2009; Falster et al., 2018; Philipson et al., 2014), higher species-level WD was associated with better survival. In addition, larger but also less acquisitive (low SLA) leaves were associated with better survival. WD and SLA can reflect multiple functions but have each been strongly associated with interspecific differences in shade tolerance for tropical seedlings (Augspurger, 1984; Kitajima, 1994; Lusk et al., 2010). Shade-tolerant species are likely to grow less quickly and thus have more resources available for lignification, thickening of cell walls and accumulating stores of non-structural carbohydrates, all of which may improve resistance to or recovery from herbivory, pathogens and drought (Augspurger, 1984; Kitajima, 1994; Lusk et al., 2010; O'Brien et al., 2017; Onoda et al., 2017).

We found no significant associations of traits with growth. This is contrary to theoretical expectations and studies that show associations of SLA with seedling and sapling growth, as well as a negative association of WD with growth across life stages (Gibert et al., 2016). Although our trees were the same age, given heterogeneous environmental conditions across the landscape, some had managed to mature more than others, and this mix of ontogenies could obscure an association of some traits with survival or growth at particular life stages (Gibert et al., 2016). We also found that the response of SLA and WD to environment differed for smaller versus larger trees, but not necessarily in ways consistent with prior theoretical modelling and meta-analysis work (Gibert et al., 2016; Falster et al. 2018).

Although trait associations with survival and growth were weak or lacking, most traits varied in relation to at least one environmental gradient, suggesting a disconnect between trait variation and seedling performance (Davidson et al., 2011), and weak environmental filtering (Kraft & Ackerly, 2010). It is more likely that within-species trait plasticity was promoting trait variation. Some authors have suggested that accounting for the allocation context of traits, whether by adjusting raw trait values to reflect leaf area or mass, or incorporating biomass allocation in trait models using a hierarchical approach, might lead to clearer associations of some traits with growth (Umana et al., 2021; Yang et al., 2018). These approaches require further development and careful consideration of the causal associations between biomass allocation, plant size, environment and traits.

In any case, identifying trait-vital rate links in a natural forest setting (despite an experimental design) is difficult because of complex interactions among traits and multiple environmental gradients. Individual-level traits may vary independently of species' general habits and thus not reflect species-level differences (Kitajima, 1994). Additionally, many traits demonstrate multiple functions and may mediate different performance trade-offs in different species (Fricke et al., 2019; Zhang et al., 2024). Finally, traits work in concert to support plant function and different trait combinations may maintain similar functional performance across environmental gradients, which would obscure the net effects of single traits on plant performance (see Zanne et al. (2010) for an example).

4.3 | Trait trade-offs and covariation

Despite a small number of significant associations between traits and vital rates, our models did suggest a typically opposite sign in the relationship of traits with survival versus growth and, hence, weak economic trade-offs between acquisitive and conservative trait values. The apparent weakness of these relationships contrasts with prior work using species mean trait values only (Philipson et al., 2014); it likely indicates large within-species variation relative to species differences (Siefert et al., 2015), resulting in non-improved predictions given individual measurements (Rodríguez-Alarcón et al., 2024). This limitation persists despite us having captured a range of ecological strategies (across species), and in young trees, where growth–mortality trade-offs are expected to be strongest (Wills et al., 2018; Wright et al., 2010). Our findings do show that weak economic trade-offs occur at small spatial and taxonomic scales and within-species (Fajardo & Siefert, 2018). The two main axes of trait covariation represented plant size, followed by trade-offs between acquisitive–conservative trait values, and then physiological and chemical responses to the environment akin to trade-offs found in other studies (Fortunel et al., 2020; Li et al., 2015; Rüger et al., 2018).

Tree size explained 32% of total trait *covariation*, demonstrating the extent to which shifting allometry with tree size can drive trait expression (Diaz et al., 2016; Rüger et al., 2018; Weiner, 2004). Although single traits commonly varied in relation to environment, only 2% of total trait *co*variation was attributable to environment after accounting for ontogenetic variation. The contrast suggests there are strong environmental cues on single traits but that trait responses are not strongly or uniformly coordinated (Richardson et al., 2013). This can occur where multiple trait combinations can

optimise performance (Westerband et al., 2021) and is consistent with the large magnitude of trait variance commonly observed within sites (Li et al., 2015).

