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RESEARCH ARTICLE

Shifts in above- and below-ground trait dissimilarity under competition mediate the future impact of neighbours

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Abstract

1. Competition drives shifts in multiple traits in plants, dynamically altering interspecific trait dissimilarity and subsequently reshaping competition intensity. Yet the directionality of trait dissimilarity changes and their effects on competition are unclear
2. In a 3-year greenhouse experiment with 5818 seedlings of seven tree species grown with and without neighbours, we quantified neighbour-induced shifts in interspecific trait dissimilarity within separate above- and below-ground multidimensional trait spaces and tested how these shifts influenced competition intensity, quantified using seedling biomass.
3. We found opposing neighbour-induced responses between above- and below-ground multidimensional trait spaces: species became more similar in above-ground traits but diverged below-ground. These contrasting shifts were significantly associated with reduced competition intensity, but their relationships unfolded at different temporal scales. Above-ground convergence corresponded to lower competition intensity within the same year, whereas below-ground divergence predicted lower competition intensity in the subsequent year.
4. *Synthesis*. Our findings reveal complementary above- and below-ground shifts in multidimensional trait dissimilarity in response to neighbours, providing new insight into potential mechanisms by which plants deal with competitive pressure. These findings suggest a dynamic feedback loop between competition and trait expression through coordinated shifts across multiple traits, and indicate that coordinated above- and below-ground trait change may contribute to plant coexistence by reducing interspecific competition.

KEYWORDS
above- and below-ground traits, competition, interspecific trait dissimilarity, intraspecific trait variability, multidimensional trait space, tree seedlings

1 | INTRODUCTION

Competition is a fundamental structural force in plant communities (HilleRisLambers et al., 2012), but its outcomes are often difficult to predict (Levine et al., 2025). Trait-based ecology has traditionally approached this challenge by linking competitive interactions to interspecific trait dissimilarity (ITD; Figure 1a), which captures functional differences among species related to resource use (Kunstler et al., 2012; Violle et al., 2009). Greater ITD is generally interpreted as evidence of divergent resource-use strategies, in line with the limiting similarity hypothesis (MacArthur & Levins, 1967) and is associated with weaker competitive interactions (Wagg et al., 2017). However, this framework typically treats traits—and therefore ITD—as fixed properties of species within a given environment (Mahaut et al., 2023; Montazeaud et al., 2020; but see Violle et al., 2012). Growing evidence shows that plant traits can shift in response to competitors (Abakumova et al., 2016; Castro Sánchez-Bermejo et al., 2025; Yang et al., 2021, 2024). When these trait responses vary among species, ITD may itself be altered by neighbour interactions, making it both a potential driver and an outcome of interspecific interactions (Hess et al., 2022; Turcotte & Levine, 2016).

Theory offers contrasting expectations for how ITD responds to neighbouring competitors. On the one hand, competition is expected to promote divergence in resource-use traits through niche differentiation, increasing ITD as species reduce overlap in resource acquisition (Figure 1c) (MacArthur & Levins, 1967; Mason et al., 2011; Violle et al., 2011). For instance, divergence in specific root length under competition has been interpreted as differentiation in soil foraging strategies (Bennett et al., 2016). In contrast, competition may reduce ITD when species—especially competitively inferior ones—shift their traits toward those of superior competitors, which is consistent with expectations from competitive hierarchies (Figure 1b; Mayfield & Levine, 2010; Yang et al., 2024). For example, competition drives shoot elongation in shorter plants, thereby reducing height-based ITD (Carmona et al., 2019). These expectations show that competition can either increase or decrease ITD, but current evidence—often mixed and largely focused on single traits or functional axes, overlooking coordinated whole-plant phenotypic responses (Bennett et al., 2016; Carmona et al., 2019; Gibbs et al., 2025)—limits our ability to predict when each outcome occurs.

We propose that these seemingly contradictory findings can be clarified by recognising that competition operates through distinct above- and below-ground mechanisms (Figure 1). Above-ground competition for light is typically size-asymmetric, favouring taller individuals who maximise light interception (DeMalach et al., 2017; Kraft et al., 2014), which is expected to promote convergence in above-ground traits and thus reduce the ITD (Figure 1b). When such convergence moderates the initial advantage of taller individuals, adjustments in above-ground ITD may flatten competitive hierarchies and, if they feed back to competitive outcomes, be associated with reduced competition intensity (Figure 1d; Puy et al., 2021). In contrast, below-ground competition is generally more size-symmetric, as plants compete for multiple resources that can be

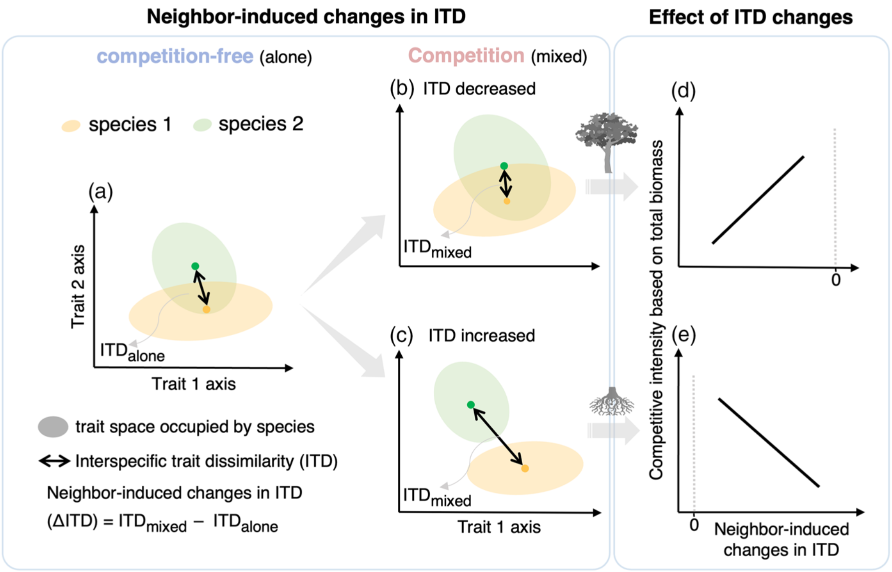


FIGURE 1 Conceptual framework linking neighbour-induced changes in interspecific trait dissimilarity (ITD) and seedling competition. (a) Trait space occupied by competing species and their ITDs under competition-free conditions. (b, c) Competition is expected to induce contrasting ITD responses depending on the dominant mechanism: Above-ground, size-asymmetric competition for light is expected to promote trait convergence and reduce ITD (b), whereas below-ground, more size-symmetric and spatially heterogeneous competition is expected to favour trait divergence and increase ITD through niche differentiation (c). (d, e) These neighbour-induced ITD changes are anticipated to feedback into competition intensity such that stronger above-ground convergence (more negative ITD change) and stronger below-ground divergence (more positive ITD change) are linked to reduced competition intensity. The coloured ellipses represent the species' trait spaces, the arrows indicate the ITD and the competition intensity is quantified as the sign-inverted relative interaction index (RII), where higher values indicate stronger net negative neighbour effects on biomass.

accessed from any direction (Del Río et al., 2014). This symmetry often encourages resource partitioning and increases the ITD in fine-root traits (Figure 1c), potentially alleviating competitive symmetry when functional differences translate into more efficient resource acquisition (Figure 1e; Bennett et al., 2016). Hence, shifts in ITD may mitigate competition, although alternative outcomes are also possible. Contrasting ITD responses above- and below-ground may offset each other, resulting in little net effect at the whole-plant level or could even intensify competition if the costs of trait adjustments outweigh their benefits (DeWitt et al., 1998). For example, increased investment in height mitigates competition only when it improves light capture; otherwise, it may be maladaptive. Despite a few studies linking ITD changes to competition, most have relied on single time points or annual plants (Gibbs et al., 2025), yielding only snapshot associations. Consequently, whether ITD dynamics consistently influence competition intensity remains a central yet unresolved question.

To address these gaps, we conducted a three-year competition experiment across biologically realistic resource environments using 5818 seedlings of seven co-occurring subtropical tree species in a subtropical broadleaf evergreen forest. Seedlings were grown either individually or with heterospecific neighbours to simulate natural multispecies competition (Levine et al., 2017). Each year for three consecutive years, we harvested a portion of the experimental seedlings and measured six above-ground and three fine-root traits per individual, capturing key functional axes hypothesised to mediate competitive interactions (Table S1). Recognising that competitive responses arise from coordinated trait syndromes rather than from isolated traits (Laughlin, 2014), we employed a multivariate approach to separately quantify above- and below-ground ITD across treatments and years. We then integrated these multidimensional ITD dynamics with seedling competitive responses, quantified as relative total biomass reduction (Armas et al., 2004), to evaluate how neighbour-induced shifts in ITD are related to the intensity of competition over time. Specifically, we aimed to address the following questions: (1) How do above- and below-ground ITDs respond differently to neighbour presence? (2) Do species that show greater neighbour-induced changes in ITD experience lower competition intensity? (3) Do these effects persist across years such that ITD changes in 1 year influence competition intensity in subsequent years?

