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ORIGINAL ARTICLE

Decoupling of above- and below-ground intraspecific trait variation along richness gradients in plants

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• **Background and Aims** How intraspecific trait variation (ITV) responds to species richness remains an unresolved question in community ecology, with two competing expectations: the niche packing hypothesis predicts ITV convergence, whereas the competitive hierarchy hypothesis predicts divergence. Given distinct competitive mechanisms for light versus soil resources, above- and below-ground ITV is likely to exhibit differential responses to species richness. However, empirical research has focused predominantly on above-ground traits, leaving a critical gap in understanding simultaneous above- and below-ground responses.
• **Methods** This study addresses these gaps through a 3-year controlled seedling experiment in Tiantong, Zhejiang, China, constructing experimental communities across species richness gradients (one, two, four and eight species) and systematically measuring 11 key above- and below-ground functional traits.
• **Key Results** Our results reveal an above-ground–below-ground decoupling pattern, in which plants responded to increasing species richness through greater ITV in traits associated with the above-ground leaf-economics axis, but exhibited more complex below-ground responses. Above-ground ITV of mean leaf area and specific leaf area increased significantly with richness, supporting the competitive hierarchy hypothesis. In contrast, ITV of root diameter decreased significantly with richness, indicating trait-specific rather than general support for the niche packing hypothesis. Species richness also drove directional shifts in mean trait values, with above-ground traits shifting towards greater resource acquisition and below-ground traits shifting towards thicker-root resource-use strategies. This decoupling indicates that plants simultaneously use divergent strategies in different organ dimensions rather than uniform responses.
• **Conclusions** The study reconciles long-standing theoretical conflicts by demonstrating that both competitive hierarchy and niche packing operate concurrently but in distinct plant compartments. These findings emphasize the necessity of integrated above- and below-ground perspectives in explaining species coexistence in diverse communities.

Key words: Above-ground–below-ground decoupling, community assembly, competitive hierarchy hypothesis, intraspecific trait variation, niche packing hypothesis, species richness.

INTRODUCTION

Understanding how biodiversity is maintained in plant communities requires examination of functional traits, i.e. the morphological, physiological and phenological characteristics that mediate species interactions (McGill *et al.*, 2006). These traits reveal species niches and differences in fitness, making trait-based approaches essential for understanding species coexistence mechanisms (Kraft *et al.*, 2015). Traditionally, community ecology has focused on interspecific trait differences, using species mean values to predict coexistence patterns. However, this approach overlooks intraspecific trait variation (ITV; i.e. variation among individuals within a species). Growing evidence shows that ITV contributes an average of 32 % of total variation among communities (Siefert *et al.*, 2015) and can respond to local selection pressures, including biotic interactions such as neighbour identity and diversity (Abakumova *et al.*, 2016; Bennett *et al.*, 2016). As species richness increases in multispecies communities, plants face increasingly complex competitive environments. How ITV responds to changing species richness thus presents a central question for theoretical ecology with practical implications for biodiversity and ecosystem functioning.

Existing ecological theories offer two contrasting predictions regarding this question, depending on whether niche differentiation or competitive hierarchy dominates community dynamics. The niche packing hypothesis posits that species interaction is driven by niche differentiation. In species-poor communities, conspecific individuals expand trait variation to use alternative resources and alleviate competition. However, as diversity increases and community niche space saturates, the risk of trait overlap grows (Walker *et al.*, 2017). According to the limiting similarity principle, coexisting species adopt niche packing strategies: resources are allocated more finely, causing conspecific traits to contract towards specific optimal ranges to avoid competitive exclusion, thereby reducing ITV with increasing species richness (Violle *et al.*, 2012; Siefert *et al.*, 2015). Empirical support for this hypothesis spans diverse ecosystems. Experiments in subtropical and temperate forests found that as tree species richness increases, ITV of key leaf traits decreases significantly (Castro Sánchez-Bermejo *et al.*, 2024, 2025). This reduction in ITV might occur because, as noted by Carmona *et al.* (2019*a*), intraspecific plasticity in competitive environments prompts disadvantaged individuals to adjust traits towards dominant species, resulting in ITV reduction.

In contrast, the competitive hierarchy hypothesis predicts that ITV increases with species richness. This theory posits that plant interactions are driven by competitive ranking, whereby traits shift towards more competitive capabilities based on nearest neighbours (Castro Sánchez-Bermejo *et al.*, 2025). As species richness increases, communities create heterogeneous biotic environments where conspecific plants face neighbours with diverse identities and competitive ranks. To alleviate homogenized competition, plants exhibit higher phenotypic plasticity, flexibly adjusting strategies according to specific neighbour identities (Uriarte *et al.*, 2010; Violle *et al.*, 2012). This specialized response enables conspecific individuals to display multiple survival strategies, expanding trait differences and increasing ITV in high-diversity communities in comparison to monocultures (Stein *et al.*, 2014; Benavides *et al.*, 2019*a*). Substantial evidence supports this view. In forest ecosystems, heterogeneous mixed neighbours prompt trees to exhibit higher variability in crown structure and leaf traits such as specific leaf area and potassium content (Benavides *et al.*, 2019*a*; Davrinche and Haider, 2021). In tropical forests and deserts, intraspecific variation of chemical elements expands with increasing intensity of competition (Jiang *et al.*, 2023; Han *et al.*, 2025). Le Bagousse-Pinguet *et al.* (2014) attribute this to equalizing mechanisms, whereby increased trait variation reduces average fitness differences, avoiding competitive exclusion.

These contrasting predictions need not be mutually exclusive but might instead reflect differential responses in distinct plant organs (Jucker *et al.*, 2015; Benavides *et al.*, 2019*a*, 2019*b*; Castro Sánchez-Bermejo *et al.*, 2025), driven by fundamentally different competitive mechanisms for above- versus below-ground resources (Semchenko *et al.*, 2018; Bricca *et al.*, 2023). In above-ground organs, competition for light is characterized by asymmetric interactions and hierarchical dominance, whereby taller individuals shade shorter ones without reciprocal effects (Vojtech *et al.*, 2007; DeMalach and Kadmon, 2017). In such conditions, plants of the same species are likely to exhibit trait divergence as species richness increases. Heightened species richness intensifies light competition asymmetry, driving conspecifics to exploit diverse light microhabitats through enhanced phenotypic plasticity, resulting in elevated ITV, which is a pattern consistent with competitive hierarchy dynamics. Conversely, in below-ground organs, soil resource acquisition operates under spatial niche constraints (e.g. nutrient patchiness) and differentiation pressures (Carvajal *et al.*, 2019; Homulle *et al.*, 2022; Bricca *et al.*, 2023). Here, conspecifics are more likely to display trait convergence, because elevated species richness induces strong environmental filtering that compels root traits to cluster around optimal values, yielding reduced ITV, which is a pattern aligning with niche packing principles. This stronger filtering might arise because species-rich communities contain species with more diverse resource-acquisition strategies and complementary patterns of soil resource use (Li *et al.*, 2017). Their combined uptake can more strongly deplete key below-ground resources, such as soil nitrogen, phosphorus or water, creating a more restrictive soil environment, in which only root trait values compatible with resource limitation and spatial niche constraints are favoured (Phoenix *et al.*, 2020; Chaves *et al.*, 2021; Wang *et al.*, 2025). For instance, root diameter variability diminishes under intense competition (Bennett *et al.*, 2016; Han *et al.*, 2025). This organ-specific perspective suggests that the two seemingly contradictory hypotheses could operate concurrently but in different plant compartments. However, current research demonstrates a pronounced above-ground–below-ground disparity. Investigations predominantly concentrate on readily measurable above-ground attributes, such as specific leaf area and plant height, which primarily capture asymmetric light competition effects (Semchenko *et al.*, 2018). Simultaneous examination of ITV responses to species richness across both above- and below-ground organs (particularly in controlled experimental settings) remains scarce, underscoring the necessity for integrated whole-plant approaches.

