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Competition-Induced Trait Variability Obscures Trait–Growth Relationships of Tree Seedlings

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Keywords: competition | individual growth | intraspecific trait variability | seedling experiment | trait–environment interactions | trait–growth relationships | trait plasticity

ABSTRACT

Trait-based ecology seeks to improve plant growth predictions by incorporating individual trait variability, yet empirical studies have shown that even individual-level traits struggle to predict growth due to unclear mechanisms. In a 3-year experiment measuring 10 functional traits and growth in 5188 seedlings, we found that individual trait–growth relationships are strongly competition-dependent. Without competition, traits strongly predicted growth, with predictive ability positively associated with trait variability, supporting theoretical expectations. However, competition significantly reduced the predictive ability of traits by simultaneously increasing individual trait variability and suppressing seedling growth rates. These results suggest that plants under competition achieve similar growth through diverse alternative strategies, obscuring trait–growth relationships. Our findings suggest that competition-induced trait variability might be a key driver of the weak trait–growth relationships frequently observed in natural communities, providing experimental evidence for the ongoing debate surrounding the weak trait–growth correlations.

1 | Introduction

Functional traits play crucial roles in plant resource acquisition strategies (Violle et al. 2007), shaping individual growth (Yang, Song, et al. 2021) and influencing community dynamics (McGill et al. 2006) and ecosystem processes (Hagan et al. 2023). Despite the promise that functional traits hold for predicting plant growth, empirical studies often reveal unexpectedly weak trait–growth relationships (Paine et al. 2015), challenging the fundamental assumption of functional ecology—traits determine individual performance, particularly growth (de Bello et al. 2025). This disconnect between theory and observation has been attributed to the widespread use of species mean traits (Yang et al. 2018), which ignore individual trait variability (Rodríguez-Alarcón et al. 2024; Siefert et al. 2015; Yang, Song, et al. 2021). Traits measured at the individual level should theoretically strengthen trait–growth relationships by better capturing plant responses to environmental conditions (Abakumova et al. 2016; Yang et al. 2018). However, recent work incorporating individual trait measurements has yielded mixed results, with some studies showing marginal improvement (Li et al. 2022) or even weaker

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trait–growth relationships (Fajardo et al. 2024; Poorter et al. 2018; Rodríguez-Alarcón et al. 2024). This inconsistency raises a critical gap in our understanding: why, despite their theoretical advantages, do individual-level traits yield divergent results in predicting plant growth?

These inconsistent findings may result from trait plasticity, particularly the diverse plastic responses induced by environmental stressors such as competition (Bittebiere et al. 2019; Yang et al. 2024), which might obscure the trait–growth relationships. According to the stress-induced plasticity hypothesis (Hoffmann and Merilä 1999), competition could trigger diverse plastic trait changes among individual plants (Novoplansky 2009) (Figure 1b). For instance, some individuals may shift toward resource-acquisition strategies (e.g., increased leaf area) that potentially enhance growth performance (Dawson et al. 2024). In contrast, others may adopt more conservative strategies or even undergo maladaptive changes (e.g., reduced height) (Lyu et al. 2017), prioritising survival over growth. Consequently, such competition-induced plasticity not only increases trait variability among individuals (Bittebiere et al. 2019; Yang et al. 2024) but also creates more individualised and divergent trait–growth relationships, making predictions of growth rates from traits more challenging. In contrast, individuals growing in the absence of competition tend to exhibit more straightforward and consistent trait–growth relationships (Figure 1a); in these cases, traits such as greater leaf area and lower stem density more reliably indicate a higher growth potential (Li et al. 2022), thereby strengthening the relationship between traits and growth (Poorter et al. 2018; Yang et al. 2018).

The observed weakening of the trait–growth relationships may also be related to the suppression of plant growth rates by competition (Beauchamp et al. 2025) (Figure 1b). Specifically, reduced growth rates first diminish interspecific differences

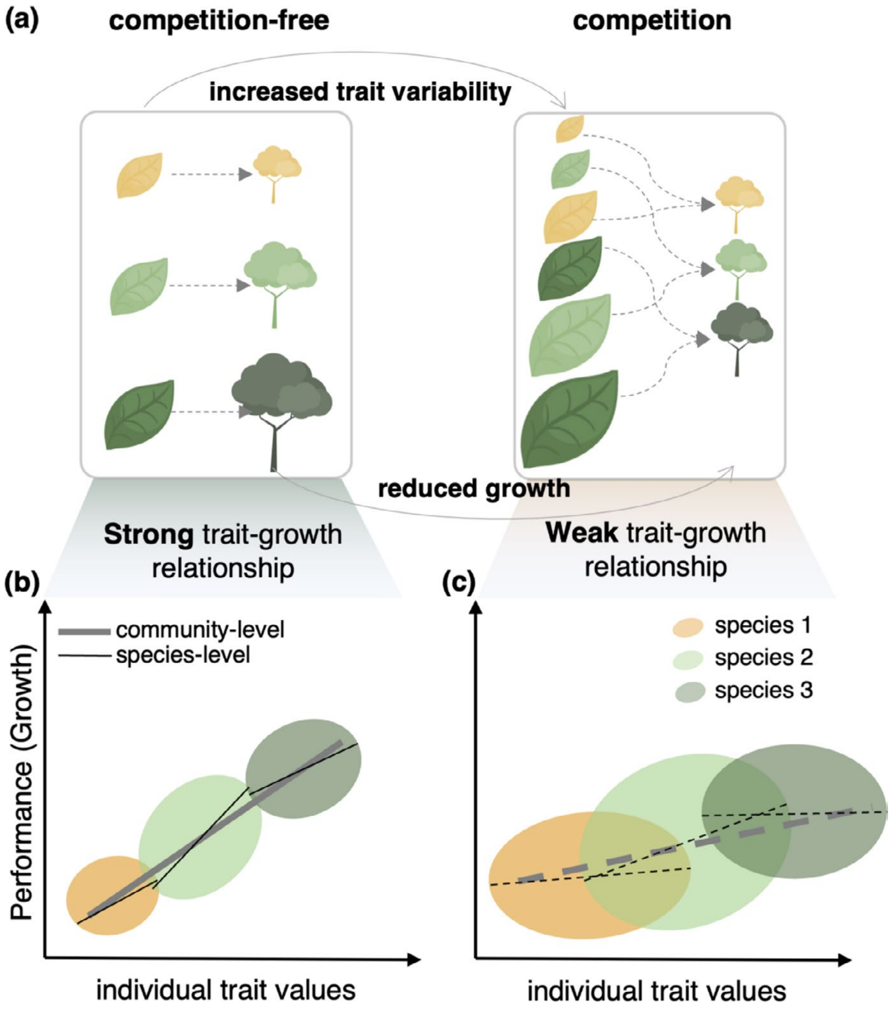

FIGURE 1 | Conceptual framework illustrating how competition alters trait–growth relationships. (a) Under competition-free conditions (left), species exhibit distinct trait values (represented by leaf size) and predictable growth performance with direct trait–growth correspondence. Under competition (right), species develop increased trait variability while growth is consistently reduced, complicating trait-based growth predictions. (b–c) Schematic trait–growth relationships showing (b) strong positive relationships under competition-free conditions, where limited trait variability and distinct growth rates yield predictable patterns (solid grey line), versus (c) weakened relationships under competition, where expanded trait variability (more expansive ellipses) coupled with compressed growth performance flattens the trait–growth relationship (dashed grey line). The coloured ellipses represent species-specific trait-performance spaces. Thin black lines depict intraspecific (within-species) relationships; thick grey lines represent community-level patterns across all species.