4.4 | Trait variation in relation to environment, size and their interaction

Here, traits varied more often in relation to tree height and less in response to environment, possibly because our selected traits likely reflect environmental conditions over moderate timescales (that reflect development of the tissues in question). For example, leaf morphological and chemical traits are largely fixed once a leaf is expanded, so reflect environmental variations on longer time scales than physiological traits may be likely to (Fortunel et al., 2020; Paine et al., 2015; Yang et al., 2018). Some observations suggest that morphological traits are strongly influenced by developmental stage or size, while forest habitat (and the associated environmental differences) drives leaf chemical traits more strongly (Fortunel et al., 2020) but this division was not clear from our results.

As suggested by the ubiquity of size-related trait changes reported here, the magnitude of trait variation with plant size is likely camouflaged in the literature by a historically uneven approach to which traits are measured at different life stages (Gibert et al., 2016). Our examination of trait differentiation among size classes in relation to multiple environmental gradients now provides scope to extend theoretical predictions of ontogenetic trait variation, which have previously been limited to WD, SLA, assimilation rates and seed mass (Falster et al., 2018; Gibert et al., 2016). Doing so will further emphasise the need to account for trait changes with plant size when attempting to examine trait responses to environment (Cavender-Bares & Bazzaz, 2000; Falster et al., 2018; Fortunel et al., 2020; Green & Harms, 2018).

The specific patterns of trait variation in our study suggest a combination of light limitation and responses to a complex edaphic environment, whereby seedlings in some parts of the landscape experience waterlogging stress while others experience water deficit (Table S1).

Trees in very low light are expected to allocate more to leaf area, chlorophyll and leaf nitrogen to compensate for decreased per unit electron transport capacity in low light (Evans, 1989). Trees in low light are also expected to allocate proportionally more to stems than roots (McConnaughay & Coleman, 1999; Reich et al., 1998). Our results do not clearly reflect these expectations. The clearest result with respect to light was that trees in low light (our low light plots experienced minimum 1.6% PAR) had greater WUE_i, which indicates reduced transpiration to prevent water loss in a light-limiting environment, thereby also reducing photosynthesis (Baltzer & Thomas, 2007; Rumman et al., 2018). Some of these relationships with light were pronounced in smaller trees—greater leaf area and lower SLA and WUE_i—but lost in larger trees. Trees growing in high light showed more contrast in leaf architecture with tree size, whereas trees growing in low light showed contrasting chlorophyll and WUE_i with tree size.

Waterlogged trees are expected to experience nutrient limitation and impaired root growth (Lopez & Kursar, 1999; Moser et al., 2019; Parent et al., 2008) which our results do not clearly demonstrate. Waterlogged trees (high soil VWC or very shallow terrain) in our experiment did have lower leaf nitrogen and less acquisitive leaves. In the riparian zone where waterlogging is most common, smaller trees typically had longer taproots, reflecting the need for anchorage in that environment (Dorval et al., 2016; Karrenberg et al., 2003). Conversely, for larger trees, longer taproots are likely more advantageous on steeper terrain, for anchorage and water scavenging (Danjon et al., 2013). Consistent with expectations in the case of water deficit, periodically droughted trees allocated relatively more to roots, had higher wood density and lower leaf osmotic potentials, as would be expected in the case of water deficit. Also, larger trees had greater WUE_i when in drier soil, but smaller trees did not, consistent with the expectation that larger trees experience greater water deficit than smaller trees growing on soils of comparable soil moisture (Bennett et al., 2015). WD for larger trees was greater in lower soil moisture conditions (35% VWC) as compared to wetter conditions (45% VWC) but was also apparently lower on steeper terrain as compared to shallow terrain, where waterlogging most frequently occurs. These complexities suggest nonlinearity in the response of WD to edaphic conditions and merit further investigation. While much prior research has focused on comparing plant traits across soil types (Baltzer et al., 2005; Dent & Burslem, 2016), our findings demonstrate that edaphic conditions can influence plant traits at local spatial scales, both within a single soil type and at the intraspecific level. Of course, further interactions between the spatial and temporal components of water availability are to be expected (Daly & Porporati, 2005).