To address these gaps, we conducted a 3-year greenhouse experiment with strict environmental controls. Controlled experiments are essential to overcome the limitation that in natural habitats, abiotic factors such as soil heterogeneity are often confounded with biotic factors, making it difficult to distinguish whether trait variation stems from richness responses or local adaptation (Biswas *et al.*, 2025). We selected ten native tree species, cultivated 3824 seedlings and constructed experimental communities across richness gradients (one, two, four and eight species), systematically measuring 11 above- and below-ground functional traits in uniform conditions. In addition to ITV, changes in mean trait values can provide complementary information on how species richness shifts the central tendency of plant functional strategies. ITV reflects the breadth of trait distributions and the extent of phenotypic differentiation within species, whereas mean trait values indicate whether communities shift directionally towards more acquisitive, conservative or alternative resource-use strategies along richness gradients. Therefore, jointly examining ITV and mean trait responses allows us to distinguish whether

species richness changes only the variability of traits or also drives directional adjustments in plant functional strategies. This study addresses two core questions.

(1) After excluding environmental noise, does high species richness force trait convergence (supporting niche packing) or promote trait differentiation (supporting competitive hierarchy)?
(2) Given different spatial properties of light and soil resources, are ITV responses consistent between above- and below-ground organs?

Additionally, we asked whether species richness also drives directional shifts in mean above- and below-ground trait values, thereby revealing coordinated changes in plant functional strategies beyond ITV. By testing these questions, we aim to clarify ITV mechanisms across organ dimensions and provide experimental evidence to understand how species richness simultaneously shapes trait variation and mean functional strategies during plant interactions.

MATERIALS AND METHODS

Study site and experimental species

This study was conducted in greenhouse facilities at Tiantong National Forest Park (29°48′N, 121°47′E) in Ningbo, Zhejiang Province, China. The region experiences a subtropical monsoon climate with hot, humid summers and dry, cold winters. Annual precipitation averages 1374.7 mm, with a mean annual temperature of 16.2 °C. The coldest month (January) averages 4.2 °C, and the hottest month (July) averages 28.1 °C. The study area soil is mountainous yellow–red soil, primarily loam and clay in texture, with pH values ranging from 4.4 to 5.1, indicating acidity. Local forest types consist of subtropical evergreen broad-leaved forests mixed with deciduous tree species (Yang *et al.*, 2011).

Based on local forest community species composition, life forms, phylogenetic relationships and seed availability, for this study we selected ten common native tree species as experimental subjects. These include two deciduous species, *Quercus chenii* (QC) and *Hovenia acerba* (HA), and eight evergreen species: *Cyclobalanopsis glauca* (CG), *Cyclobalanopsis myrsinifolia* (CM), *Quercus sessilifolia* (QS), *Lithocarpus harlandii* (LH), *Castanopsis sclerophylla* (CS), *Elaeocarpus decipiens* (ED), *Schima superba* (SS) and *Daphniphyllum oldhami* (DO). To minimize interference from intraspecific genetic variation and maternal effects, mature seeds were collected from only one healthy mother tree per species within the study area from September to December 2019. After collection, seeds were surface disinfected with imidacloprid and carbendazim, then stored through winter via sand stratification or dry storage according to species-specific requirements. In March 2020, seeds were sown in seedling trays under full light with adequate water supply. After seedlings were firmly established, individuals of similar size and health status were selected and transplanted into pots for the experiment.

Experimental design

A 3-year controlled experiment (2020–2023) was conducted to investigate the effects of species richness on ITV. In June 2020, eight healthy seedlings were transplanted into each pot, establishing four species richness gradients (one, two, four and eight species) to construct plant communities.

All ten species were grown in monoculture (richness = 1), with each species replicated in eight pots. Owing to low germination rates of some species, a fully factorial design was not feasible. To encompass species combinations with varying phylogenetic distances while considering seedling availability, the following combinations were implemented, For two-species combinations there were nine groups: QS-QC, QC-LH, CM-CG, CM-QC, QC-HA, QC-ED, LH-ED, SS-ED and SS-DO. Each pot contained four individuals per species, with each combination replicated 12 times. For four-species combinations, there were five groups: QS-QC-CS-LH, CM-CG-QC-LH, HA-CM-CG-QC, HA-QC-LH-ED and SS-HA-ED-DO. Each pot contained two individuals per species, with each combination replicated 24 times. For eight-species combinations, there were three groups: HA-CM-CG-QS-QC-CS-LH-ED, SS-HA-CM-CG-QS-QC-LH-ED and SS-HA-CM-CG-QC-LH-ED-DO. Each pot contained one individual per species, with each combination replicated 48 times.

All treatments maintained identical planting density (eight individuals per pot). Initial seedling height and basal diameter were standardized across pots to ensure comparability. During the first week post-transplantation, missing seedlings were replaced with conspecifics of similar size. Pots were spaced 15–20 cm apart to prevent cross-pot interference, and positions were randomized every 2 weeks to minimize microenvironmental variation. Insect nets and necessary pesticide applications were used throughout the experiment to maintain seedling health.

Functional trait measurements

All surviving seedlings were sampled and measured for traits from July to August 2023. Entire pots were processed, with roots carefully washed and separated by individual. We measured seven above-ground and four below-ground traits for each surviving seedling. Above-ground traits included mean leaf area (MLA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf toughness (LTO), chlorophyll content (Chl), height (Height) and stem specific density (SSD). Below-ground fine root traits included specific root length (SRL), root diameter (RD), root tissue density (RTD) and specific root area (SRA). All trait measurements followed standardized protocols (Pérez-Harguindeguy *et al.*, 2013).

Above-ground trait measurements. Before plant harvest, plant height was measured using a ruler to determine main stem length from base to apex. Daily morning relative chlorophyll content was measured *in situ* using a SPAD-502Plus chlorophyll meter (Konica-Minolta, Japan) on five mature, intact leaves per seedling (Marenco *et al.*, 2009). Ten randomly selected intact, healthy mature leaves were collected for leaf trait determination. Leaf fresh weight was measured using a precision balance, and leaf area was

obtained by scanning leaves with a leaf area meter (LI-3100C, Li-Cor, USA). Leaf toughness was measured on three randomly selected leaves using a digital force gauge (precision 0.001 N; HADPI, Leqing, China) with a puncture test method. The sensing needle (1 mm diameter) moved downwards at 10 mm s^{-1}, penetrating non-major and secondary vein areas. Measurements were repeated three times at different positions, with the average of maximum penetration forces recorded as leaf toughness (Pérez-Harguindeguy *et al.*, 2013; He *et al.*, 2019). Leaves were then placed in a 105 °C oven for 30 min to deactivate enzymes, followed by drying at 75 °C to constant weight to obtain leaf dry weight. Specific leaf area was calculated as leaf area divided by leaf dry weight, and leaf dry matter content as leaf dry weight divided by leaf fresh weight. After leaf trait measurements, all seedlings were harvested. For stem specific density estimation, one main stem segment ~5 cm above the base was collected from each seedling. Stem fresh weight was measured using a precision balance, stem fresh volume was determined by water displacement, and stems were dried at 75 °C to constant weight to obtain stem dry weight. Stem specific density was calculated as stem dry weight divided by fresh volume.