2 | METHODS

2.1 | Study site and tree species

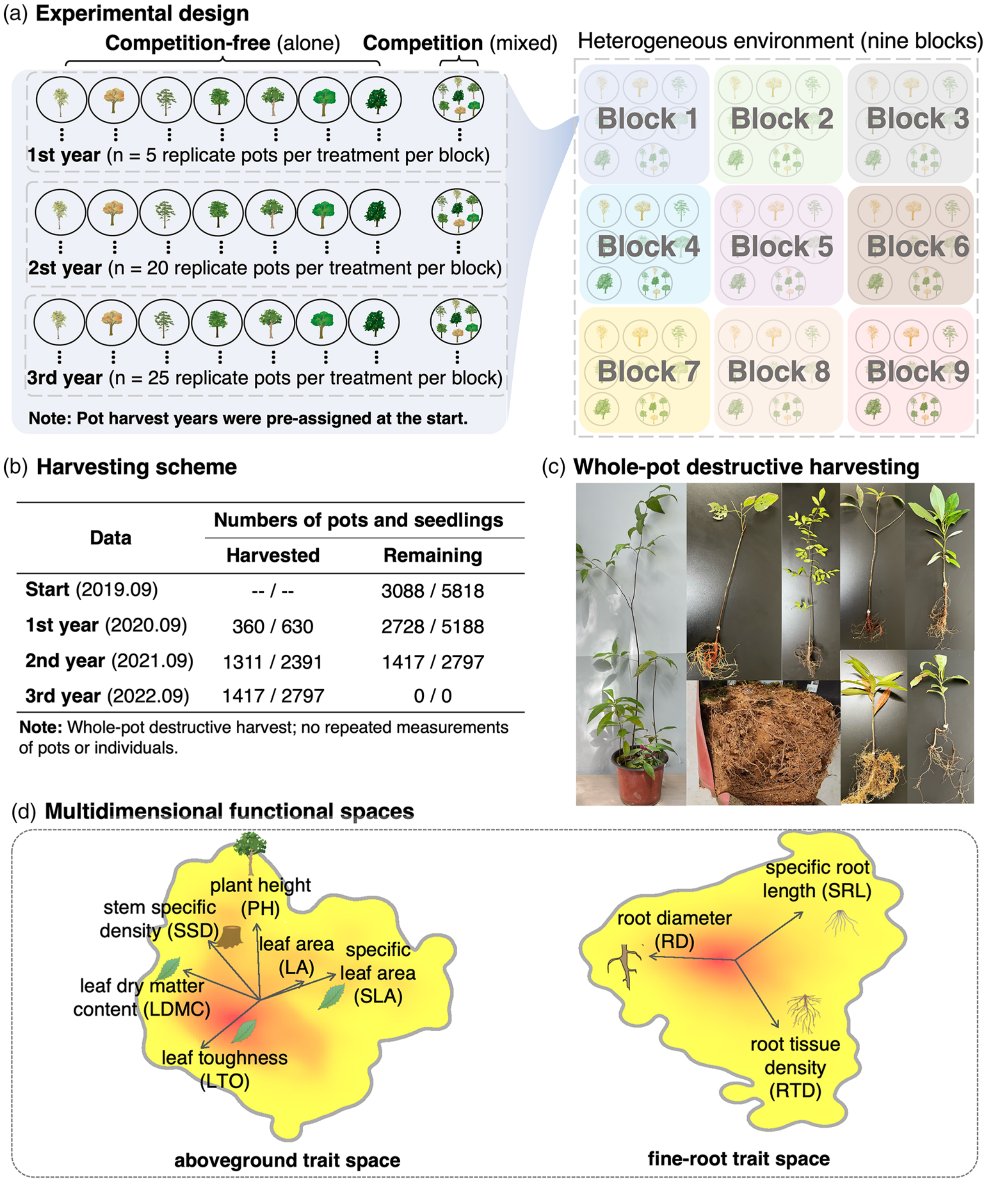
We conducted a multispecies competition experiment in a greenhouse at Tiantong National Forest Park, which is located in a subtropical monsoon climate zone in eastern China. The region has a mean annual temperature of 16.2°C and receives approximately 1375 mm of annual precipitation (Yang et al., 2011), characteristic of subtropical evergreen broadleaf forests. To maintain ecological realism, both plant material and soil were sourced locally. The experimental soil was collected from the same forest at a depth of 15–30 cm, excluding the nutrient-rich topsoil layer. The soil was sieved and homogenised to ensure uniform growing conditions. It exhibited low nutrient availability (6.10 $g\cdot kg^{-1}$ total carbon, 0.4 $g\cdot kg^{-1}$ total nitrogen and 0.45 $g\cdot kg^{-1}$ total phosphorus) and a slightly acidic pH (5.21), which is consistent with the highly weathered, phosphorus-limited substrates typical of this region (Cui et al., 2022).

We initially selected 13 co-occurring tree species (eight evergreen and five deciduous; Table S2) to encompass a range of growth forms, phylogenetic distances and seed availability representative of the local forest community. To minimise genetic and maternal effects, more than 2000 healthy seeds per species were collected from a single mature individual per species in a nearby forest between October and December 2018. Seeds were thoroughly mixed, and seedlings were randomly assigned to experimental treatments. Seeds were sown in nursery trays in April 2019 and grown under full sunlight with regular irrigation prior to transplantation. Due to variable germination success across species, we ultimately focused on seven species for the experiment: *Daphniphyllum oldhami* (DO), *Cyclobalanopsis glauca* (CG), *Castanopsis sclerophylla* (CS), *Lithocarpus glaber* (LG), *Schima superba* (SS), *Hovenia acerba* (HA) and *Quercus chenii* (QC). All are common trees in the subtropical evergreen broadleaf forests at Tiantong and frequently co-occur in the field.

2.2 | Experimental design

We conducted a three-year seedling competition experiment (2019–2022) to examine how neighbour presence alters interspecific trait dissimilarity across ontogenetic and environmental contexts. Two planting arrangements were established: a competition-free treatment with a single seedling per pot and a competition treatment in which seven seedlings (one per species) were grown together in the same pot (Figure 2a). This multispecies design reflects natural neighbourhood assemblages in subtropical forests and allows for a direct assessment of neighbour effects on interspecific trait dissimilarity (Snaydon, 1991). To evaluate the robustness of neighbour effects across realistic resource heterogeneity, both planting treatments were replicated within nine environmental blocks defined by orthogonal gradients of light availability, soil moisture and soil phosphorus (Table S3). These variables were selected because they represent the dominant and largely independent resource axes that constrain seedling establishment in subtropical forests: light regulates carbon acquisition under closed canopies, soil moisture influences seedling survival in monsoon climates (Liu et al., 2021) and phosphorus—rather than nitrogen—limits growth in the highly weathered soils at Tiantong (Cui et al., 2022; Zheng et al., 2020). The ranges of these gradients were defined based on field measurements from a nearby 20-ha forest dynamics plot (He et al., 2022) (Figure S1), ensuring that experimental conditions captured ecologically realistic variation while minimising confounding environmental covariation.

To realise these environments, we manipulated resource availability at three levels (low, medium and high). Light availability was



Data	Numbers of pots and seedlings	
	Harvested	Remaining
Start (2019.09)	-- / --	3088 / 5818
1st year (2020.09)	360 / 630	2728 / 5188
2nd year (2021.09)	1311 / 2391	1417 / 2797
3rd year (2022.09)	1417 / 2797	0 / 0

Note: Whole-pot destructive harvest; no repeated measurements of pots or individuals.