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in growth performance, causing diverse individual trait values to be linked to similar growth, thereby potentially complicating trait–growth linkages (Rodríguez-Alarcón et al. 2024). Although slow tree growth is prevalent in various forests (Li et al. 2022; Poorter et al. 2018; Rodríguez-Alarcón et al. 2024) and is projected to increase due to climate change (Augusto et al. 2025), the effects of slow growth rates have rarely been tested, largely due to methodological constraints associated with isolating competition-free individuals within natural communities. Consequently, whether competition-induced trait variability and suppression of the growth rate collectively explain the observed weak individual-level trait–growth relationships remains unclear, and this leaves a critical gap in our understanding of the mechanisms underlying plant growth dynamics in natural communities.

To address these gaps, we conducted a 3-year greenhouse experiment in which 5188 seedlings of seven co-occurring subtropical tree species were raised under competition-free and competition conditions. We measured 10 functional traits and monitored the increase in the height of the plants, constructing separate univariate growth models for each trait under both competition conditions. This controlled experimental approach allowed us to rigorously investigate the following questions: (1) Do individual traits consistently predict growth under both competition-free and competition conditions, and in which scenario are traits more predictive? (2) How does individual trait variability influence the trait–growth relationship under different competition conditions? (3) How does the seedling growth rate itself affect the trait–growth relationship? We hypothesised that traits would better predict growth under competition-free conditions, as evidenced by the higher R^2 values of the growth model and by the larger standardised regression coefficients of traits. Additionally, we predicted that trait variability would enhance the predictive ability of traits under competition-free conditions but weaken trait–growth relationships through greater individual trait variability in plants under competition, reflecting the use of diverse alternative functional strategies by the plants. Furthermore, we expected that a reduction in growth rates under competition conditions would diminish the strength of the trait–growth relationship.

2 | Materials and Methods

2.1 | Study Site and Species

Our experiment was conducted in a greenhouse at Tiantong National Forest Park (29°48.817′N, 121°47.116′E), Zhejiang Province, eastern China. This region has a subtropical monsoon climate with a mean annual temperature of 16.2°C and a mean annual precipitation of 1374.7 mm. The forest is dominated by evergreen tree species but also includes deciduous species growing on slightly acidic yellow–red mountain soils with pH values ranging from 4.4 to 5.1 (Yang et al. 2011). Thirteen native tree species, including eight evergreen and five deciduous species that naturally coexist in the local forest, were initially selected on the basis of life form diversity, phylogenetic relationships and seed availability (Table S1). To minimise confounding genetic variation and maternal effects, more than 2000 healthy seeds per species were collected from a single mature tree between October and December 2018. The seeds were disinfected, stored over the winter and sown in nursery trays in April 2019 under full sunlight with adequate irrigation. Owing to differences in germination success, the final experiment included seven species: *Daphniphyllum oldhamii*, *Cyclobalanopsis glauca*, *Castanopsis sclerophylla* , *Lithocarpus glaber*, *Schima superba*, *Hovenia acerba* and *Quercus chenii* . When the seedlings were well established, individuals of similar size and health status were transplanted into pots for the experiment.

2.2 | Experimental Design

We conducted a 3-year (2019–2022) greenhouse experiment (Yang et al. 2024) that fully crossed two competition treatments with nine abiotic environments. This design enabled us to assess how competition influences trait–growth relationships across diverse resource conditions and to test the generality of these effects within environmentally heterogeneous settings.

The experiment included two treatments: a competition-free baseline (one seedling per pot) and a competition treatment (seven seedlings, one from each of seven species, planted 3–5 cm apart). Seedling positions in competition pots were fully randomised to avoid spatial bias. Both treatments were replicated across nine environmental blocks (see Figure S1 for full details). Each block represented a unique combination of light (L), soil moisture (M) and soil phosphorus (P), established via a three-factor, three-level (low, medium and high; coded 1–3) orthogonal design (Table S2). The greenhouse was thus divided into nine blocks, each corresponding to a specific combination of resource levels (see Appendix S1 for details on abiotic setup). Environmental factor levels were based on measurements from a nearby 20-ha forest plot (Yang et al. 2011), and comparison with natural forest data (Figure S2) confirmed that experimental conditions were fully nested within the natural range of the understory, ensuring an ecologically realistic resource landscape.

To maximise statistical power, we established 40 replicate pots per species for the competition-free treatment and 50 replicate pots per species for the competition treatment within each of the nine environmental blocks. During a 1-month establishment period, any seedlings that died were replaced with healthy, size-matched individuals. Subsequent minor losses resulted in final effective replications of 35–40 pots (competition-free) and 45–48 pots (competition) per species per block, which yielded a final dataset of 2728 pots and 5188 seedlings.

All seedlings were grown in uniform pots (15 cm height, 18.5/12 cm top/bottom diameter; Figure S3), each filled with 2 ± 0.01 kg of homogenised forest soil collected from 15 to 30 cm depth and sieved to remove coarse particles and organic debris. All pots were spaced 15–20 cm apart to prevent cross-pot interference and were randomly repositioned within each block every 2 weeks to minimise microenvironmental variation. Pest control measures, including insect-proof netting and insecticide application, when necessary, were used to ensure seedling health. Pot size was selected based on previous experimental experience (Yang, Lu, et al. 2021; Yang et al. 2024) to balance the need for detectable interspecific competition against the risk of unnatural root confinement (Appendix S2).

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2.3 | Measurement of Functional Traits and Construction of Multidimensional Trait Axes

We used a two-phase destructive harvest with temporal replication to link seedling functional strategies with growth across temporal and environmental gradients. Seedlings were randomly preassigned at the start to two harvests: 2391 in year two (2021) and a larger group of 2797 for year three (2022) to offset higher expected mortality. For each harvest, entire pots were processed, with roots carefully washed and, in competition pots, separated by individuals. We measured five aboveground and four belowground traits for every surviving seedling (Figure S4), reflecting diverse ecological strategies of seedlings (Laughlin 2023). The aboveground traits included leaf area (LA, cm^2), specific leaf area (SLA, cm^2/g), leaf dry matter content (LDMC, g/g), leaf toughness (LTO, N/m) and stem specific density (SSD, g/cm^3). The fine-root traits included specific root length (SRL, m/g), root diameter (RD, mm), root tissue density (RTD, g/cm^3) and specific root area (SRA, cm^2/g). All trait measurements followed standardised protocols (Pérez-Harguindeguy et al. 2013). See Appendix S3 for detailed methods and Table S3 for trait-specific sample sizes ($n = 3400–4005$).