Root trait measurements. For root trait measurements, below-ground roots were placed in a 2 mm fine mesh sieve and gently washed with clean water to remove soil and attached organic particles. Fine roots (<2 mm diameter, ~2 g) were randomly selected for analysis. Fine root images were scanned at 400 dpi resolution using an Epson Expression 10000XL Scanner, with roots spread in trays without overlap. Images were manually cleaned of background impurities using Adobe Photoshop and analysed with WinRHIZO software (Arabidopsis v.2012b; Regents Instruments Inc., Quebec, Canada) to obtain total root length, root diameter, root surface area and fine root volume. Fine roots were then dried at 75 °C to constant weight to obtain root dry weight. Specific root length was calculated as total root length divided by root dry weight, specific root area as root surface area divided by root dry weight, and root tissue density as root dry weight divided by root volume.

Intraspecific trait variability metrics

ITV was quantified for each focal species within each species-composition treatment, defined as a unique species assemblage at a given richness level (e.g. QS-QC at richness = 2 or CM-CG-QC-LH at richness = 4). For a given focal species in a species-composition treatment, all surviving individuals across replicate pots of that assemblage were pooled into a single population. Consequently, our calculated ITV metric captures both the variation among individuals experiencing the same competitive neighbourhood (within-pot variation) and the variation among replicate pots (between-pot variation). From this pooled population, ITV was quantified using both single-trait and multidimensional approaches, because both methods offer complementary insights into ITV relationships with species richness.

To assess competition effects on intraspecific variability of individual traits, we calculated intraspecific variability for each trait of each species using the improved coefficient of variation (Bao's CV) (Yang *et al.*, 2020). All trait values were initially normalized to a scale ranging from zero to one. To reduce potential effects of unequal sample sizes across treatments, a rarefaction approach was applied (Yang *et al.*, 2020). When the number of individuals was >20, 20 individuals were randomly sampled 999 times, and the mean Bao's CV value was used as the ITV estimate. When the number of individuals was ≤20, all individuals were included in the calculation. For multidimensional trait variation, we used the trait probability density (TPD) method (Carmona *et al.*, 2016). Initially, principal component analysis was performed separately on above- and below-ground functional traits to identify principal axes of functional variation and reflect their independence (Carmona *et al.*, 2021). Before principal component analysis, trait data underwent logarithmic transformation and standardization. Horn's parallel analysis determined the number of principal components (PCs) to retain (Horn, 1965), with varimax rotation applied to improve interpretability (Yang *et al.*, 2025).

ITV in multidimensional trait space was then quantified using the TPDs function from the TPD package. This framework uses multidimensional Gaussian kernel density estimation, which captures trait probability distributions in space more sensitively than traditional convex hull methods. We constructed multidimensional trait probability densities for each population (conspecific individuals within specific species composition groups). Optimized bandwidth algorithms were used in density estimation, with a 5 % quantile threshold set to define trait space boundaries and mitigate extreme outlier influence. Based on estimated TPDs, functional richness was calculated using the REND function. Functional richness represents the total volume occupied by a population in two-dimensional functional trait space, directly reflecting realized niche size and ITV. Additionally, to analyse ITV across different functional dimensions, we calculated one-dimensional TPD and functional richness for PC1 and PC2 axes separately.

Asymmetry of competition

To elucidate the underlying competitive mechanisms driving trait variation patterns, we used the Gini coefficient (G) as a metric of size inequality. Ecological theory posits that size inequality among individuals is driven primarily by size-asymmetric competition; consequently, the Gini coefficient has been widely used to quantify the intensity of asymmetric competition within plant populations or communities (Weiner and Solbrig, 1984; Cordonnier and Kunstler, 2015).

Specifically, we calculated the Gini coefficient for above-ground biomass and below-ground biomass of plants within each experimental unit based on the Lorenz curve (Equation 1). The calculation formula is as follows:

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}|x_i - x_j|}{2n^2\bar{x}} \quad (1)$$

where x_i and x_j represent the biomass of plant individuals i and j, respectively; n is the total number of plant individuals within the experimental unit; and $\bar{x}$ is the mean biomass.

Given the potentially small number of individuals (n) within each experimental unit in this study, the directly calculated standard Gini coefficient might underestimate the real population inequality. To eliminate estimation bias caused by small sample sizes, we applied the correction method recommended by Weiner and Solbrig (1984) to obtain the unbiased Gini coefficient (G_{corr}) (Equation 2):

$$G_{corr} = G \times \frac{n}{n-1} \quad (2)$$

The corrected Gini coefficient (G_{corr}) ranges from zero to one. A larger G_{corr} value indicates a more pronounced disparity in individual sizes within the community, implying a strict competitive hierarchy and strong asymmetric competition. Conversely, a smaller G_{corr} value suggests stronger symmetric competition (resource sharing or niche packing). All Gini coefficient calculations were performed using the ineq package in R.

Statistical analysis

Linear mixed-effects models were used to test the effects of species richness on ITV. Response variables included multidimensional functional richness, one-dimensional functional richness along individual principal component axes, and Bao's coefficient of variation for individual traits. Each observation represented the ITV of one focal species within one species composition. Log-transformed species richness was included as a fixed effect, and species identity was included as a random intercept to account for species-specific differences in baseline ITV. Species composition was evaluated as an additional crossed random intercept to account for variation among assemblages within richness levels (retained when it significantly improved model fit in a likelihood-ratio test, $P < 0.05$; Supplementary Data Table S1) (Matuschek *et al.*, 2017). The candidate full model was: ITV ~ $\log_2$-(Richness) + (1|Species) + (1|Composition), with the final random-effect structure for each ITV metric reported in Supplementary Data Table S1. Accordingly, the fixed effect of richness was interpreted as the average richness–ITV relationship across the ten focal species rather than as a species-specific response. To compare richness–ITV relationships between above- and below-ground compartments, we subsequently combined all ITV metrics after z-score standardizing values separately within each metric. Standardized ITV was modelled as a function of $\log_2$-transformed species richness, compartment and their interaction using the same random-effects selection procedure. The candidate full model for this comparison was: ITV ~ $\log_2$(Richness) × Compartment + (1|Species) + (1|Composition). The richness × compartment interaction tested whether the richness–ITV relationship differed between above- and below-ground compartments. To assess potential among-species variation in richness–ITV relationships further, we also fitted separate simple bivariate linear regressions of each ITV metric against $\log_2$-transformed species richness for each species.