FIGURE 2 Experimental design and multidimensional trait spaces. (a) A multispecies competition experiment was conducted across nine heterogeneous abiotic environments (blocks) under two treatments: Competition-free (one seedling per pot) and competition (seven heterospecific seedlings per pot). Abiotic environments were designed to reflect natural heterogeneity in nearby forest communities (Table S3). Pots were preassigned at the start of the experiment, and they were assigned to one of three destructive harvest years, with the number of replicates per treatment and block increasing over time to maintain statistical power. (b) Numbers of pots and seedlings harvested and remaining at each census; minor deviations from planned harvests reflect stochastic seedling mortality. (c) Whole-pot destructive harvesting, showing intact pots before harvest and representative seedlings after excavation and root separation; no individuals or pots were measured repeatedly across years. (d) Multidimensional functional trait spaces constructed from six above-ground and three fine-root traits. Principal component analyses were conducted separately for above- and below-ground traits, and the resulting trait spaces were used to quantify interspecific trait dissimilarity.

adjusted using zero, one or two layers of six-needle shade netting, yielding mean (±SE) midday photosynthetically active radiation (PAR) in summer of 1237 ± 195 (high), 503 ± 103 (medium) and 15 ± 2 μmol m^{-2} s^{-1} (low), respectively. Soil moisture was regulated by watering every 2, 4 or 6 days (adjusted for ambient temperature), and the mean volumetric water contents were maintained at 33.0% ± 0.3% (high), 28.8% ± 0.2% (medium) and 21.4% ± 0.3% (low), respectively. Soil phosphorus was controlled through monthly additions of NaH_2PO_4 solution (0.4, 0.2 or 0 g/mL), resulting in final total soil phosphorus concentrations of 1.07 ± 0.05 (high), 0.89 ± 0.02 (medium) and 0.49 ± 0.04 g/kg (low). All realised conditions were monitored throughout the study to ensure treatment stability.

We grew seedlings in standardised pots (15 cm tall, 18.5/12 cm top/bottom diameter), each filled with 2 ± 0.01 kg of homogenised local forest soil. We selected this pot size to maximise the detectability of competition while minimising root restriction, drawing on previous experimental experience (Yang et al., 2024). To reduce initial size variation, we selected seedlings of comparable height and health status within species. We controlled for 3–5 cm spacing between the seedlings within pots to facilitate interspecific competition while maintaining a sufficient distance (15–20 cm) between the pots to prevent cross-pot interference. During the first month after transplantation, we monitored seedling survival daily and replaced dead individuals with size-matched conspecifics to maintain experimental integrity. Subsequent minor unavoidable losses resulted in a final effective replication of 40–45 pots (competition-free) and 50–53 pots (competition) per species per block, which yielded a final dataset of 3088 pots and 5818 seedlings. To minimise bias from environmental variation within the greenhouse, we randomly repositioned pots biweekly within each block and controlled herbivory with insect nets and insecticides when necessary.

2.3 | Above- and below-ground trait measurements from independent annual harvests

Building on the experimental design described above, we quantified seedling functional traits and biomass through a series of temporally stratified, independent destructive harvests. At the start of the experiment, pots were randomly assigned to one of three non-overlapping harvest cohorts corresponding to the first, second or third year of growth, ensuring statistical independence among censuses. To compensate for cumulative mortality and maintain sufficient statistical power for ITD estimation, sampling intensity increased over time: 5, 20 and 25 pots were harvested per species, treatment and environmental block in years one, two and three, respectively (Figure 2a). This approach ensured robust trait representation through the final census (Table S4; Figure 2b).

At each scheduled harvest, entire pots were destructively sampled, and all surviving seedlings were collected and processed individually (Figure 2c). Seedlings were carefully excavated intact, washed to remove soil and examined to clearly identify stem–root connections. In multispecies pots, root systems were separated at the individual level before trait measurements. By tracing root architecture from the stem base to fine-root tips and leveraging distinct interspecific differences in root morphology, we reliably assigned below-ground tissues to the correct species. Fine roots were subsampled for trait measurements only after complete individual-level separation was confirmed.

For each harvested seedling, we measured nine functional traits (Figure S2) selected to capture major axes of the global plant trait spectrum and to test contrasting competition mechanisms (Table S1). Above-ground traits reflected variation along two dimensions: plant size, represented by plant height (cm) and leaf area (LA, cm^2), and leaf–stem economics, represented by specific leaf area (SLA, cm^2/g), leaf dry matter content (LDMC, g/g), leaf toughness (LTO, gram-force) and stem-specific density (SSD, g/cm^3). Below-ground traits represented the root economic axis, quantified by root tissue density (RTD, g/cm^3) and the root collaboration axis, quantified by specific root length (SRL, m/g) and root diameter (RD, mm). Collectively, these traits capture key above- and below-ground functional axes related to resource acquisition, conservation and competitive interactions (Laughlin, 2023). In addition to trait measurements, total biomass was quantified for each individual as the sum of oven-dried above- and below-ground mass and was used to calculate interaction intensity. All measurements followed standardised protocols (Pérez-Harguindeguy et al., 2013), with detailed procedures provided in Appendix S1.

2.4 | Construction of multidimensional functional spaces

To quantify interspecific trait dissimilarity in a multidimensional framework while avoiding redundant weighting of correlated traits, we constructed separate above- and below-ground functional spaces using principal component analysis (PCA; Figure 2d). This approach allowed correlated traits to be integrated into orthogonal axes, ensuring that Euclidean distances reflected coordinated functional differences rather than covariance structure alone. Specifically, the above-ground PCA used six traits from a subset of 4009 seedlings, and the below-ground PCA used three root traits from 4505 seedlings, all without missing values (Table S5). The number of retained dimensions was determined using Horn's parallel analysis (Horn, 1965). For above-ground traits, the first three axes explained 66.9% of the variance and represented the leaf economic spectrum (SLA vs. LDMC and LTO), plant size (SSD and height), and leaf area. For below-ground traits, the first two axes explained nearly all of the variance (94.9%), reflecting root collaboration strategies (SRL vs. RD) and root economics (RTD) (Figure S3). These axes align with established global functional spectra (Beccari & Carmona, 2024; Bergmann et al., 2020; Carmona et al., 2021; Díaz et al., 2016; Weigelt et al., 2021). All subsequent distance calculations were performed within these reduced, orthogonal PCA axes.

2.5 | Estimation of interspecific trait dissimilarity

In this section, we quantify ITD under both competition-free and competitive conditions, establishing a basis for evaluating whether the presence of neighbours systematically alters ITD.

2.5.1 | ITD estimation for the competition-free treatment

We estimated species-level ITD using an individual-based resampling framework that explicitly incorporated within-species trait variability. For each species and census year, ITD was estimated in the PCA-derived functional trait spaces by averaging the trait dissimilarities between a focal species and all potential heterospecific neighbours. All calculations were performed separately for above-ground and fine-root trait spaces. The estimation followed three steps.

First, we defined individual-level trait dissimilarity. For a given year *y*, the dissimilarity between two individuals *k* and *l* grown without neighbours was quantified as their Euclidean distance in the corresponding T-dimensional PCA space ($T=3$ for above-ground traits; $T=2$ for fine-root traits):

$$D^{\text{alone}}_{k,l,y} = \sqrt{\sum\nolimits_{t=1}^{T} \left(x^{\text{alone}}_{k,y,t} - x^{\text{alone}}_{l,y,t}\right)^2} \tag{1}$$

where $x^{\text{alone}}_{k,y,t}$ and $x^{\text{alone}}_{l,y,t}$ are the scores of individuals *k* and *l* on the *t*-th principal component, respectively.

Second, we aggregated individual-level distances to estimate pairwise interspecific dissimilarity across environmental contexts. For each focal species *i* and each potential neighbouring species *j*, all surviving individuals were pooled across experimental blocks for a given year and trait space. To account for within-species variability and unequal sample sizes, we applied a standardised resampling procedure. In each iteration, we randomly drew $n=35$ individuals from each species and calculated the mean of all pairwise individual distances ($35\times35=1225$ comparisons). This procedure was repeated $R=999$ times, and the pairwise interspecific dissimilarity was defined as the mean across all iterations:

$$\text{PD}^{\text{alone}}_{i,j,y} = \frac{1}{R}\sum\nolimits_{r=1}^{R}\left(\frac{1}{n^2}\sum\nolimits_{k=1}^{n}\sum\nolimits_{l=1}^{n} D^{\text{alone}}_{k,l,y}\right) \tag{2}$$

Third, we summarised the ITD for each focal species *i* by averaging its dissimilarities to all six heterospecific neighbours in the seven-species community:

$$\text{ITD}^{\text{alone}}_{i,y} = \frac{1}{6}\sum\nolimits_{j=1}^{6} \text{PD}^{\text{alone}}_{i,j,y} \tag{3}$$

This individual-based approach fully utilises trait variation within species and avoids reliance on centroid distances, which can obscure within-species variability (Carmona et al., 2016). A higher ITD value indicates greater trait dissimilarity between a focal species and its potential competitors. Because seedlings grown alone do not co-occur with heterospecific neighbours, this resampling framework provides a species-level estimate of ITD that is directly comparable to the ITD quantified under competition. The full workflow is illustrated in Figure S4.