Given that plant traits covary due to physiological and evolutionary constraints, we used principal component analysis (PCA) to reduce above- and below-ground trait data into multidimensional axes (Table S4). Analyses were performed separately for above- and belowground traits to reflect their functional independence (Beccari and Carmona 2024; Carmona et al. 2021), using only individuals with complete data for all nine traits ($n = 3306$). Prior to PCA, all traits were $\log_{10}$-transformed (except the near-normal LDMC, LTO and RD) and standardised. We used Horn's parallel analysis (Horn 1965) to determine the number of retained components and applied varimax rotation to improve interpretability. For both above- and below-ground traits, two main axes were identified (Figure 2), explaining 56% and 97% of the variance, respectively. These axes captured key ecological trade-offs: the leaf economics spectrum (Above_PC1, 35%), stem construction (Above_PC2, 21%), root collaboration (Below_PC1, 49%) and root economics spectrum (Below_PC2, 48%). These multidimensional axes, closely aligned with global plant functional spectra (Bergmann et al. 2020; Carmona et al. 2021; Díaz et al. 2016), were used as predictors in subsequent growth models.

2.4 | Seedling Growth Rate

We quantified seedling relative growth rate (RGR) as a size-corrected metric of average annual growth. Height was measured from the stem base to the apical leaf at transplant (August 2019; H_{initial}) and again at final harvest (2021 for 2-year-old seedlings, 2022 for 3-year-old; H_{final}). RGR was calculated as $(\log(H_{\text{final}}) - \log(H_{\text{initial}})) / (t_{\text{final}} - t_{\text{initial}})(\log(H_{\text{initial}}) - \log(H_{\text{final}})) / (t_{\text{final}} - t_{\text{initial}})$ (Hoffmann and Poorter 2002; Weemstra et al. 2021), where H denotes the height and t represents the measurement time in years. This approach standardises growth relative to initial size, capturing average annual height gain over the measurement interval. We used height as a proxy for growth due to the nondestructive repeatability and strong correlation with biomass (Pearson's $r = 0.68$, Figure S5), providing a viable alternative to destructive single-harvest biomass assessments. We excluded seedlings that died before harvest ($n = 1077$), showed negative growth ($n = 38$), or were statistical outliers (RGR > ±4 SD, $n = 3$) (Yang, Song, et al. 2021). The final dataset comprised 4070 seedlings (2256 2-year-old and 1814 3-year-old) with validated annual RGR values.

2.5 | Modelling Trait–Growth Relationships at Community and Species Levels

To quantify how interspecific competition alters trait–growth relationships, we developed a hierarchical modelling framework. This

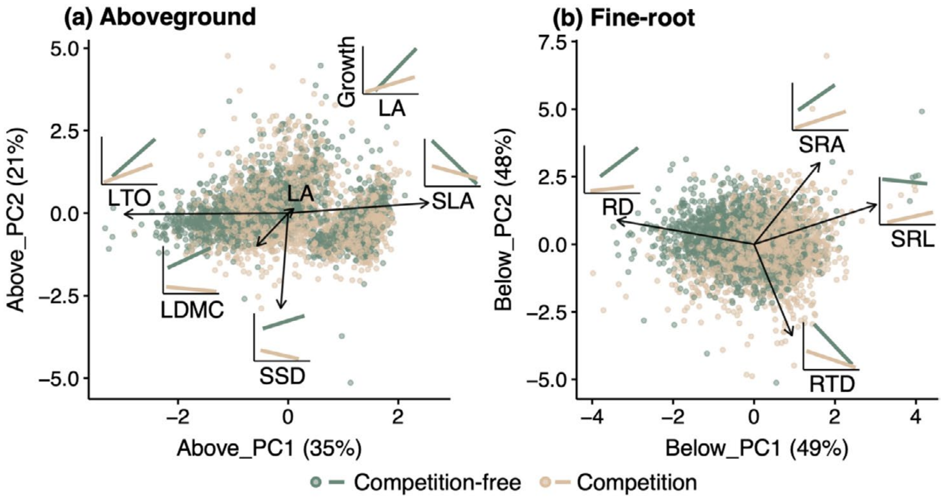

FIGURE 2 | Major axes of functional trait variation. Principal component analysis (PCA) was performed separately on the five aboveground and four belowground traits ($n = 3306$ seedlings). Two axes were retained for each PCA via Horn's parallel analysis with varimax rotation, explaining 56% (aboveground) and 97% (belowground) of the total variance. The resulting axes capture key ecological strategies: The leaf economics spectrum (Above_PC1, 35%) and stem construction (Above_PC2, 21%) and a root collaboration spectrum (Below_PC1, 49%) and the root economics spectrum (Below_PC2, 48%). Points are individual seedlings, coloured by treatment (green: Competition-free; yellow: Competition). The inset plots show the bivariate relationship between each trait and the relative growth rate, with regression lines for the competition-free (green) and competition (yellow) treatments. See Figure S7 for complete trait–growth correlations.

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involved fitting a series of growth models to both competition-free and competition treatment datasets, systematically comparing their outcomes. Our core analysis modelled standardised seedling relative growth rate as a function of a given multidimensional trait axis. The general model structure was as follows:

$$\mathrm{RGR} \sim \alpha + \beta_1 \mathrm{Trait} + \beta_2 \mathrm{Year} + \beta_3 \mathrm{Trait{:}\,Year} + \gamma_{sp}$$

where α is the intercept, β variables represent estimated coefficients for the standardised trait axis, growth year (2 vs. 3) and their interaction, and γ denotes random effects of species identity to account for inherent baseline growth differences. To preserve clear ecological interpretability, we modelled each of the four orthogonal trait axes separately (Bongers et al. 2020; Li et al. 2022). This axis-by-axis approach yields a slope that can be directly interpreted as the predictive ability of a specific functional strategy, without confounding effects from other orthogonal axes. By keeping year covariates constant and varying only trait predictors, differences in R^2 directly quantify each trait axis's contribution to growth prediction, facilitating fair comparisons of competition effects.

We implemented this core model within a hierarchical framework to ensure generalisability (Figure S6). To isolate competition effects while holding the environment constant, models were fitted separately within each of nine environmentally homogeneous blocks. To capture both overall and species-specific patterns, analyses were conducted at two levels: community-level mixed-effects models with species identity as a random intercept, and species-level linear models fitted separately for each species within each block. This yielded 72 community-level models and 344 species-level models, excluding 18 species–block combinations with fewer than 10 individuals.