To test how competition asymmetry varied along the species-richness gradient, we fitted linear mixed-effects models separately for above- and below-ground biomass. G_{corr} was included as the response variable, log-transformed species richness as a fixed effect, and species composition as a random intercept. The model structure was: G_{corr} ~ $\log_2$-(Richness) + (1|Composition). Furthermore, to evaluate one aspect of the hypothesised decoupling between above- and below-ground competition modes, we used a paired t-test to compare corrected Gini coefficients for above- and below-ground biomass within the same pot. This analysis tested the directional prediction that above-ground biomass inequality, hence inferred size asymmetry, was consistently greater than below-ground biomass inequality because of the contrasting physical properties of light and soil resources.

To examine whether the richness-related increase in biomass inequality was accompanied by changes in the relative importance of within- and between-species biomass differences, we partitioned the total squared deviations in log-transformed individual biomass into additive within- and between-species components following Schmid *et al.* (2017). The analysis was conducted separately for above- and below-ground biomass at the pot level. Within each pot, the within-species component quantified deviations of individual biomass from the corresponding species mean, whereas the between-species component quantified differences between species means and the overall pot mean, weighted by the number of individuals per species. We then calculated the fraction of total squared deviations attributable to between-species differences. Linear mixed-effects models were used to test the relationships of the within-species squared deviations and the between-species fraction with log-transformed species richness, with species composition included as a random intercept. Within-species squared deviations were evaluated at richness levels 1, 2 and 4, whereas the between-species fraction was evaluated at richness levels 2, 4 and 8.

In addition to ITV, we examined whether species richness was associated with shifts in species-level mean trait values, which might indicate directional changes in functional strategies along the richness gradient. For each species within each richness and composition treatment, mean trait values were calculated by averaging across all individuals. Richness effects were tested using the same linear mixed-effects modelling framework and random-effect selection procedure described above, with $\log_2$-transformed species richness as a fixed effect and with species identity and, where supported, species composition included as random intercepts. The richness effect was therefore interpreted as the average richness–mean-trait relationship across the ten focal species. This analysis was applied to all individual traits and principal component axes (PC1 and PC2 for above- and below-ground traits).

All statistical analyses and plotting were conducted in the R v.4.4.3 statistical computing environment (R Core Team, 2025). The linear mixed-effects models mentioned above were fitted using the lmer function in the lme4 package (Bates *et al.*, 2015), with parameters estimated using restricted maximum likelihood (REML) to obtain unbiased variance components. To assess the statistical significance of fixed effects (i.e. log-transformed species richness), we used the lmerTest package (Kuznetsova *et al.*, 2017), with the significance of regression coefficients (Estimate) obtained based on t-tests using Satterthwaite's approximation

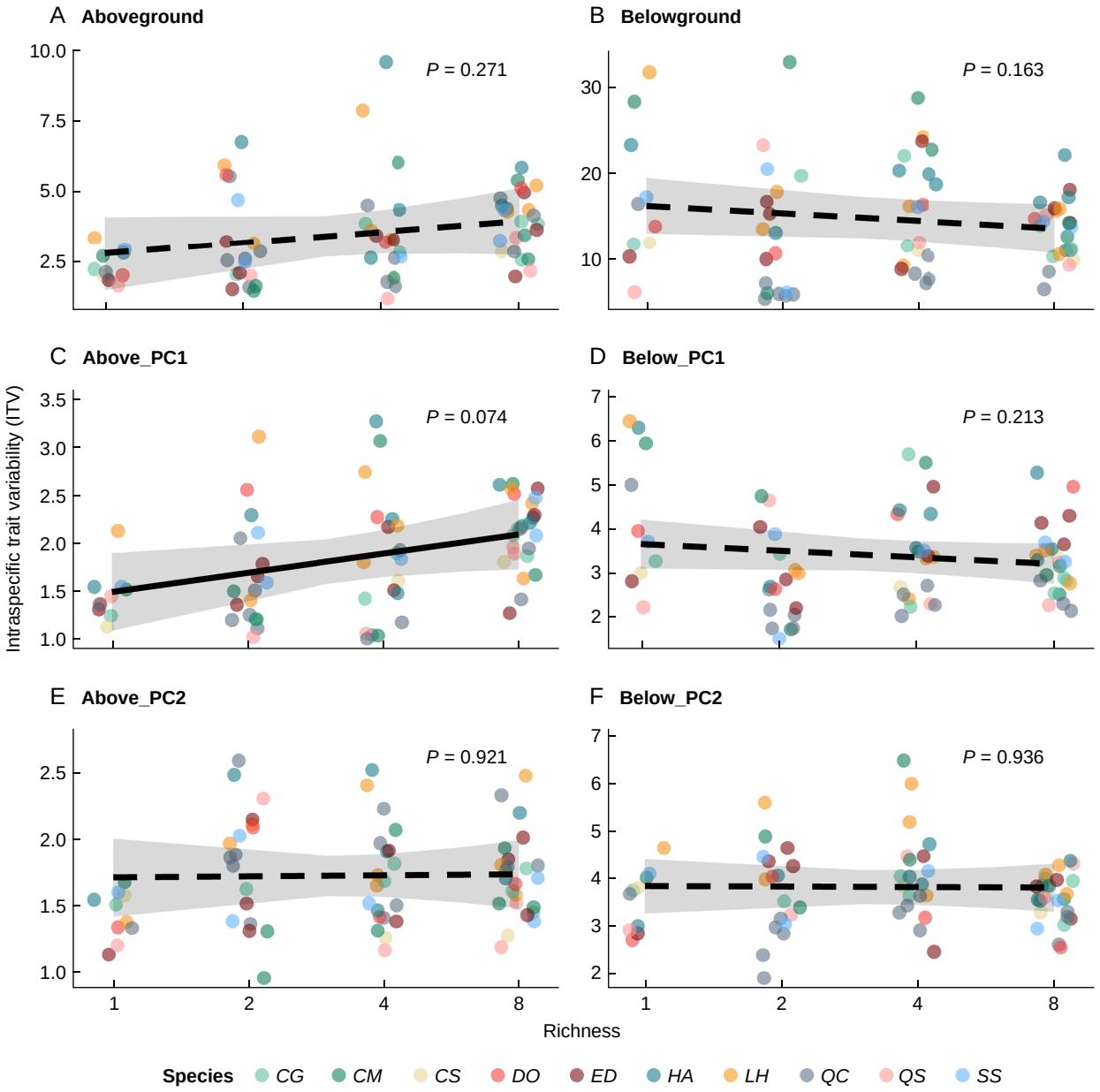

FIG. 1. Relationships between species richness and above- and below-ground intraspecific trait variability (ITV). (A, B) Two-dimensional ITV for above- (A) and below-ground traits (B). (C–F) One-dimensional ITV along the principal functional axes: (C) above-ground PC1, representing the leaf economics spectrum; (D) below-ground PC1, primarily associated with specific root area and root tissue density; (E) above-ground PC2, representing plant size and structural traits; and (F) below-ground PC2, representing the root economics spectrum. Each point represents the ITV of one species within a given richness level and species composition, with colours identifying the ten focal species. Lines and grey shading show predictions and 95 % confidence intervals, respectively, from the final linear mixed-effects models. All models included species identity as a random intercept; model-specific random-effect structures are reported in Supplementary Data Table S1. Solid lines denote relationships with $P < 0.1$, whereas dashed lines denote relationships with $P \geq 0.1$. Model-derived P-values for the fixed effect of $\log_2$-transformed species richness are shown in each panel. Species richness is displayed on a $\log_2$-scaled axis.

for degrees of freedom. Additionally, predicted means and 95 % confidence intervals for the models across richness gradients were extracted using the allEffects function in the effects package (Fox and Weisberg, 2019) to visualize regression trends. Multidimensional trait variation was quantified using the TPD package (Carmona *et al.*, 2016; Carmona *et al.*, 2019*b*). Principal component analysis and parallel analysis were conducted using the psych package (Revelle, 2023) and the paran package (Dinno, 2018), respectively. The Gini coefficient was calculated using the ineq package (Zeileis, 2014). Data manipulation and visualization were performed using dplyr (Wickham *et al.*, 2023*a*), tidyr (Wickham *et al.*, 2023*b*) and ggplot2 (Wickham, 2016).