2.5.2 | ITD estimation for the competition treatment

In the competition treatment, seedlings grew alongside heterospecific neighbours within the same pots, enabling the quantification of ITD at both the species and the pot scale. We employed two complementary approaches. First, to maintain direct comparability with the competition-free treatment, we applied the same species-level resampling framework described earlier. All surviving individuals of a given species from mixed-species pots were pooled across environmental blocks within each year and trait space, and ITD was estimated by resampling $n=35$ individuals per species. Second, to capture realised neighbourhood interactions, we quantified ITD at the pot level. For each surviving focal individual, we calculated ITD as the mean Euclidean distance between that individual and its actual surviving heterospecific neighbours within the same pot, which ranged from one to six species.

2.6 | Quantifying neighbour-induced changes in interspecific trait dissimilarity

To quantify how the presence of neighbours alters ITD (Question 1), we calculated annual changes in ITD for each focal species as the difference between ITD under competition and competition-free conditions: $\text{Change in ITD}_{i,y} = \text{ITD}^{\text{mixed}}_{i,y} - \text{ITD}^{\text{alone}}_{i,y}$, where both terms represent the mean dissimilarity of species *i* relative to its six heterospecific competitors in year *y*. Because all seedlings in both treatments originated from the same maternal seed pool (see Section 2.1) and were randomly assigned, the presence versus absence of neighbours constitutes the only systematic difference between treatments. We therefore interpret changes in ITD as a neighbour-induced response in interspecific trait dissimilarity. Positive values indicate increased dissimilarity (trait divergence), while negative values indicate decreased dissimilarity (trait convergence).

To evaluate whether neighbour presence systematically altered ITD across species and years (Question 1), we tested whether changes in ITD differed from zero using Wilcoxon signed-rank tests. We treated ITD values measured under competition and competition-free conditions as paired observations for each species within each census year, reflecting the matched experimental design. All tests were conducted separately for above-ground and below-ground functional trait spaces.

To assess sensitivity to realised neighbourhood composition, we additionally quantified pot-level ITD changes by matching observed species subsets in competition pots to richness-matched expectations from the competition-free treatment. Species-level and pot-level ITD changes showed highly consistent patterns and were robust to species loss due to mortality or missing trait data (Figures S5 and S6). Given this consistency, we report species-level ITD changes in the main text to maintain scale symmetry across treatments while providing pot-level results in the Supporting Information (Figures S6 and S7).

2.7 | Estimation of the competition intensity among seedlings

To examine whether neighbour-induced changes in ITD are associated with competition intensity within and across years (Questions 2 and 3), we quantified competition intensity for all seedlings grown with neighbours using sign-inverted relative interaction index (RII; Armas et al., 2004). Hereafter, RII refers to this sign-inverted index (i.e. the original RII multiplied by −1), ensuring that higher values consistently represent stronger net negative (competitive) neighbour effects. For a seedling *k* of species *i* grown with neighbours in year *y* and block *b*, the RII was calculated as follows:

$$\mathrm{RII}_{i,k,y,b} = \left(\overline{\mathrm{BM}}^{\mathrm{alone}}_{i,y,b} - \mathrm{BM}^{\mathrm{mixed}}_{i,k,y,b}\right) / \left(\overline{\mathrm{BM}}^{\mathrm{alone}}_{i,y,b} + \mathrm{BM}^{\mathrm{mixed}}_{i,k,y,b}\right) \tag{4}$$

where $\mathrm{BM}^{\mathrm{mixed}}_{i,k,y,b}$ is the total biomass of the focal seedling grown with heterospecific neighbours and $\overline{\mathrm{BM}}^{\mathrm{alone}}_{i,y,b}$ is the mean biomass of conspecific seedlings grown without neighbours within the same environmental block and year. Biomass was measured as the total dry mass of the above- and below-ground parts after oven-drying for 72 h.

The RII thus provides a standardised proxy for the net outcome and intensity of neighbour interactions based on the differences in biomass between seedlings grown with and without neighbours (Figure S8a), and it is directly comparable across species, environments and years (Armas et al., 2004; Feng et al., 2020). Our experiment revealed only a weak association between RII and seedling height ($R^2 = 0.17$, $p < 0.001$; Figure S9), indicating limited size-related confounding. Neighbourhood effects were overwhelmingly negative: 97.1%, 96.7% and 89.1% of the seedlings presented positive RII values in years 1, 2 and 3, respectively (Figure S10), indicating that facilitation was rare (<6%) and that RII primarily reflects competition intensity in our study.

To avoid survivorship bias—which would systematically underestimate competitive intensity—we followed Bennett et al. (2016) and assigned a minimal biomass value (0.01 g) to dead seedlings. This adjustment was critical because mortality increased over time (0.32%, 4.68% and 34.50% in years one to three), and excluding dead individuals substantially distorted species-level competitive rankings (Figure S8b). Although ITD was calculated only from survivors, the resulting mismatch was minor, as mortality was negligible in the first 2 years and unavoidable in the third, when traits could not be measured on dead seedlings (Table S4). Therefore, incorporating mortality allowed us to capture competition dynamics more comprehensively across developmental stages while maintaining the reliability of ITD-competition comparisons.

2.8 | Modelling associations between neighbour-induced ITD change and competition intensity

To test whether neighbour-induced changes in interspecific trait dissimilarity are associated with competition intensity within and across years, we used linear mixed-effects models that link species-level trait responses to individual-level competition intensity. Competition intensity was quantified for each seedling using the sign-inverted relative interaction intensity (RII; Section 2.7), while changes in ITD were quantified at the species × year level (Section 2.6).

2.8.1 | Same-year associations between ITD change and competition intensity

We first examined whether species exhibiting greater neighbour-induced changes in interspecific trait dissimilarity experienced weaker or stronger competition within the same census year (Question 2). Specifically, we modelled the competition intensity of individual *k* belonging to species *i* in year *y* as follows:

$$\mathrm{RII}_{i,k,y} \sim \beta_1 \mathrm{ITD\ change}_{i,y} + \beta_2 \mathrm{ITD}^{\mathrm{mixed}}_{i,y} + \beta_3 \mathrm{Year} + \gamma_{\mathrm{species}} + \alpha_{\mathrm{blocks}} + \varepsilon \tag{5}$$

where the coefficient β_1 captures the association between changes in ITD and competition intensity within the same year. To distinguish the effects of trait responses to competition from those of constitutive interspecific differences, we included ITD under competition as a covariate, such that β_2 represents static interspecific trait dissimilarity under competitive conditions. Although changes in ITD were derived from ITD values, correlations between predictors were weak (above-ground: $r = 0.17$; below-ground: $r = 0.02$; Figure S11), and the conclusions of the model remained robust when ITD measured under competition was excluded (Figure S12), indicating minimal collinearity.

To ensure robust inference, we included the experimental year as a numeric covariate to capture temporal variation in competition intensity across censuses. We specified species identity and environmental block as crossed random effects to account for repeated measures within species and spatial heterogeneity among blocks. We fitted models separately for above- and below-ground trait spaces to maximise sample size and reflect their distinct ecological roles. This approach did not affect our conclusions because the results were consistent with those from a combined model, and because above- and below-ground ITDs were only weakly correlated ($r = -0.22$) and their changes were uncorrelated ($r = -0.05$; Figure S11).