To test competition effects, we compared two key metrics derived from the model when fitted to the competition-free versus the competition datasets: (1) marginal R^2, the proportion of variance explained solely by the fixed effects, interpreted here as predictive ability in line with trait-based ecology literature and for conceptual clarity (de Bello et al. 2025); and (2) the standardised slope of the trait axis, indicating effect size per trait standard deviation. To formally test for differences, we compared the sets of marginal R^2 values and standardised slopes from the 36 community-level or 180 species-level pairs using paired *t*-tests or Wilcoxon rank-sum tests, as determined by Shapiro–Wilk normality tests. All predictors and responses were standardised, allowing direct comparisons of coefficients across traits (Schielzeth 2010). Analyses used data from 3306 seedlings with complete multidimensional trait and growth records. Finally, we used hierarchical partitioning to quantify the independent effects of trait axis, year and their interaction (Lai et al. 2022), and repeated the above main analysis with individual traits instead of multidimensional axes to confirm the consistency of our findings (Figures S7 and S8).

2.6 | Effects of Trait Variability and Growth Rate on Trait–Growth Relationships

To further explore the drivers of the varying trait–growth relationships, we tested how trait variability and mean seedling growth rate influenced the model's predictive ability, as measured by marginal R^2. The response variable for this analysis was the marginal R^2 derived from each growth model. We calculated two corresponding predictor variables: (1) trait variability, which was quantified as functional richness (i.e., the extent of occupied trait space) using the trait probability density (TPD) method (Carmona et al. 2016, 2019), which integrates both inter- and intra-specific variation, and (2) mean growth rate, which was calculated as the arithmetic mean of the relative growth rates for all seedlings within each model. For trait variability, at the species level, we pooled individual trait values and estimated continuous TPDs using Gaussian kernel density estimation with an optimised bandwidth, applying a 5% quantile threshold to mitigate the influence of outliers. At the community level, we aggregated the species-level TPDs (Carmona et al. 2019).

We then fitted these variables using generalised linear mixed-effects models with a beta error distribution, appropriate for modelling proportion data bounded between 0 and 1. The full theoretical model included trait variability, the interaction between trait variability and competition (to capture potential context-dependent effects), and mean RGR as fixed effects, with trait identity and environmental block specified as random effects. However, at the community level, a preliminary analysis revealed strong collinearity between mean RGR and the competition treatment (Pearson's $r = 0.77$), preventing their simultaneous inclusion. We therefore adopted a two-model strategy: the first model included trait variability and its interaction with competition to test our primary hypothesis, while a second, separate model tested the effect of mean RGR alone, which in this context served as a proxy for the competition treatment. At the species level, the collinearity between mean RGR and competition was weaker ($r = 0.59$), allowing us to include all predictors in a single model, with species identity as a random effect. We further explored these species-level effects using a Bayesian structural equation model to disentangle the direct and indirect causal pathways (see Appendix S4 for details).

To test the robustness of our findings, this entire workflow was then repeated using the results from the 162 community-level and 910 species-level growth models based on individual traits (Figure S9). To address potential statistical concerns regarding the use of R^2 as a response variable, we performed a null-model analysis which confirmed the robustness of our findings (see Appendix S5 for methods; Figure S10 for results). To assess whether competition effects were robust to environmental heterogeneity, we fitted linear mixed-effects models to the entire dataset pooled across all nine environmental blocks, in contrast to our block-specific analyses. Separate models for the competition and competition-free treatments included the four multidimensional trait axes, year, three primary environmental variables (light, moisture and phosphorus), and all two-way interactions as fixed effects, with block and species identity (for community-level models) as random effects. Results from these heterogeneous models were qualitatively consistent with our main findings (Figures S11–S13), confirming that competition effects persist across the full resource gradient.

Analyses were performed in R (v4.4.2) using TPD for trait variability, lme4 and glmmTMB for mixed models, lmerTest for significance testing, MuMIn for marginal R^2 and glmm.hp for variance partitioning.

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3 | Results

3.1 | Trait–Growth Relationships Are Consistently Weaker Under Competition

Competition consistently weakened the relationship between functional traits and seedling growth, as evidenced by a significant reduction in both the variance explained (marginal R^2) and the magnitude of trait effects (standardised absolute slopes). At the community level, the average marginal R^2 across four multidimensional trait axes decreased by 59% under competition, from 0.11 to 0.047 (paired Wilcoxon test, $V=648$, $p<0.001$; $n=36$; Figure 3a). This reduction was most pronounced for the leaf economics spectrum (Above_PC1), with marginal R^2 declining by 65% (Figure S8a). A similar pattern was observed at the species level, where the average marginal R^2 dropped by 53%, from 28% to 13.2%, under competition ($V=14{,}725$, $p<0.001$; $n=180$; Figure 3a and Figure S8b), despite higher baseline values without competition.

The absolute trait slopes were generally reduced under competition (Figure 3b). Although this trend was not statistically significant for the multidimensional axes at the community level (−29%, $V=428$, $p=0.14$; Figure 3b), it was more pronounced and marginally significant at the species level (−7.9%, $V=9362$, $p=0.08$; Figure 3b), particularly for Above_PC1, whose *slope* was halved (Figure S8c). Analyses of nine individual traits further supported these results and revealed additional trait-specific differences (Figure S7).

3.2 | Increased Trait Variability Weakens Trait–Growth Relationships Under Competition

Competition consistently increased trait variability among seedlings, as measured by the extent of occupied trait space (Figure 4). At the community level, trait variability across the four multidimensional axes was on average 15% greater under competition (increasing from 4.16 to 4.78; $V=161$, $p=0.006$;