RESULTS

The effect of species richness on ITV depended on trait dimensionality and plant compartment (Fig. 1). The first two PCs

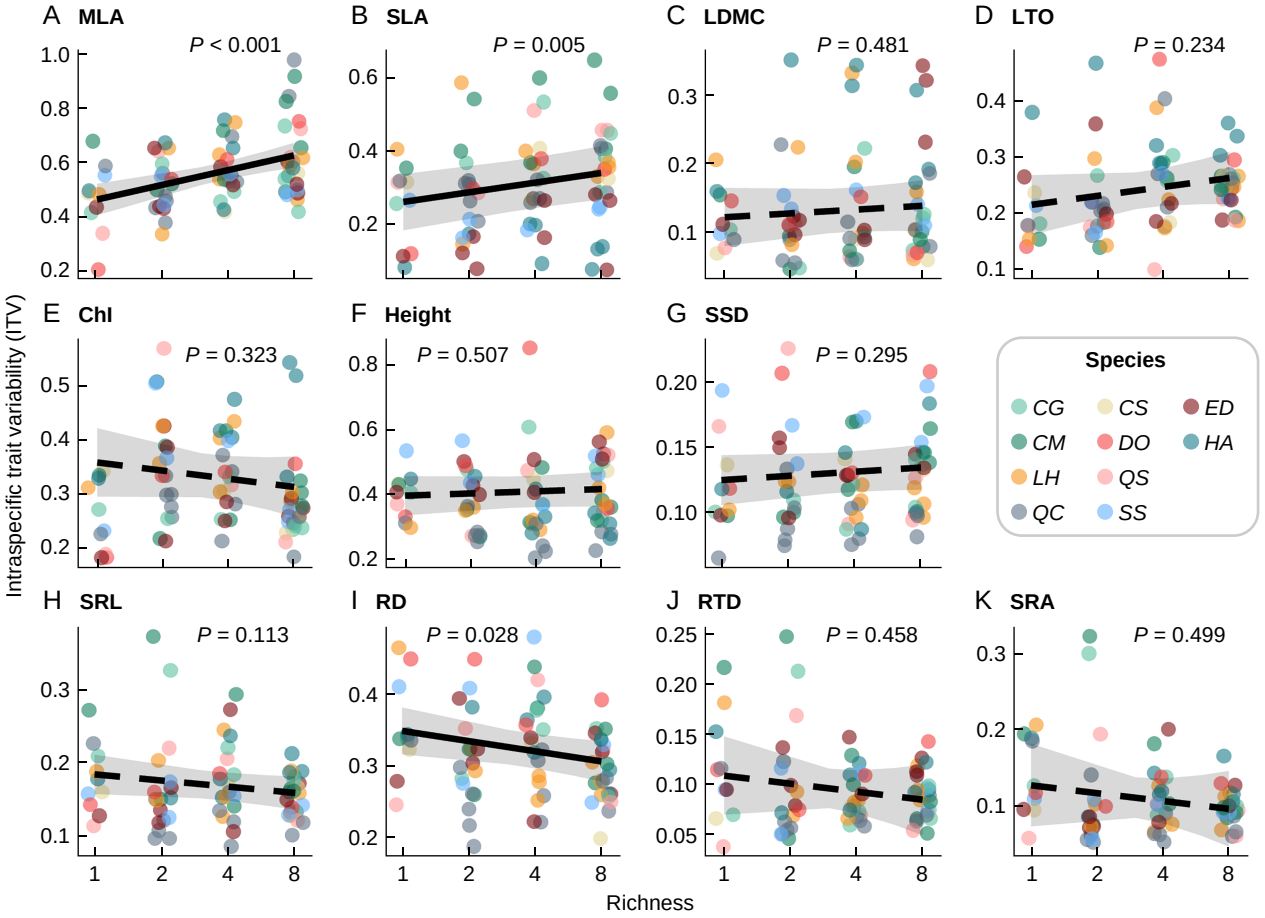

FIG. 2. Relationships between species richness and intraspecific variability in individual functional traits. (A–G) Relationships are shown for seven above-ground traits: (A) mean leaf area (MLA); (B) specific leaf area (SLA); (C) leaf dry matter content (LDMC); (D) leaf toughness (LTO); (E) chlorophyll content (Chl); (F) plant height; and (G) stem specific density (SSD). (H–K) Relationships are also shown for four below-ground fine-root traits: (H) specific root length (SRL); (I) root diameter (RD); (J) root tissue density (RTD); and (K) specific root area (SRA). Each point represents the ITV of one species within a given species richness and composition treatment, with colours identifying the ten focal species. Lines and grey shading show predictions and 95 % confidence intervals, respectively, from the final linear mixed-effects models. All models included species identity as a random intercept; model-specific random-effect structures are reported in Supplementary Data Table S1. Solid lines denote relationships with $P < 0.05$, whereas dashed lines denote relationships with $P \geq 0.05$. Model-derived P-values for the fixed effect of $\log_2$-transformed species richness are shown in each panel. Species richness is displayed on a $\log_2$-scaled axis.

explained 66.2 and 99.3 % of the total variation in above- and below-ground traits, respectively (Supplementary Data Fig. S1). At the multidimensional level, species richness had no significant effect on either above- or below-ground ITV ($P = 0.271$ and $P = 0.163$, respectively; Fig. 1A, B). When the functional axes were analysed separately, above-ground ITV tended to increase with richness along PC1, representing the leaf-economics spectrum associated with SLA, MLA and LDMC (*slope* = 0.286, $P = 0.074$; Fig. 1C; Supplementary Data Fig. S1A). No effect was detected along above-ground PC2, representing plant size and structural traits ($P = 0.921$; Fig. 1E; Supplementary Data Fig. S1A). Below-ground ITV was unrelated to richness along either PC1, primarily associated with SRA and RTD ($P = 0.213$; Fig. 1D; Supplementary Data Fig. S1B), or PC2, associated with RD and SRL ($P = 0.936$; Fig. 1F; Supplementary Data Fig. S1B).