2.8.2 | Interannual associations between ITD change and subsequent competition intensity

To examine whether neighbour-induced changes in ITD persisted beyond the year in which they occurred (Question 3), we fitted lagged mixed-effects models that related species-level changes in ITD in year *y* to the competition intensity experienced by conspecific seedlings in year *y* + 1. These analyses were conducted for two consecutive intervals (year 1 → 2 and year 2 → 3). Since the seedlings were destructively harvested at each census, these lagged models linked species-level trait responses to the competitive outcomes of different cohorts of individuals in subsequent years. The model

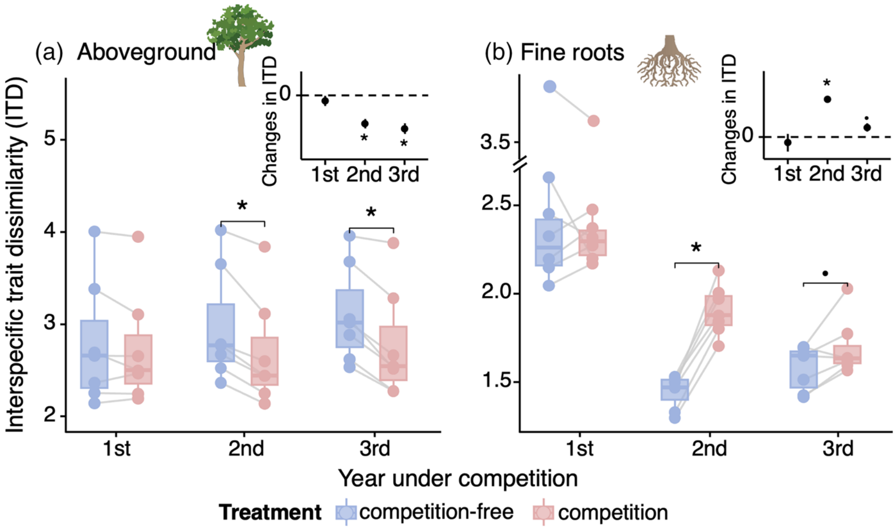


FIGURE 3 Interspecific trait dissimilarity (ITD) under competition-free and competition treatments across 3 years. Interspecific trait dissimilarity (ITD) in (a) above-ground and (b) fine-root trait spaces under competition-free (blue) and competition (pink) treatments for each of the 3 years. ITD quantifies the mean Euclidean distance between a focal species and others in multivariate trait space, with larger values indicating greater trait dissimilarity. The coloured points represent species-specific ITD values ($N=7$ species), with grey lines connecting the same species across treatments. The top-right subpanels display the mean neighbour-induced changes (± SEs) in the ITD across the seven species, calculated as the ITD under competition minus the ITD under competition-free conditions. The black asterisks indicate significant changes in the ITD (Wilcoxon signed-rank test; $\cdot p<0.1$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$).

structure and random-effects specifications matched those used in the same-year analyses.

Given the pronounced abiotic heterogeneity across experimental blocks, we further assessed whether the associations between ITD change and competition intensity depended on environmental context. We extended both same-year and lagged models to include interaction terms between changes in ITD and key abiotic factors (light availability, soil moisture and available phosphorus). Including these interactions did not alter the main patterns reported in the main text (Figure S12), indicating that the observed associations were robust across environmental conditions. All mixed-effects models were fitted using the lme4 package, marginal and conditional R^2 values were calculated using MuMIn (function r.squaredGLMM) and all analyses were conducted in R version 4.3.0 (R Core Team, 2023). The data and code used in this study are publicly available from figshare (Yang, 2025).

3 | RESULTS

3.1 | Neighbour-induced reduction in above-ground interspecific trait dissimilarity

Above-ground and fine-root trait dissimilarities exhibited contrasting responses to the presence of neighbours. Specifically, compared with the competition-free condition, the competition treatment consistently reduced above-ground ITD at all three time points, resulting in an average reduction of 8% (average change in ITD $=-0.22\pm0.04$; Wilcoxon signed-rank: $V=9$, $p<0.001$; Figure 3a; Figure S13). The key contributors to this reduction were leaf area (−36.89%), plant height (−25.54%) and leaf toughness (−13.85%), although the dissimilarity of the other individual traits slightly increased under competition (Figures S14 and S15).

3.2 | Neighbour-induced increase in below-ground interspecific trait dissimilarity

In contrast to above-ground traits, the presence of neighbours significantly increased the ITD between the target species and their competitors within the fine-root trait space. This increase was substantial, reaching 12.8% overall (0.15 ± 0.05, $V=188$, $p=0.010$; Figure 3b; Figure S13) and peaking at 28.3% in the second year (0.43 ± 0.04, $V=28$, $p=0.016$). An analysis of individual traits revealed that the primary drivers of this increased ITD were root tissue density, of which ITD increased by 33.67%, and specific root length, of which ITD increased by 20.37% (Figure S14). However, not all fine-root traits followed this pattern. Root diameter dissimilarity decreased by 5% in the presence of neighbours, a trend contrary to the overall divergence observed in the fine-root trait space (Figure S14).

Further analysis revealed that these decoupled dynamics were driven primarily by the pairing of deciduous species with evergreen species and with other deciduous species (Figure S16). Specifically, neighbour presence reduced above-ground dissimilarity more between deciduous and other species (-0.25 ± 0.03) than did evergreen species pairs (-0.20 ± 0.04), while the increase in below-ground ITD was more pronounced in interactions between deciduous and evergreen species (0.20 ± 0.04) than between pairs of evergreen species (0.11 ± 0.05) (Figure S16).

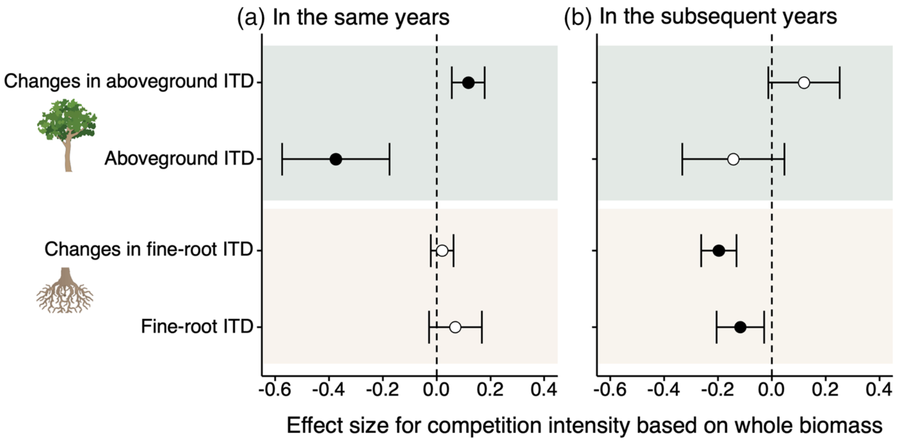


FIGURE 4 Associations between neighbour-induced changes in interspecific trait dissimilarity (ITD) and seedling competition intensity. Mixed-effects models examining the relationships between neighbour-induced ITD changes and competition intensity in the same year (a, $N=3185$ seedlings) and subsequent year (b, $N=2870$ seedlings; e.g. first-year ITD metrics predict second-year competition intensity). Models also included ITD values under competition conditions and competitive year as additional fixed effects, with species identity and environmental blocks as random effects to ensure robust analysis of competition intensity variation. Effect sizes were estimated as standardised coefficients derived from mixed-effects models fitted separately for above-ground and fine-root trait spaces. The solid circles denote significant effects ($p<0.05$), whereas the hollow circles denote nonsignificant effects ($p \geq 0.05$). Competition intensity was measured using the sign-inverted relative interaction index (RII), where higher values indicate stronger net negative neighbour effects (competition) on seedling biomass.

3.3 | Effects of changes in interspecific trait dissimilarity on competitive pressure

Neighbour-induced ITD shifts were linked to competition intensity, but in contrasting ways and at different temporal scales. For above-ground traits, changes in ITD were positively associated with concurrent competition intensity (slope $=0.29$, $p<0.001$, marginal $R^2=0.13$; Figure 4; Figure S17a). As the species responded to neighbours by reducing ITD, changes in above-ground traits thus served to reduce the competition intensity among species. At the same time, above-ground ITD per se showed a significant negative relationship with competition intensity (slope $=-0.23$, $p<0.001$; Figure 4a). These relationships, however, were confined to the same experimental year, as above-ground ITD in a given year was not significantly related to competition intensity in the subsequent year (Figure 4b).

In contrast, below-ground ITD exerted lagged effects. Neighbour-induced changes in fine-root ITD were not significantly associated with competition intensity in the same experimental year (Figure 4a; Figure S17b; Table S6). Instead, they were negatively related to competition intensity in the subsequent year (slope $=-0.23$, $p<0.001$, marginal $R^2=0.02$; Figure 4b; Figure S17d; Table S7). Similarly, fine-root ITD itself was negatively associated with competition intensity (slope $=-0.12$, $p=0.010$; Figure 4b).

4 | DISCUSSION

Plant traits can be modulated in response to competition, altering trait differences within and among species and ultimately shaping the intensity and outcomes of competition (Turcotte & Levine, 2016). Previous studies have focused on single above-ground traits, yielding inconsistent results and overlooking the complexity of trait integration (Funk & Wolf, 2016; Holden & Cahill, 2024; Yin et al., 2021) as well as the largely unexplored fine-root traits (Carmona et al., 2019; Hess et al., 2022). Integrating above- and below-ground trait measurements from 5818 tree seedlings over 3 years, we show that neighbourhood interactions—which are overwhelmingly competitive in our system (Figure S10)—drive contrasting shifts across trait domains: species converge above-ground but diverge below-ground, with the former alleviating competitive pressure within the same year and the latter doing so with a lag into the subsequent year (Figures 3 and 4). These findings reconcile conflicting views on neighbour-induced ITD shifts, reveal dynamic feedback linking traits and competition, and provide direct experimental evidence that complementary above- and below-ground strategies jointly mitigate competitive pressure on seedlings.