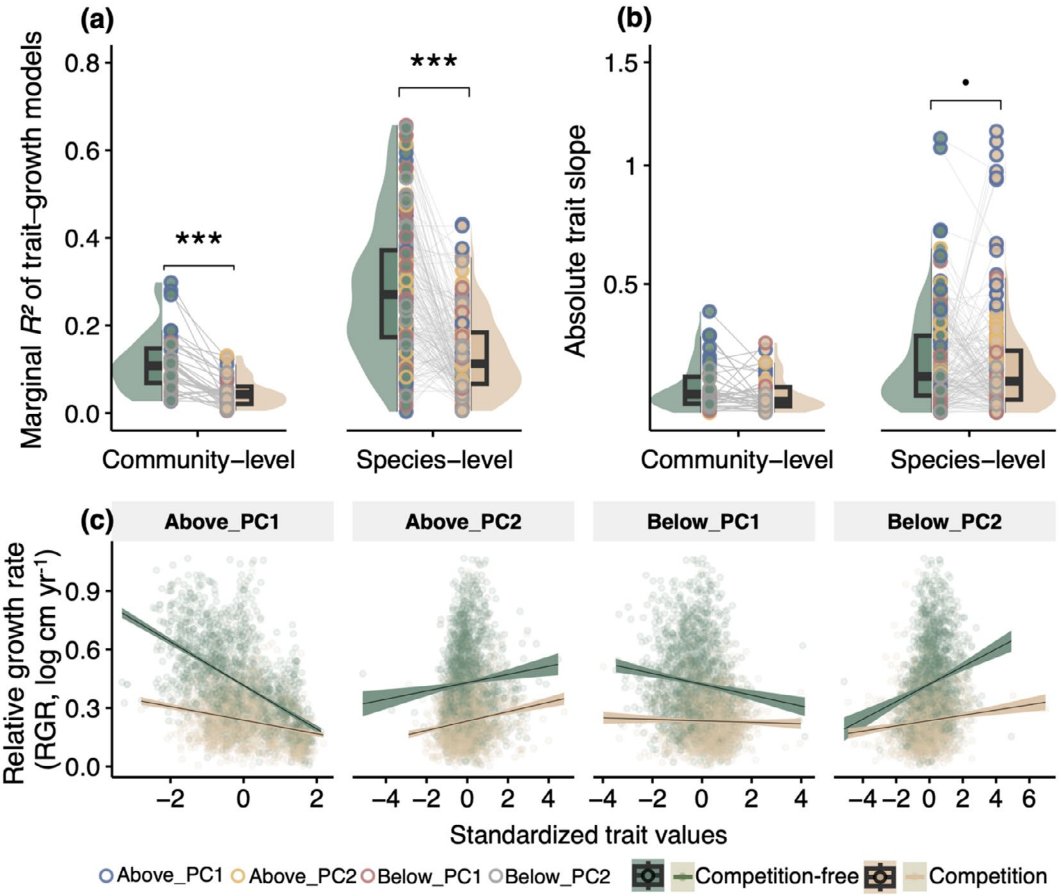

FIGURE 3 | Multidimensional trait–growth relationships under competition-free and competition treatments in within-block homogeneous environments. (a) Marginal R^2 (predictive ability) and (b) absolute slope of multidimensional trait axes from growth models under competition-free (green) and competition (yellow) treatments. Each point represents a trait–growth model, with border colour indicating trait identity and fill colour denoting treatment. The grey lines connect matched models across treatments. All analyses were conducted within environmentally homogeneous blocks to minimise abiotic heterogeneity and isolate the effects of competition. Models were fitted at both the community level ($n=36$; 4 trait axes ×9 environmental blocks) and the species level ($n=180$; after 18 block–species combinations with fewer than 10 observations were excluded). Both models included one of the multidimensional trait axes, year and their interaction as fixed effects. At the community level, species identity was incorporated as a random effect, whereas the species-level models were simple linear regressions without random effects. Statistical significance ($^{***}p<0.001$; $^{\cdot}0.05<p<0.1$) was determined using paired Wilcoxon rank-sum tests. (c) Bivariate relationships between standardised multidimensional trait axes and the relative growth rate (RGR) under competition-free (green) and competition (yellow) conditions.

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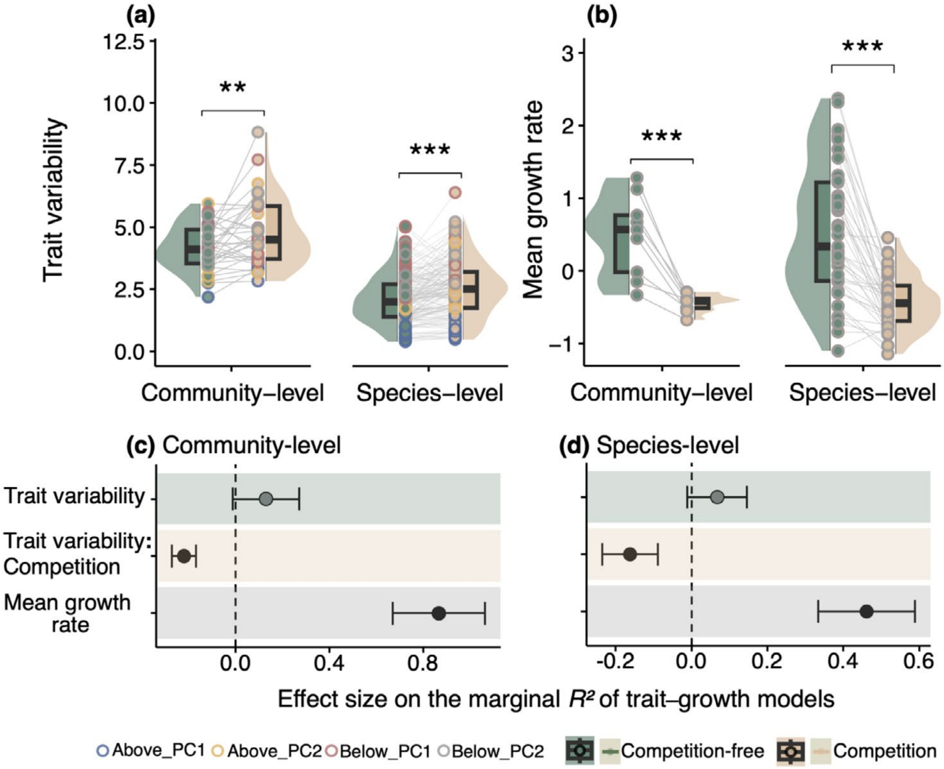

FIGURE 4 | Trait variability and mean growth rate modulate the predictive ability of multidimensional trait–growth models in within-block homogeneous environments. (a) Variability in multidimensional trait axes and (b) mean standardised relative growth rates (RGRs) for each trait–growth model, shown separately for community-level and species-level analyses under competition-free (green) and competition (yellow) conditions. For community-level models, trait variability encompasses both within- and between-species differences, whereas for species-level models, it reflects only within-species variation. Each point represents a trait–growth model, with border colour indicating trait identity and fill colour denoting treatment. The grey lines connect matched models across treatments. Statistical significance (***$p < 0.001$; **$p < 0.01$) was determined using paired Wilcoxon rank-sum tests. (c, d) Effects of trait variability, its interaction with competition and the mean growth rate on model predictive ability (marginal R^2), evaluated using generalised linear mixed-effects models (beta distribution, logit link). At the community level (c), trait variability and its interaction with competition were included in one model, and the mean growth rate was included in a separate model to avoid collinearity with competition. At the species level (d), all three predictors were included in a single model due to their low correlation. The models included trait identity and environmental block as random effects at the community level, with species identity added at the species level. The black points indicate significant effects ($p < 0.05$), and the grey points indicate marginal significance ($0.05 \leq p < 0.1$).

Figure 4a). This pattern was even more pronounced at the species level, where trait variability increased by 21% (from 2.08 to 2.52; $V = 666$, $p < 0.001$; Figure 4a).

The influence of trait variability on marginal R^2 was strongly context-dependent. In the absence of competition, greater trait variability was associated with a marginally positive effect on R^2 at both the community (slope $= 0.07$, $p = 0.09$; Figure 4c) and species (slope $= 0.13$, $p = 0.07$; Figure 4d) levels. However, the interaction between trait variability and competition was significantly negative at both levels (community: slope $= -0.22$, $p < 0.001$; species: slope $= -0.16$, $p < 0.001$; Figure 4c,d), indicating that increased trait variability corresponded to lower R^2 values under competition. These patterns were further supported by supplementary analyses based on individual traits (Figure S9).