Single-trait analyses revealed more specific responses to species richness (Fig. 2). Above-ground ITV increased for MLA (*slope* = 0.079, $P < 0.001$) and SLA (*slope* = 0.038, $P = 0.005$), whereas no significant effects were detected for LDMC, LTO, chlorophyll content, height or stem specific density (Fig. 2A–G). Among below-ground traits, ITV decreased for root diameter (*slope* = −0.021, $P = 0.028$), whereas specific root length, root tissue density and specific root area showed no significant responses (Fig. 2H–K). When all standardized ITV metrics were analysed jointly, the average effect of richness on above-ground ITV was positive but not significant (*slope* = 0.217, $P = 0.060$; Supplementary Data Table S2). Importantly, the richness × compartment interaction was significant (slope difference = −0.424, $P < 0.001$), showing that the average effect of richness on ITV was lower below- than above-ground. Species-specific regressions broadly supported this contrast: relationships along the above-ground leaf-economics axis were predominantly positive, whereas below-ground relationships were more heterogeneous in direction and magnitude (Supplementary Data Figs S2 and S3).

Biomass inequality increased with species richness in both plant compartments (Fig. 3). The corrected Gini coefficient increased for above-ground biomass (*slope* = 0.067,

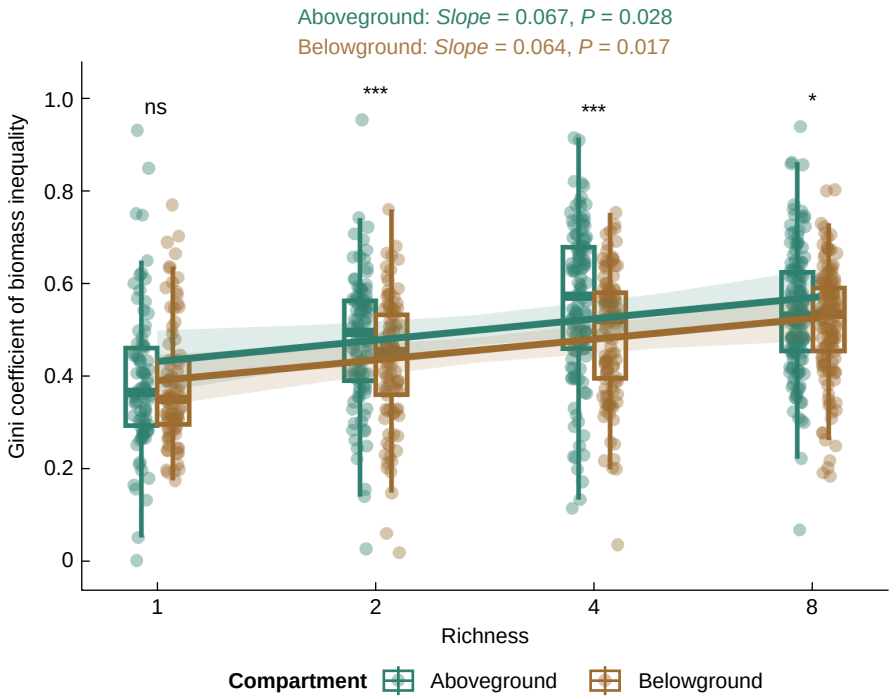

FIG. 3. Asymmetry in above-ground versus below-ground competition along species richness gradients. Each point shows the bias-corrected Gini coefficient of biomass inequality (Weiner and Solbrig, 1984), calculated separately for the above- and below-ground compartments within a single pot ($n = 80$, 108, 120 and 144 pots at richness levels 1, 2, 4 and 8, respectively); boxplots summarize the distribution at each richness level, with teal and brown denoting the above- and below-ground compartments, respectively. Lines and shading show model predictions ± 95 % confidence intervals from linear mixed-effects models with species composition as a random intercept; slope estimates and *P*-values for the effect of richness on each compartment are given in the corresponding colour. Asterisks above each richness level indicate the significance of a paired *t*-test comparing above- and below-ground Gini coefficients within the same pots (ns, $P \geq 0.1$; $\cdot P < 0.1$; $^{*}P < 0.05$; $^{***}P < 0.001$). Species richness is displayed on a $\log_2$-scaled axis.

$P = 0.028$) and below-ground biomass (*slope* = 0.064, $P = 0.017$). Paired comparisons further showed greater above- than below-ground biomass inequality at richness levels 2, 4 and 8, but not in monocultures (Fig. 3). Thus, biomass became increasingly unevenly distributed among individuals in both compartments, with generally greater above-ground inequality in species mixtures. A complementary sum-of-squares partition showed that within-species squared deviations decreased with richness for above-ground (*slope* = −1.488, $P = 0.017$) and below-ground biomass (*slope* = −1.533, $P = 0.038$), whereas the between-species fraction of total squared deviations increased in both compartments (above-ground: *slope* = 0.384, $P < 0.001$; below-ground: *slope* = 0.397, $P < 0.001$; Fig. 4). Thus, an increasing share of the observed biomass heterogeneity was associated with differences among species at higher richness.

Species richness was also associated with shifts in several species-level mean traits (Fig. 5). Above-ground mean MLA (*slope* = 0.250, $P = 0.028$), SLA (*slope* = 0.286, $P = 0.010$) and PC1 scores (*slope* = 0.323, $P = 0.002$) increased with richness, whereas mean LTO (*slope* = −0.112, $P < 0.001$) and SSD (*slope* = −0.328, $P = 0.004$) decreased. Mean LDMC showed a marginal decrease with richness (*slope* = −0.112, $P = 0.059$), whereas chlorophyll content, height and above-ground PC2 showed no significant responses. Below-ground mean SRL (*slope* = −0.134, $P = 0.017$) and PC2 scores (*slope* = −0.197, $P < 0.001$) decreased with richness, whereas mean RD increased (*slope* = 0.201, $P < 0.001$). No significant effects were detected for RTD, SRA or below-ground PC1. Overall, the richness-related shifts in mean traits differed between above- and below-ground compartments.

DISCUSSION

This study demonstrates that species richness modulates above- and below-ground ITV differentially, revealing a decoupling between the two plant compartments. Above-ground ITV increased significantly for key leaf traits and showed a positive tendency along the leaf-economics axis, whereas below-ground ITV decreased for root diameter and exhibited greater species-specific heterogeneity. The significant richness × compartment interaction supported this contrast. These patterns suggest that different assembly processes might shape ITV across plant compartments and functional dimensions. Beyond ITV, species richness also shifted species-level mean trait values, indicating coordinated changes in both the variability of selected traits and the central tendency of trait distributions.

The increase in ITV of leaf-economic traits with species richness is consistent with the competitive hierarchy hypothesis, which proposes that asymmetric competition can promote trait differentiation (Weiner, 1990). Above-ground biomass inequality increased with richness and was generally greater than below-ground inequality in species mixtures, consistent with a more pronounced size hierarchy in the