Factors additional to those captured here may influence trait variation and the degree to which traits mediate survival and growth outcomes. A prior study of demographic data, traits and soil variables from a 20 ha warm temperate forest dynamics plot showed that biotic neighbourhood context (density of heterospecific neighbours) and soil nutrient levels modulated trait effects on seedling survival (Zhang et al., 2026). Trait associations with vital rates can also vary seasonally and with climate. For example, hydraulic traits may best predict individual growth under drought, while light-acquisition traits may be more predictive for non-droughted trees (Rowland et al., 2021). These additional factors driving trait variation will serve to further complicate the picture presented here.

5 | CONCLUSION

We used a series of Bayesian models with variables for environment and tree height (drivers of within-species variation) to link traits with vital rates in a seedling translocation experiment in Bornean rainforest. Species WD and SLA were associated with species-level survival, and no traits were associated with species-level growth, consistent with prior work that shade tolerance and persistence may dominate seedling dynamics. Trait variation and covariation were driven by tree size and to a lesser extent by environment, clearly

demonstrating the need to further incorporate plant size or ontogeny in studies of trait variation. Trait covariation reflected morphometric shifts associated predominantly with tree size but also a spectrum of acquisitive versus conservative trait trade-offs both within and among species. Broadly speaking, our results demonstrate that within-species variation contains rich ecological information that can help to identify the complex links between traits, environment and plant performance and that these links vary as trees grow in size.

AUTHOR CONTRIBUTIONS

Michael O'Brien designed and established the planting experiment. Hannah J. Carle and Michael O'Brien led all aspects of scientific development, manuscript writing and review. Additionally, Patrick Meir, Adrienne B. Nicotra, Andrew Hector and Timothée Bonnett contributed to the ideas and methodology; Timothée Bonnett contributed to analysis of the data; Elia Godoong and Andrew Hector contributed on logistics, project administration and resources. All authors contributed critically to the drafts and gave approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Trait data are available on the Zenodo Repository: https://doi.org/10.5281/zenodo.17189187 (Carle et al., 2025). Growth, survival, light and neighbourhood data are available via the SEARRP Research Database. Tropospheric CO_2 and $\delta^{13}C$ data used to calculate WUE_i are available via the NOAA GML Data Repository.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Establishment of the experiment and rainfall exclusion.

Appendix S2. Details of environmental data collection.

Appendix S3. Trait measurements and calculations.

Appendix S4. Extended modelling and statistical analysis.

Figure S1. Posterior draws of species trait values. Summarised with median highest density intervals (HDI) at 0.66 and 0.95.

Figure S2. No evidence that tree size mediated species growth (blue) and survival (orange) outcomes in relation to species traits. Posterior estimates of the association of (a) species trait-size slopes with species growth/survival intercepts and (b) species trait intercepts with growth/survival-size slopes. Posterior draws from Bayesian hierarchical models are summarised with median highest density intervals (HDI) at 0.66.

Table S1. Summary of environmental variables. Plot-level means for each environmental factor were derived either from repeat measurements through time (n_t), repeat measurements within subplots (sbp) or plots (plot) (n_{sp}) or both. Half the subplots were periodically droughted, half kept under normal rainfall conditions.

Table S2. Summary of associations among environmental variables used in the trait models. From linear mixed models.

Table S3. Summary of measured traits. Carbon isotopes ($\delta^{13}C$) were used to calculate water-use efficiency (WUE_i) so $\delta^{13}C$ was not included as an independent trait in further analyses.

Table S4. Characteristics of select plots where plants were harvested for destructive sampling of above- and below-ground biomass. Plots were selected to represent the suite of available light and soil moisture conditions within each site and to provide a mix of tree sizes.

Table S5. PCA loadings for first five dimensions (Figure 3, main text).

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