3.3 | Low Seedling Growth Rates as a Factor in Weakening the Trait–Growth Relationships

Over the 3 years, competition consistently and significantly reduced the mean standardised seedling growth ($p < 0.001$; Figure 4b). In turn, lower mean growth was strongly associated with lower marginal R^2 values in the trait–growth models. This positive relationship was evident at both the community (slope $= 0.46$, $p < 0.001$; Figure 4c) and species levels (slope $= 0.87$, $p < 0.001$; Figure 4d). Bayesian structural equation modelling at the species level further confirmed that competition weakened trait–growth models via reduced growth (competition → mean growth: standardised path coefficient $\beta = -0.98$; mean growth → R^2: $\beta = 0.08$; Figure S14a). The indirect effect of competition on marginal R^2 via mean growth accounted for 53% of the total effect (-0.078 of -0.149; Figure S14b). Repeating the main analyses on a dataset pooled across all nine environmental blocks revealed that competition remained a significant factor that reduced both the marginal R^2 and the absolute *slopes* of the trait–growth relationships (Figures S11–S13; see Table S5 for model details).

4 | Discussion

Although intraspecific trait variability has been proposed to improve plant growth predictions by capturing microenvironmental

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responses (Yang et al. 2018), empirical studies increasingly report weak trait–performance relationships among individuals in natural communities (Fajardo et al. 2024; Li et al. 2021; Poorter et al. 2018; Rodríguez-Alarcón et al. 2024). This paradox may result from oversimplified frameworks of trait–environment dynamics, particularly the inadequate integration of competition as a critical driver of phenotypic expression (Novoplansky 2009). Through a 3-year field experiment encompassing 5188 seedlings across diverse environmental gradients, we demonstrate that competition fundamentally restructures trait–growth relationships. Under competition-free conditions, trait variability strengthens traits' predictive ability (marginal R^2) for individual growth as expected. Conversely, competition decouples traits from growth performance by increasing trait variability and reducing growth rates (Figure 4). Our findings identify competition as a pivotal modulator of trait–performance relationships, providing direct evidence and new insight into the limited predictive ability of traits in natural communities, and reconciling previously conflicting empirical observations.

4.1 | Strong Trait–Growth Relationships Under Competition-Free Conditions

By experimentally removing competition, we found that trait-based models could explain substantial growth variation (2.7%–40.3%, Figure S12a), a level of predictive ability rarely achieved in complex field studies (Li et al. 2021; Paine et al. 2015; Poorter et al. 2018). However, these relationships were highly trait-specific and context-dependent (e.g., they varied with both abiotic conditions and temporal factors). For example, leaf economics axis (Above_PC1, primarily associated with SLA) was the most powerful predictor of growth (Figures S8a and S13a), but revealed an unexpected pattern (Wright et al. 2004): a consistent negative association with growth that amplified significantly under high-light conditions (Figure S12g). In such environments, elevated physiological stress may cause the metabolic and structural costs of high-SLA leaves to outweigh their photosynthetic advantages. These results are consistent with similar findings in seedlings (Iida et al. 2014) and suggest a developmental contingency, further supported in our study by widespread trait × year interactions (Figures S8g and S12c). In contrast, belowground trait effects, which explained 2.9%–14.1% of growth variation, were more variable in their direction: the relationship between the root economics axis (Below_PC2) and growth shifted from positive under low light (favouring acquisitive strategies) to negative under high light (favouring conservative strategies) (Roumet et al. 2016). These divergent trait-specific relationships highlight the need for growth performance models that explicitly account for the interactive effects of traits, environmental conditions, and developmental stage (Dun et al. 2025; Kamimura et al. 2023; Laughlin 2018, 2023, 2024).

4.2 | Weak Trait–Growth Relationships Under Competition

Compared with those under competition-free conditions, the overall predictive ability (0.5%–16%) of trait–growth models declined by 63% in homogeneous environments, with main effects, trait–year interactions and year alone reduced by 44%, 39% and 66%, respectively (Figure S15a). This weakening occurs through three pathways. First, competition attenuated the main effects of key functional traits, such as the complete loss of the positive influence of aboveground conservative traits like LDMC (Figures S8e and S12b). Second, competition suppressed trait–environment and trait–year interactions, with all belowground trait × light interactions becoming nonsignificant (Table S5). This likely occurred because shading by taller neighbours homogenised the understory light environment, thus removing the light gradient with which root traits could interact. Third, competition weakened the effects of abiotic drivers, particularly light availability and developmental stage (3- vs. 3-year-old seedlings), consistent with a crowded canopy with homogeneous light conditions (Figure S16). These findings collectively highlight that competition, a ubiquitous feature of communities (Freckleton et al. 2009; McGill et al. 2006), acts as a strong ecological filter that broadly decouples plant growth from both functional traits and environmental factors. This explains the limited predictive ability of growth models, even when higher-order trait–environment interactions are included (Li et al. 2021).

Notably, the competition filter does not uniformly suppress all trait effects. Some relationships are maintained or even amplified, revealing which strategies are favoured under intense resource competition. For instance, the positive effect of total leaf area (LA) on growth is retained and strengthened under competition (Figure S8c,e), consistent with recent studies highlighting the high predictive value of LA (Fajardo et al. 2024). This suggests that in crowded, light-limited stands, the capacity to intercept light becomes a decisive advantage (Goud et al. 2023), potentially overriding other functional trade-offs. Moreover, belowground traits shift from environment-dependent influences to strong direct effects under intense competition (Table S5), reflecting a transition from multiple coexisting root strategies shaped by abiotic heterogeneity (Weemstra et al. 2016) to the dominance of a specific competitive strategy—thicker fine roots, low specific root length and low root tissue density—that enables rapid, low-cost soil exploration and resource preemption (Sanaei et al. 2025). Thus, even under strong biotic filtering, LA and key belowground attributes remain potential predictors of growth, offering promising avenues for future research in trait-based ecology.

4.3 | What Drives the Weaker Trait–Growth Relationships Under Competition?

Our results indicate two synergistic mechanisms can dismantle trait–growth relationships under competition. First, competition-induced trait variability may potentially weaken trait–growth relationships through two distinct but synergistic mechanisms: phenotypic noise caused by plasticity-driven trait variability and the blurring of interspecific trait differences. On the one hand, competition induces diverse phenotypic responses (Figure 4a, Figures S9 and S13), including nonadaptive plasticity (e.g., competition-induced compensatory increases in SLA in our study) and shifts in the adaptive strategies (e.g., shifting from growth-focused strategies to survival-focused strategies) (Iida et al. 2014). Such diverse plastic responses may introduce functional noise, resulting in the decoupling of traits from growth outcomes. Even adaptive plastic responses, such

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as reduced SSD to improve resource acquisition, may not necessarily translate into growth benefits (Auld et al. 2009), potentially leading to a failure to predict growth. On the other hand, competition-driven changes in traits predominantly emerge within species (Figure S5). This increased intraspecific variation could blur interspecific differences by masking each species' inherent functional signature. This resulting pattern of interspecific trait convergence aligns with observations in Amazonian forests, complicating trait-based growth predictions (Poorter et al. 2018). Experiments further confirm that hard traits (e.g., hydraulic traits) with high intraspecific variability exhibit weaker growth predictive ability than less plastic soft morphological traits do (Li et al. 2022). This dual effect—the ambiguity of functional signals and species identity—potentially alters the direction and strength of trait–growth relationships at multiple ecological scales, ultimately reducing the predictability of growth.