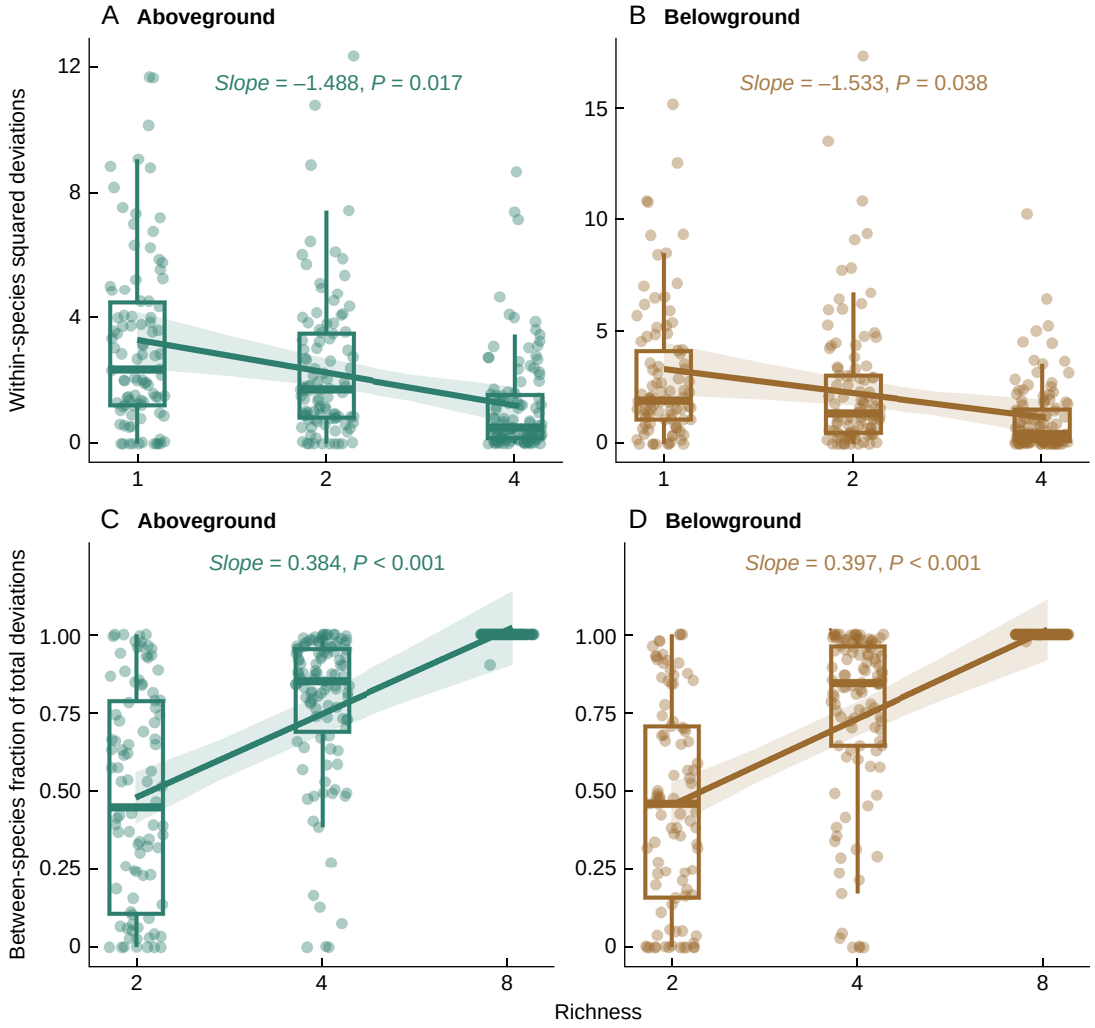

FIG. 4. Partitioning of observed squared deviations in individual biomass across species richness levels. (A, B) Sum of squared deviations in $\log_2$-transformed biomass among conspecific individuals within each pot at richness levels 1, 2 and 4 for above- (A) and below-ground biomass (B). (C, D) Fraction of the total squared deviations assigned to differences among species, calculated as the between-species sum of squared deviations divided by the sum of the between- and within-species squared deviations, at richness levels 2, 4 and 8 for above- (C) and below-ground biomass (D). Each point represents one pot. In eight-species pots, each species was represented by one individual; consequently, the within-species component was zero, and the fraction assigned to differences among species equalled one by construction. These observations were included in the mixed-effects analysis. Species richness is displayed on a $\log_2$-scaled axis.

canopy (Fig. 3). During competition for light, taller or better-positioned individuals can shade shorter neighbours without equivalent reciprocal effects, creating size-asymmetric competition for light (Del Río *et al.*, 2014; DeMalach *et al.*, 2016). Such asymmetric interactions might generate heterogeneous light environments and thereby contribute to differentiation in leaf strategies within populations, consistent with previous evidence linking competitive position to intraspecific variability (DeMalach *et al.*, 2017; Guo *et al.*, 2017; Yang *et al.*, 2024). Accordingly, ITV increased significantly for specific leaf area and leaf area, while ITV along the leaf-economics axis showed a positive tendency that was broadly supported by the species-specific relationships (Figs 1 and 2). In contrast, multidimensional above-ground ITV and ITV along the plant size and structural axis showed no detectable relationships with richness, indicating that the above-ground response was concentrated in leaf-economic traits. At the same time, species-level mean above-ground traits also shifted towards a more acquisitive strategy, with increasing specific leaf area and leaf area and decreasing LTO and stem specific density (Fig. 5). Thus, increasing richness was associated with both enhanced variability in selected leaf-economic traits and a directional shift in the central tendency of above-ground trait distributions, consistent with a coordinated response to increasing competition for light (Bittebiere *et al.*, 2012; Mahaut *et al.*, 2023).

Below-ground competition exhibited a more complex pattern. Although below-ground biomass inequality was generally lower than above-ground inequality in species mixtures, the below-ground Gini coefficient also increased significantly with species richness (Fig. 3). This increase indicates that below-ground biomass became progressively more unevenly distributed among individuals and is consistent with below-ground competition not being entirely size