4.1 | Decoupled responses of above- and below-ground trait dissimilarity to neighbours

Competition elicited opposite shifts in above- and below-ground ITD. Above-ground, interspecific dissimilarity decreased, leading to convergence in multivariate trait space, aligning with height-based, single-trait results in herbaceous communities (Bennett et al., 2016; Kraft et al., 2014, 2015). Taking a multivariate perspective extends these findings in two ways. First, convergence arose from coordinated shifts across multiple traits, not from changes along a single axis, indicating a net reduction in above-ground phenotypic differentiation. Second, although the pattern mirrors that reported for herbs, the mechanism likely differs for tree seedlings. Whereas herbaceous seedlings can outgrow their neighbours rapidly (Carmona et al., 2019), tree seedlings face a greater challenge in reaching the forest canopy because of the greater vertical distance from the ground to the canopy. Rapid height growth can deplete resources and increase mortality risk (DeWitt et al., 1998) and may compromise resource allocation to below-ground competition and defenses (Herms & Mattson, 1992), further increasing mortality risk under the canopy. Instead, tree seedlings often grow conservatively until a canopy gap opens above them (Modrow et al., 2020), which can confer them a competitive advantage once their main competitors for light are fellow juvenile trees (Gross et al., 2009).

In contrast, below-ground competition increased ITD, which is consistent with expectations based on niche differentiation in resource acquisition and observational evidence of diverse fine-root strategies among co-occurring trees in subtropical (Luo et al., 2021) and temperate forests (Valverde-Barrantes et al., 2013). This divergence may reflect the size-symmetric nature of root interactions (Brown & Cahill, 2022; Weiner, 1990), in which larger individuals do not gain a disproportionate advantage in resource uptake (Beckett & Webster, 1971). Consequently, root trait shifts may be less consistently directed toward a single competitive optimum, allowing co-occurring species to respond in different ways to heterogeneous soil conditions. Such divergence in fine-root strategies may increase below-ground ITD by promoting niche differentiation and reducing competition (Casper & Jackson, 1997; Lyu & Alexander, 2024).

Beyond these general patterns, ITD shifts also varied with trait identity and life form. For example, root diameter dissimilarity decreased under competition (Figure S14), which is in line with previous findings, explaining the seemingly contradictory results based on single traits (Kraft et al., 2015) and highlighting the necessity of a multi-trait approach to disentangle the ITD response to competition. Moreover, deciduous pairs showed stronger above-ground convergence and greater below-ground divergence than evergreen pairs, indicating that ITD shifts were largely driven by deciduous species in our experiment, consistent with our earlier findings (Yang et al., 2021). These results collectively suggest that, compared with evergreen species, later-evolved deciduous trees (Axelrod, 1966) are not only more responsive to abiotic factors (e.g. shedding leaves in response to drought) but also more sensitive to biotic competition.

4.2 | Divergent strategies toward the common goal of competition mitigation

Plants achieve the same goal of reducing competitive pressure through contrasting strategies: decreasing above-ground ITD and increasing below-ground ITD. Above-ground, reductions in ITD alleviated competition within the same year, consistent with evidence that global trait space is structured mainly by plant size, a key determinant of light acquisition (Carmona et al., 2021; Díaz et al., 2016). Minimising differences in these traits would thus equalise species' abilities to compete for light and alleviate overall competition intensity on target species seedlings in our study. Paradoxically, above-ground ITD itself was negatively associated with competition intensity, suggesting that above-ground convergence could also intensify competition as predicted by limiting similarity (MacArthur & Levins, 1967). As above-ground ITD values and their changes were only minimally correlated ($r = 0.17$, $p < 0.001$; Figure S11), reduced above-ground ITD among interacting species probably alleviated competition through two processes. First, reduction in above-ground ITD was driven mainly by larger plants becoming smaller (e.g. height), suggesting that competition suppressed the growth of taller species. This reduction in size likely decreased competition suppression for shorter species but also reflected intense competition acting on those taller plants. Second, when trait dissimilarities were maintained, taller species experienced less competition, highlighting the dual role of above-ground ITD in shaping competitive dynamics.

In contrast, the negative relationship between below-ground ITD and competitive intensity, coupled with the observed increase in fine-root ITD under competition, suggests that as fine-root ITD rises in a target species, competitive pressure on its seedlings tends to diminish in the following year. This finding implies that competition-driven variation within the fine-root trait space may help mitigate competitive pressure over time. Supporting this interpretation, we also detected a significant negative effect of fine-root ITD on competition intensity (Table S7), indicating limiting similarity in fine-root traits, consistent with earlier single-trait studies (Bennett et al., 2016; Kraft et al., 2015). As many of these studies focused on individual traits, we concur *with* (Kraft et al., 2015) that competition effects on below-ground ITD can be trait-specific and that multidimensional trait dissimilarity is more closely tied to niche differentiation than any single trait. Furthermore, the strength of these above- and below-ground effects was not uniform but varied predictably with environmental conditions. Above-ground ITD convergence most strongly reduced competition under low light in the same year (Figure S12c), whereas increases in fine-root ITD were linked to weaker competition in the subsequent year under higher soil moisture and phosphorus availability (Figure S12d,e). This context dependence indicates that, within each trait domain, the competitive advantages of neighbour-induced ITD shifts are finely adjusted by the locally limiting resource.

The existence of these contrasting strategies strongly suggests that above- and below-ground trait spaces function as distinct, independent domains (Carmona et al., 2021). These findings were further confirmed by the lack of correlation between above-ground and below-ground ITD shifts and the lack of significant overall ITD changes (-0.05 ± 0.04, $V = 96$, $p = 0.52$; Figures S13 and S18). Contrasting above-ground and below-ground patterns may offset each other in the combined trait space, obscuring detectable changes. These findings not only highlight the differing response strategies of above- and below-ground traits but also underscore the importance of distinguishing them when studying the ITD-competition relationship (Bueno et al., 2023). Failing to make this distinction can obscure unique responses of below-ground traits, limiting our understanding of how plants adapt to changing environments.

4.3 | Temporal dynamics differentiate the impact of trait responses

Above- and below-ground traits are related to competition at different time scales (Figure S19). The current year's above-ground traits were not significantly related to competition in the subsequent year, although the general pattern was the same across years (Table S7). This result suggests that the relationship between above-ground trait dissimilarity and competition may initially be strong in seedlings, but that it weakens over time. Conversely, below-ground traits showed a lagged effect on competition, mitigating competition in the subsequent year. Plants often respond more slowly to below-ground than above-ground competition. While light availability can be rapidly detected by leaves, triggering immediate responses (Gundel et al., 2014), root growth and adjustment, necessary for responding to below-ground competition, take longer (Casper & Jackson, 1997). Furthermore, competition for light is more likely to lead to competitive exclusion than competition for soil resources (Lamb et al., 2009), making an immediate response to competition for light more necessary, whereas changes in root traits are less imperative for continued existence.

By extending research from herbaceous plants to trees, incorporating spatially distinct environments and spanning a longer duration (3 years vs. a few months in earlier studies) (Bennett et al., 2016; Carmona et al., 2019; Kraft et al., 2014), our study represents a significant step forward. However, three limitations warrant attention. First, while comparing competition-free and mixed treatments effectively captures trait responses to neighbour presence, it proxies the net outcome of interactions rather than estimating density-dependent competition coefficients. As a result, it does not allow ITD to be linked directly to species coexistence. Future studies should therefore adopt response-surface competition designs with orthogonal density gradients (Hart et al., 2018), which enable estimation of intra- and interspecific interaction coefficients and thereby provide a more direct basis for linking ITD to species coexistence. Second, although we analysed 5818 seedlings across nine morphological traits related to competitive ability and resource-use strategies (Carmona et al., 2021), logistical constraints precluded the inclusion of physiological traits (e.g. photosynthetic and hydraulic). Incorporating these traits would strengthen the robustness of our findings (Carmona & Beccari, 2025). Finally, although the controlled greenhouse allowed precise observations, it may not capture natural community complexity and 3 years reflect only an early life stage. Extending our findings to natural communities and predicting persistence in mature forests therefore requires caution.