The suppression of plant growth rates by competition emerged as another mechanism. Competition reduced interspecific growth differences by 31% (Figure S18), compressing the growth performance landscape and making it inherently difficult to detect trait effects on growth. This detection difficulty was compounded by technical limitations in measuring small growth increments. For instance, obvious measurement errors in height (e.g., negative or zero growth) increased 7.5-fold under competition, with 34 such instances recorded versus only four in the competition-free treatment. Although these outliers were excluded from our growth models, their elevated frequency indicates that measurement uncertainty remained high among retained seedlings. Such heightened noise in growth measurement likely further constrains the predictive ability of trait-growth models. Our results thus experimentally support the previously untested assumption that observed weak trait–growth correlations in slow-growing hyperdiverse Amazonian forests (Poorter et al. 2018) and Colombian tropical dry forests (Rodríguez-Alarcón et al. 2024) are mechanistically constrained by low growth rates.

Importantly, these mechanisms are not unique to competition but likely constitute a general stress signature in plant responses to intense ecological pressures. For example, harsh abiotic conditions, such as drought and nutrient limitation, are known to induce similar patterns of increased trait plasticity and reduced growth (Niu et al. 2020). Supporting this inference, in our most resource-poor environments (as indicated by average biomass in the absence of competition), trait–growth correlations remained weak even without competition (Figure S17), suggesting that strong abiotic stress may decouple traits from performance through mechanisms similar to those under competition. This points to the possibility of a unifying framework to explain the persistent erosion of trait–performance linkages across biotic and abiotic stress gradients, from highly competitive communities to resource-limited environments (Fajardo et al. 2024; Goud et al. 2023; Li et al. 2021; Paine et al. 2015; Poorter et al. 2018; Rodríguez-Alarcón et al. 2024). Such integrative frameworks are urgently needed under accelerating global change, as increased phenotypic plasticity and reduced growth—two key drivers of weakened trait–performance linkages—are becoming increasingly prevalent under intensifying climate stress (Augusto et al. 2025; Chen et al. 2017).

5 | Conclusion

Our 3-year experiment demonstrated that competition generally weakened trait–growth correlations in seedlings (except for leaf area) by increasing trait variability and reducing seedling growth rates. This helps explain the weak trait–growth relationships frequently observed in natural forests. We further show that individual trait variability enhances the predictive ability of trait–growth models under competition-free conditions but reduces it under competition, thereby providing evidence that reconciles recent inconsistencies over its role in trait–growth relationships. More broadly, our study highlights that growth prediction is context dependent, shaped not only by abiotic factors but also by biotic competition and ontogeny, underscoring the need to integrate both environmental and developmental stages.

Author Contributions

J.Y. conceived this study. C.P.C. and G.S. further developed the idea. G.S., J.Y. and X.W. designed the experiments. J.Y. conducted the experiments, collected and analysed the data and performed the visualisation. J.Y. wrote the first draft of the manuscript, and all authors substantially contributed to revisions.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and analysis code supporting this study are openly available on Figshare: https://doi.org/10.6084/m9.figshare.30121870.v2.

Peer Review

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References

Abakumova, M., K. Zobel, A. Lepik, and M. Semchenko. 2016. "Plasticity in Plant Functional Traits Is Shaped by Variability in Neighbourhood Species Composition." *New Phytologist* 211: 455–463.

Augusto, L., R. Borelle, A. Boča, et al. 2025. "Widespread Slow Growth of Acquisitive Tree Species." *Nature* 640: 395–401.

Auld, J. R., A. A. Agrawal, and R. A. Relyea. 2009. "Re-Evaluating the Costs and Limits of Adaptive Phenotypic Plasticity." *Proceedings of the Royal Society B: Biological Sciences* 277: 503–511.

14610248, 2025, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70259 by East China Normal University, Wiley Online Library on [11/11/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Beauchamp, N., G. Kunstler, L. Touzot, et al. 2025. “Light Competition Affects How Tree Growth and Survival Respond to Climate.” *Journal of Ecology* 113: 672–688.

Beccari, E., and C. P. Carmona. 2024. “Aboveground and Belowground Sizes Are Aligned in the Unified Spectrum of Plant Form and Function.” *Nature Communications* 15: 9199.

Bergmann, J., A. Weigelt, F. van der Plas, et al. 2020. “The Fungal Collaboration Gradient Dominates the Root Economics Space in Plants.” *Science Advances* 6: eaba3756.

Bittebiere, A.-K., H. Saiz, and C. Mony. 2019. “New Insights From Multidimensional Trait Space Responses to Competition in Two Clonal Plant Species.” *Functional Ecology* 33: 297–307.

Bongers, F. J., B. Schmid, Z. Sun, et al. 2020. “Growth–Trait Relationships in Subtropical Forest Are Stronger at Higher Diversity.” *Journal of Ecology* 108: 256–266.

Carmona, C. P., C. G. Bueno, A. Toussaint, et al. 2021. “Fine-Root Traits in the Global Spectrum of Plant Form and Function.” *Nature* 597: 683–687.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. “Traits Without Borders: Integrating Functional Diversity Across Scales.” *Trends in Ecology & Evolution* 31: 382–394.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2019. “Trait Probability Density (TPD): Measuring Functional Diversity Across Scales Based on TPD With R.” *Ecology* 100: e02876.

Chen, L., J.-G. Huang, S. A. Alam, et al. 2017. “Drought Causes Reduced Growth of Trembling Aspen in Western Canada.” *Global Change Biology* 23: 2887–2902.

Dawson, W., J. Bòdis, A. Bucharova, et al. 2024. “Root Traits Vary as Much as Leaf Traits and Have Consistent Phenotypic Plasticity Among 14 Populations of a Globally Widespread Herb.” *Functional Ecology* 38: 926–941.

de Bello, F., F. M. Fischer, J. Puy, et al. 2025. “Raunkiæran Shortfalls: Challenges and Perspectives in Trait-Based Ecology.” *Ecological Monographs* 95: e70018.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. “The Global Spectrum of Plant Form and Function.” *Nature* 529: 167–171.

Dun, L. P., E. H. Wenk, D. S. Falster, M. Westoby, and I. J. Wright. 2025. “Do Trait–Growth Relationships Vary With Plant Age in Fire-Prone Heathland Shrubs?” *Journal of Ecology* 113: 1164–1184.

Fajardo, A., A. Siefert, and D. C. Laughlin. 2024. “Wood Density and Leaf Size Jointly Predict Woody Plant Growth Rates Across (But Not Within) Species Along a Steep Precipitation Gradient.” *Journal of Ecology* 112: 374–388.

Freckleton, R. P., A. R. Watkinson, and M. Rees. 2009. “Measuring the Importance of Competition in Plant Communities.” *Journal of Ecology* 97: 379–384.