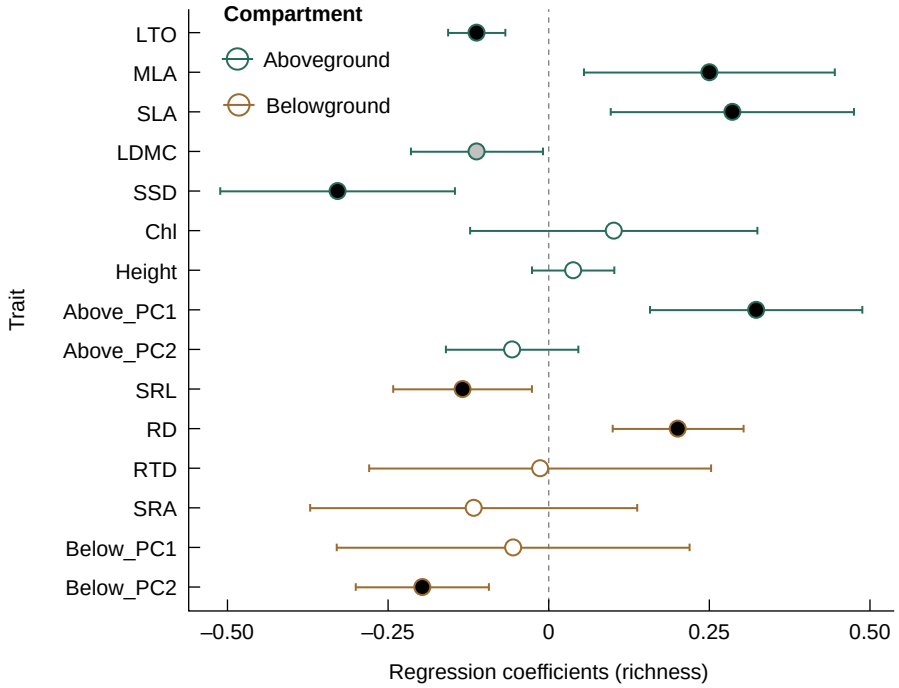

FIG. 5. Effects of species richness on species-level mean functional traits. Effects of species richness on mean trait values of 11 functional traits and principal component axes, estimated from linear mixed-effects models. The horizontal axis represents regression coefficients (estimate) of log-transformed species richness. The vertical axis lists traits and principal component axes in the order shown in the figure: leaf toughness (LTO), mean leaf area (MLA), specific leaf area (SLA), leaf dry matter content (LDMC), stem specific density (SSD), chlorophyll content (Chl), height (Height), Above_PC1, Above_PC2, specific root length (SRL), root diameter (RD), root tissue density (RTD), specific root area (SRA), Below_PC1 and Below_PC2. Above- and below-ground traits are shown in teal and brown, respectively. Points represent estimated effect sizes of species richness on mean trait values, and horizontal error bars indicate 95 % confidence intervals (±1.96 s.e.). The vertical dashed line at zero indicates no effect of species richness. Symbols with black centres denote statistically significant effects ($P < 0.05$), symbols with grey centres denote relationships with $0.05 \leq P < 0.1$, and open symbols denote non-significant effects ($P \geq 0.1$). Positive coefficients indicate increasing mean trait values with species richness, whereas negative coefficients indicate decreasing trends.

symmetric (Schwinning and Weiner, 1998; Mayfield and Levine, 2010). The sum-of-squares partition showed that within-species squared deviations in below-ground biomass decreased with richness, whereas the between-species fraction of total squared deviations increased significantly (Fig. 4). Thus, at higher richness, a greater share of below-ground biomass heterogeneity was associated with differences among species. This reorganization coincided with increasing biomass inequality among individuals, indicating that species richness altered both the degree and the structure of below-ground biomass heterogeneity.

Among the below-ground traits examined, only ITV in root diameter decreased significantly with species richness, whereas ITV in specific root length, root tissue density and specific root area, in addition to multidimensional and PC axis ITV, showed no detectable relationships with richness (Figs 1 and 2). The decrease in root diameter ITV suggests increasing constraints on the range of diameter-related strategies expressed within species, providing trait-specific evidence consistent with niche packing below-ground (MacArthur and Levins, 1967; Cahill and McNickle, 2011). One possible explanation is that complementary resource use in species-rich communities might have promoted more complete exploitation of soil resources, thereby intensifying resource limitation along particular root trait dimensions (Flombaum and Sala, 2012; Siebenkäs *et al.*, 2016; Shen *et al.*, 2022). Root diameter and specific root length jointly describe a root collaboration gradient, ranging from autonomous soil exploration by roots with high specific root length to outsourcing strategies associated with thicker roots and greater potential for mycorrhizal resource acquisition (Bergmann *et al.*, 2020). At the level of mean trait values, root diameter increased whereas specific root length decreased with richness (Fig. 5), indicating a shift towards thicker roots with lower specific root length (Yang *et al.*, 2026). Root diameter therefore changed in both its mean and ITV, whereas specific root length shifted in its mean but not in ITV. Root tissue density changed in neither its mean nor ITV, providing little evidence for a coordinated response along the tissue-conservation dimension (Fort *et al.*, 2014; Weemstra *et al.*, 2016; Erktan *et al.*, 2023). These contrasting responses indicate that support for below-ground niche packing was confined to particular root trait dimensions, potentially reflecting differences in their ecological functions (Bruelheide *et al.*, 2018; Carvajal *et al.*, 2019; Freschet *et al.*, 2021). Overall, richness shifted the position of below-ground trait distributions along the root collaboration gradient while selectively reducing variation in root diameter, with no detectable change in multidimensional ITV (Mason *et al.*, 2011; Carvajal *et al.*, 2019).

Several limitations define the scope of these findings. First, the experiment was conducted with tree seedlings in

controlled pot conditions. Although all richness treatments shared the same pot volume, planting density and soil conditions, thereby facilitating controlled comparisons, restricted rooting volume might have constrained below-ground development, and responses of adult trees in field conditions might differ from those observed here. Second, our focus on macroscopic morphological traits might not fully capture the physiological, anatomical and symbiotic processes underlying plant competition (Shipley *et al.*, 2016). Below-ground competition strategies often manifest in anatomical structures (e.g. vessel diameter) or physiological processes (e.g. root exudates), rather than purely morphological indicators (Kirfel *et al.*, 2017; Han *et al.*, 2025). Future research should integrate long-term field monitoring with analyses of root physiology and mycorrhizal fungal communities to assess the effects of biodiversity on whole-plant functional traits more comprehensively. Third, this experiment was conducted during seedling stages, although the resource allocation strategies and competitive abilities of trees undergo significant changes throughout their life histories. Adult plant responses to biodiversity might differ from those observed in seedlings. Future studies should expand to different life-history stages to examine how trait responses evolve with plant development.

Conclusion

In summary, this study provides experimental evidence that species richness shapes plant ITV in an organ- and trait-specific manner, revealing a decoupled pattern between above- and below-ground responses. Above-ground ITV responses were concentrated along the leaf-economics dimension and were predominantly positive across species, whereas below-ground responses were more heterogeneous, with a reduction in ITV confined to root diameter. This organ specificity extended to the central tendency of trait distributions: above-ground traits shifted towards greater resource acquisition, while below-ground traits shifted towards thicker roots with lower specific root length. These changes occurred alongside increasing biomass inequality in both compartments, indicating that richness simultaneously reshaped trait distributions and community size structure. The contrasting responses are consistent with evidence that root morphological strategies can be partly decoupled from whole-plant economic spectra and respond to environmental conditions differently from above-ground traits (Shen *et al.*, 2019). Together, these findings suggest that competitive hierarchy and niche-related constraints leave distinct signatures across plant organs and functional dimensions. Recognizing this organ specificity will be essential for developing a whole-plant understanding of how biodiversity reorganizes functional strategies and competitive structure within communities (Yang *et al.*, 2026).

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Table S1: random-effect structure selection for the intraspecific trait variability (ITV) metrics presented in Figs 1 and 2 and for the species-level mean trait values presented in Fig. 5. Table S2: statistical results of the linear mixed-effects model testing the divergence between above- and below-ground intraspecific trait variation responses to species richness. Figure S1: principal component analysis of functional traits. Species distribution patterns in multidimensional trait space for above- (A) and below-ground traits (B). Figure S2: species-specific relationships between species richness and above- and below-ground intraspecific trait variability (ITV). Figure S3: species-specific relationships between species richness and intraspecific variability in individual functional traits.

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DATA AVAILABILITY

The individual-level trait and biomass data, together with the complete R code used for all analyses and figure generation, are openly available on GitHub at https://github.com/Jingyangecnu/AoB-decoupling-ITV-richness.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Guochun Shen and Jing Yang conceived and designed the study and established the experimental system. Xiya Wang, Congling Zhang, Jia Yao and Jing Yang collected the data. Jing Yang and Jia Yao curated and analysed the data. Jia Yao, Jing Yang and Guochun Shen drafted the manuscript. Jing Yang led the additional statistical analyses, revision of the manuscript and preparation of the response to reviewers. All authors reviewed and approved the final version of the manuscript.

AI USE

ChatGPT (GPT-5.5) was used to assist with English language polishing during the preparation of this revised manuscript. The authors reviewed all AI-assisted edits to ensure that the scientific content and meaning were not altered.

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