5 | CONCLUSION

Our study revealed that trait responses to competition are widespread among plants, challenging trait-based predictions of competitive dynamics. In a three-year multispecies competition experiment with multidimensional trait analysis, we found a consistent pattern: plants converge above-ground but diverge below-ground, and although these two strategies contrast, they ultimately mitigate competition. By capturing coordinated shifts across multiple traits, we demonstrate decoupled above- and below-ground responses as a novel mechanism by which plants adjust their phenotypes to alleviate competitive pressure among coexisting seedlings. This unified perspective reconciles contradictory hypotheses about competition-driven trait differentiation and provides a more robust framework for understanding community assembly and species coexistence.

AUTHOR CONTRIBUTIONS

Jing Yang, Carlos P. Carmona and Guochun Shen conceived the research idea. Guochun Shen, Jing Yang, and Xihua Wang designed the experiment. Jing Yang and Siyu Wu collected the data. Jing Yang analysed the data and performed the visualisations with input from Carlos P. Carmona, Guochun Shen, Shengman Lyu and Enrico Tordoni. Jing Yang and Guochun Shen wrote the first draft of the manuscript and Carlos P. Carmona, Jonathan A. Bennett, Shengman Lyu and Enrico Tordoni contributed substantially to revisions. All authors critically revised the manuscript and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code are publicly available from figshare (Yang, 2025): https://doi.org/10.6084/m9.Figshare.28250756.v2 (54).

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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. Trait measurements.

Table S1. Functional traits measured in this study and expected trait-specific responses of interspecific trait dissimilarity (ITD) to competition.

Table S2. Tree species initially selected for our experiment and their growth forms. Species names in bold indicate those ultimately included in this study; others were excluded because of low germination rates.

Table S3. Light intensity, soil moisture and soil phosphorus (total and effective) measurements across nine environmental blocks.

Table S4. Effective annual sample sizes and their proportions relative to the total sample size used to construct multidimensional trait spaces (above-ground, below-ground and total) and unidimensional traits. Leaf area, specific leaf area, leaf dry matter content, leaf toughness and stem-specific density were used for the above-ground trait space; specific root length, root diameter and root tissue density were used for the below-ground space; and all traits were used for the total space.

Table S5. Principal component analysis (PCA) results showing trait loadings and variance explained for above-ground traits, fine-root traits and combined traits. The first three principal components were retained for the above-ground trait space (66.91% of the variance explained), the first two components were retained for the fine-root trait space (94.87% of the variance explained) and the first four components were retained for the combined trait set. Component selection was guided by Horn's parallel analysis.

Table S6. Summary of the model evaluating the effects of interspecific trait dissimilarity (ITD) and ITD changes on seedling competition intensity in the corresponding year. The model includes ITD and its changes in the first, second and third years to predict seedling ($N=3185$) competition intensity for the same year (e.g. ITD and ITD changes in the first year predict seedling competition in the first year). Fixed effects include ITD, ITD changes and year, whereas species and environmental blocks are treated as random effects.

Table S7. Summary of the model used to evaluate the effects of interspecific trait dissimilarity (ITD) and ITD changes on seedling competition intensity in the following year. The model incorporates the ITD and its changes within the first and second years to predict seedling competition intensity in the subsequent years (i.e. the second and third years; $N=2870$). Fixed effects include ITD, ITD changes and year, whereas species and environmental blocks are included as random effects.

Figure S1. Comparison of abiotic environmental conditions between the greenhouse experiment and the natural Tiantong Forest. (a–c) The three discrete levels (low, medium and high) of light availability, soil moisture and total soil phosphorus were manipulated in our greenhouse experiment. Detailed measurement protocols are provided in Appendix S1. (d–f) The corresponding continuous environmental gradients were measured in situ across the Tiantong plot. Corresponding continuous gradients of light, soil moisture and total soil phosphorus across the 20-ha Tiantong Forest Dynamics Plot. Understory light availability was quantified using the LESS (Leaf-Environment Spatial Structure) model (Qi et al., 2019), which integrates LiDAR-derived canopy structure, topography and spatial heterogeneity to estimate incident light at the forest floor (Yu et al., 2022). Soil moisture and phosphorus were sampled at 20-m intervals following standardised methods (He et al., 2022).

Figure S2. Pearson correlation matrix of six above-ground traits and three fine-root traits for all the seedlings across the three experimental years. The orange points represent seedlings under the competition-free condition, whereas the blue points represent seedlings under the competition condition. The leftmost and topmost columns of the matrix display trait distributions and histograms for seedlings under the competition-free and competition conditions, respectively. The lower-left triangle of the matrix contains scatter plots showing the relationships between each pair of traits. The diagonal includes probability density functions for each trait under both conditions. The upper-right triangle presents correlation coefficient values for each trait pair. Trait abbreviations: LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LT, leaf toughness; Height, shoot height; SSD, specific stem density; SRL, specific root length; RD, root diameter and RTD, root tissue density.

Figure S3. Principal component analysis (PCA) of seedling functional traits under different competitive conditions. PCA of six above-ground (a, c) and three below-ground (b, d) traits from seedlings with complete datasets under competition-free (a, b; hollow points) and competition (c, d; solid points) conditions. Different colours represent different species. The density distribution curves show the trait distributions along the first two principal components. Table 3 shows the trait loadings and variance explained by each component.

Figure S4. Workflow for quantifying interspecific trait dissimilarity (ITD). (a) Hierarchical, individual-based calculation of ITD. Pairwise Euclidean distances were first calculated between individuals in a principal component analysis (PCA)-derived trait space. Interspecific pairwise dissimilarity between a focal species i and a neighbouring species j was then estimated using repeated randomised subsampling (999 iterations; $n = 35$ individuals per species) to standardise the sample size. Species-level ITD was obtained by averaging pairwise dissimilarities between the focal species and its six heterospecific neighbours. Neighbour-induced change in ITD was calculated $\Delta \text{ITD} = \text{ITD}_{\text{mixed}} - \text{ITD}_{\text{alone}}$. (b) ITD estimation under spatially heterogeneous environments. Species-specific individual pools were constructed by pooling all individuals of each species across the nine environmental blocks, representing the full range of abiotic conditions in the experiment. Pairwise dissimilarities were calculated by random sampling from these pools (colours indicate blocks; shapes indicate species). (c) Sensitivity analyses under environmentally homogeneous conditions. ITD was recalculated using individuals drawn from the same pot or within-pot species assemblages in the competition treatment. Consistent results across heterogeneous (block-level) and homogeneous (pot-level) analyses indicate that ITD patterns are robust to environmental heterogeneity.

Figure S5. Availability of seedlings for constructing the above-ground trait space under competition. (a) Distribution of the number of individuals per pot with complete above-ground trait data across three annual harvests in the competition treatment, pooled across all nine environmental blocks. (b) Corresponding distributions shown separately for each environmental block. The bars show the number of pots in which 0–7 individuals with complete above-ground trait measurements were retained, where 7 indicates that all the species in a pot were included in the analysis. Reductions in individual number reflect seedling mortality or missing above-ground traits (e.g. loss of leaves), both of which prevent inclusion in the above-ground multivariate trait space used to estimate ITD. The colour shading indicates the number of individuals per pot, and the numbers within the bars denote pot counts.

Figure S6. Pot-level interspecific trait dissimilarity (ITD) and sensitivity to species loss. (a, b) Pot-level ITD for above-ground (a) and fine-root (b) traits across 3 years. Each point represents the ITD of a focal seedling calculated from its surviving heterospecific neighbours within the same competition pot (two to seven species). To account for variation in species richness due to mortality or missing trait data, each competition pot was paired with a richness-matched expectation generated by resampling individuals from the competition-free treatment ($R = 999$). Split–violin plots show density distributions with medians and interquartile ranges; grey lines connect observed values to their paired expectations. Asterisks indicate paired test results (**$p < 0.01$; ***$p < 0.001$; ns). (c, d) Sensitivity of pot-level changes in ITD to species loss. The mean change in ITD (±SE) is shown as a function of the minimum number of species retained per pot for the above-ground (c) and fine-root (d) traits. Analyses were restricted to pots meeting each threshold and paired with richness-matched virtual pots from the competition-free treatment.

Figure S7. Pot-level effects of interspecific trait dissimilarity (ITD) on competition intensity. Mixed-effects models relating pot-level ITD metrics to competition intensity (relative interaction index (RII)) in the same year (a) and the subsequent year (b). ITD was calculated at the pot level between each focal seedling and its surviving neighbours; competition-free expectations were generated using richness-matched, resampled virtual pots. Effect sizes are standardised coefficients from models fitted separately for above-ground and fine-root trait spaces. Solid circles indicate significant effects ($p < 0.05$), open circles indicate nonsignificant effects. Pot-level results are qualitatively consistent with species-level analyses, indicating that the relationship between dynamic ITD shifts and competition intensity is robust to analytical scale.