Goud, E. M., A. A. Agrawal, and J. P. Sparks. 2023. “A Direct Comparison of Ecological Theories for Predicting the Relationship Between Plant Traits and Growth.” *Ecology* 104: e3986.

Hagan, J. G., J. J. Henn, and W. H. A. Osterman. 2023. “Plant Traits Alone Are Good Predictors of Ecosystem Properties When Used Carefully.” *Nature Ecology & Evolution* 7: 332–334.

Hoffmann, A. A., and J. Merilä. 1999. “Heritable Variation and Evolution Under Favourable and Unfavourable Conditions.” *Trends in Ecology & Evolution* 14: 96–101.

Hoffmann, W. A., and H. Poorter. 2002. “Avoiding Bias in Calculations of Relative Growth Rate.” *Annals of Botany* 90: 37–42.

Horn, J. L. 1965. “A Rationale and Test for the Number of Factors in Factor Analysis.” *Psychometrika* 30: 179–185.

Iida, Y., T. S. Kohyama, N. G. Swenson, et al. 2014. “Linking Functional Traits and Demographic Rates in a Subtropical Tree Community: The Importance of Size Dependency.” *Journal of Ecology* 102: 641–650.

Kamimura, V. d. A., P. d. P. Loiola, C. P. Carmona, et al. 2023. “Trait Interactions Effects on Tropical Tree Demography Depend on the Environmental Context.” *Perspectives in Plant Ecology, Evolution and Systematics* 59: 125732.

Lai, J., Y. Zou, S. Zhang, X. Zhang, and L. Mao. 2022. “Glmm.Hp: An R Package for Computing Individual Effect of Predictors in Generalized Linear Mixed Models.” *Journal of Plant Ecology* 15: 1302–1307.

Laughlin, D. C. 2018. “Rugged Fitness Landscapes and Darwinian Demons in Trait-Based Ecology.” *New Phytologist* 217: 501–503.

Laughlin, D. C. 2023. *Plant Strategies*. Oxford University Press.

Laughlin, D. C. 2024. “Unifying Functional and Population Ecology to Test the Adaptive Value of Traits.” *Biological Reviews* 99: 1976–1991.

Li, Y., Y. Jiang, B. Shipley, et al. 2021. “The Complexity of Trait–Environment Performance Landscapes in a Local Subtropical Forest.” *New Phytologist* 229: 1388–1397.

Li, Y., Y. Jiang, K. Zhao, et al. 2022. “Exploring Trait–Performance Relationships of Tree Seedlings Along Experimentally Manipulated Light and Water Gradients.” *Ecology* 103: e3703.

Lyu, S., X. Liu, P. Venail, and S. Zhou. 2017. “Functional Dissimilarity, Not Phylogenetic Relatedness, Determines Interspecific Interactions Among Plants in the Tibetan Alpine Meadows.” *Oikos* 126: 381–388.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. “Rebuilding Community Ecology From Functional Traits.” *Trends in Ecology & Evolution* 21: 178–185.

Niu, K., S. Zhang, and M. J. Lechowicz. 2020. “Harsh Environmental Regimes Increase the Functional Significance of Intraspecific Variation in Plant Communities.” *Functional Ecology* 34: 1666–1677.

Novoplansky, A. 2009. “Picking Battles Wisely: Plant Behaviour Under Competition.” *Plant, Cell & Environment* 32: 726–741.

Paine, C. E. T., L. Amissah, H. Auge, et al. 2015. “Globally, Functional Traits Are Weak Predictors of Juvenile Tree Growth, and We Do Not Know Why.” *Journal of Ecology* 103: 978–989.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, et al. 2013. “New Handbook for Standardised Measurement of Plant Functional Traits Worldwide.” *Australian Journal of Botany* 61: 167–234.

Poorter, L., C. V. Castilho, J. Schietti, R. S. Oliveira, and F. R. C. Costa. 2018. “Can Traits Predict Individual Growth Performance? A Test in a Hyperdiverse Tropical Forest.” *New Phytologist* 219: 109–121.

Rodríguez-Alarcón, S., R. González-M, C. P. Carmona, and E. Tordoni. 2024. “Trait–Growth Relationships in Colombian Tropical Dry Forests: Incorporating Intraspecific Variation and Trait Interactions.” *Journal of Vegetation Science* 35: e13233.

Roumet, C., M. Birouste, C. Picon-Cochard, et al. 2016. “Root Structure–Function Relationships in 74 Species: Evidence of a Root Economics Spectrum Related to Carbon Economy.” *New Phytologist* 210: 815–826.

Sanaei, A., F. van der Plas, H. Chen, et al. 2025. “Tree Growth Is Better Explained by Absorptive Fine Root Traits Than by Transport Fine Root Traits.” *Communications Biology* 8: 1–11.

Schielzeth, H. 2010. “Simple Means to Improve the Interpretability of Regression Coefficients.” *Methods in Ecology and Evolution* 1: 103–113.

Siefert, A., C. Violle, L. Chalmandrier, et al. 2015. “A Global Meta-Analysis of the Relative Extent of Intraspecific Trait Variation in Plant Communities.” *Ecology Letters* 18: 1406–1419.

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Violle, C., M.-L. Navas, D. Vile, et al. 2007. “Let the Concept of Trait Be Functional!” *Oikos* 116: 882–892.

Weemstra, M., L. Mommer, E. J. W. Visser, et al. 2016. “Towards a Multidimensional Root Trait Framework: A Tree Root Review.” *New Phytologist* 211: 1159–1169.

Weemstra, M., J. Zambrano, D. Allen, and M. N. Umaña. 2021. “Tree Growth Increases Through Opposing Above-Ground and Below-Ground Resource Strategies.” *Journal of Ecology* 109: 3502–3512.

Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. “The Worldwide Leaf Economics Spectrum.” *Nature* 428: 821–827.

Yang, J., M. Cao, and N. G. Swenson. 2018. “Why Functional Traits Do Not Predict Tree Demographic Rates.” *Trends in Ecology & Evolution* 33: 326–336.

Yang, J., J. Lu, R. Wang, X. Wang, S. Li, and G. Shen. 2021. “Importance and Benefit of Incorporating the Responses of Species Mean Trait Values in Trait-Based Community Assembly.” *Ecological Indicators* 130: 108095.

Yang, J., X. Song, J. Zambrano, et al. 2021. “Intraspecific Variation in Tree Growth Responses to Neighbourhood Composition and Seasonal Drought in a Tropical Forest.” *Journal of Ecology* 109: 26–37.

Yang, J., X. Wang, C. P. Carmona, X. Wang, and G. Shen. 2024. “Inverse Relationship Between Species Competitiveness and Intraspecific Trait Variability May Enable Species Coexistence in Experimental Seedling Communities.” *Nature Communications* 15: 2895.

Yang, Q., Z. Ma, Y. Xie, et al. 2011. “Community Structure and Species Composition of an Evergreen Broad-Leaved Forest in Tiantong's 20 Ha Dynamic Plot, Zhejiang Province, Eastern China.” *Biodiversity Science* 19: 215.

Supporting Information

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