Figure S8. Species-specific competition intensity across 3 years in heterogeneous environments. Mean competition intensity (sign-inverted relative interaction index, RII; mean ± SE) for seven experimental species measured over the first, second and third years of competition. Panel (a) shows competition intensity calculated for all individuals of each species, whereas panel (b) shows competition intensity calculated only for surviving seedlings. Competition intensity is based on total biomass, with higher RII values indicating stronger net negative neighbour effects (greater biomass reduction). Different colours represent each species: *Daphniphyllum oldhami* (DO), *Cyclobalanopsis glauca* (CG), *Castanopsis sclerophylla* (CS), *Lithocarpus glaber* (LG), *Schima superba* (SS), *Hovenia acerba* (HA) and *Quercus chenii* (QC). Additional species details are provided in Table S2.

Figure S9. Relationship between seedling height (cm) and competition intensity. Competition intensity was quantified using the relative interaction intensity (RII), calculated as $(\text{BM}_{\text{alone}} - \text{BM}_{\text{mixed}})/(\text{BM}_{\text{alone}} + \text{BM}_{\text{mixed}})$, where BM_{mixed} is the biomass of a focal seedling grown with neighbours and BM_{alone} is the mean biomass of conspecific seedlings grown in the competition-free treatment. Points represent individual seedlings, and the solid line shows the fitted linear regression with 95% confidence intervals. Height is measured in centimetres. The weak but significant relationship ($R^2=0.17$, $p<0.001$) indicates that seedling size explains only a modest fraction of variation in competition intensity.

Figure S10. Year-specific distributions of competition intensity (relative interaction intensity (RII)) for seedlings grown with neighbours. Competition intensity was quantified using the relative interaction intensity, which is based on the formulation of Armas et al. (2004) but multiplied by −1 for analytical clarity, and calculated as $(BM_{alone}-BM_{mixed})/(BM_{alone}+BM_{mixed})$ where BM_{mixed} is the biomass of a focal seedling grown with neighbours and BM_{alone} is the mean biomass of conspecific seedlings grown in the competition-free treatment. Under this definition, higher positive values indicate stronger net negative (competitive) interaction outcomes, whereas negative values indicate net positive (facilitative) outcomes. Points represent individual seedlings. The numbers above and below the zero line indicate the count and proportion of seedlings experiencing facilitative and competitive interaction outcomes, respectively.

Figure S11. Pearson correlation matrix showing relationships between interspecific trait dissimilarity (ITD) values and their competition-induced changes across above-ground and fine-root trait spaces. The closer the colour is to red, the stronger the positive correlation between the two variables; the closer the colour is to blue, the stronger the negative correlation. The numbers represent correlation coefficients, with blank spaces indicating nonsignificant correlations ($p>0.05$).

Figure S12. Context dependence of the relationship between neighbour-induced changes in interspecific trait dissimilarity (ITD) and competition intensity. Panels (a, b) show standardised coefficients (±95% CI) from mixed-effects models relating competition intensity (sign-inverted relative interaction intensity (RII)) to neighbour-induced changes in above-ground and fine-root ITD, environmental conditions (light availability, soil moisture and available phosphorus), experimental year and their two-way interactions for the same year (a) and the subsequent year (b). Species identity and environmental block were included as random intercepts. Positive coefficients indicate stronger net competitive effects (higher RII), whereas negative coefficients indicate weaker competition; vertical dashed lines denote zero effects. Panels (c–e) visualise the fitted marginal relationships corresponding to key significant interactions, illustrating how the associations between ITD change and competition intensity varies across environmental contexts. Specifically, panel (c) shows the changes in above-ground ITD under contrasting light availability conditions in the same year, whereas panels (d) and (e) show the changes in fine-root ITD under contrasting soil moisture and soil phosphorus availability conditions, respectively, in the subsequent year. Lines represent fixed-effect predictions and shaded bands indicate 95% confidence intervals; low, medium and high environmental levels correspond to representative values observed across experimental blocks.

Figure S13. Relative changes in interspecific trait dissimilarity (ITD) from competition-free to competition conditions in above-ground, fine-root and total trait spaces over the first, second and third years. Interspecific trait dissimilarity (ITD) quantifies the mean Euclidean distance between a focal species and others in multivariate trait space. Relative changes were calculated as the ratio of the absolute ITD change to the baseline ITD under competition-free conditions. The different point colours indicate different species ($N=7$). Red asterisks indicate significant ITD changes (paired Wilcoxon rank-sum test; $^{*}p<0.1$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$).

Figure S14. Changes in interspecific trait dissimilarity (ITD, mean ± SE) from competition-free to competition conditions in individual traits over the first, second and third years. Each black dot represents the mean change (±SE) in ITD between treatments across seven species, calculated as the ITD under competition minus the ITD under competition-free conditions. Red asterisks indicate significant ITD changes (Wilcoxon signed-rank test; $^{*}p<0.1$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$).

Figure S15. Mean trait values for seven tree species under competition-free (hollow circles) and competition (solid circles) conditions across nine environmental blocks. Different colours represent environmental blocks, highlighting the variation in average trait values between competition treatments for each species across environments. The species included *Daphniphyllum oldhami* (DO), *Cyclobalanopsis glauca* (CG), *Castanopsis sclerophylla* (CS), *Lithocarpus glaber* (LG), *Schima superba* (SS), *Hovenia acerba* (HA) and *Quercus chenii* (QC).

Figure S16. Competition effects on trait dissimilarity (ITD) across species pairs with different growth forms. (a) Absolute and (b) relative changes in ITD for species pairs grouped by growth form across above-ground, fine-root and total trait spaces over 3 years. Species combinations include deciduous-deciduous (DD, yellow, $n=1$ pair), deciduous-evergreen (DE, light green, $n=10$ pairs) and evergreen-evergreen (EE, dark green, $n=10$ pairs) combinations. Changes in ITD were calculated as ITD under competition minus ITD under competition-free conditions, with positive values indicating increased trait dissimilarity under competition. Relative changes were calculated by dividing absolute changes by competition-free ITD values. Red asterisks indicate significant ITD changes (Wilcoxon signed-rank test, $\cdot p<0.1$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$).

Figure S17. Relationship between interspecific trait dissimilarity (ITD) changes and competition intensity in the current year (a, b) and subsequent years (c, d) for above-ground (a, c) and fine-root (b, d) trait spaces. Each point represents an individual seedling, with colours indicating first (blue), second (purple) and third (red) years of competition. Changes in ITD were calculated as the ITD under competition minus the ITD under competition-free conditions. The competition intensity was measured via the inverse relative interaction index (RII) based on total biomass, with higher values indicating greater biomass reduction. The grey lines represent simple linear regression relationships across all years, with equations and significance values displayed.

Figure S18. Competition effects on interspecific trait dissimilarity (ITD) in total trait space across 3 years. ITD in total trait space under competition-free (blue) and competition (pink) treatments across 3 years. ITD quantifies the mean Euclidean distance between a focal species and others in a four-dimensional trait space derived from principal component analysis of nine functional traits, with larger values indicating greater trait dissimilarity. The coloured points represent species-specific ITD values ($N=7$), with grey lines connecting the same species across treatments. The top-right inset shows the mean changes (±SEs) in the ITD between treatments, calculated as the ITD under competition minus the ITD under competition-free conditions. Positive values indicate greater dissimilarity under competition, whereas negative values suggest trait convergence under competitive pressure. NS indicates nonsignificant changes between treatments (Wilcoxon signed-rank test).

Figure S19. Temporal dynamics of competition-induced inter-specific trait dissimilarity (ITD) changes across species. Mean changes in ITD for above-ground (a) and fine-root (b) trait spaces across 3 years of competition. ITD represents the mean Euclidean distance between focal species and competitors in multivariate trait space. Changes in ITD were calculated as ITD under competition minus ITD under competition-free conditions for each species, with negative values indicating reduced trait dissimilarity under competition. The black curves show locally weighted smoothing (loess regression) with 95% confidence intervals (grey shading). The coloured points represent individual species: *Daphniphyllum oldhami* (DO), *Cyclobalanopsis glauca* (CG), *Castanopsis sclerophylla* (CS), *Lithocarpus glaber* (LG), *Schima superba* (SS), *Hovenia acerba* (HA) and *Quercus chenii* (QC).

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