Title: Climate and soil nutrients drive global variations in community-level root nutrient acquisition strategies

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Abstract

Fine root traits critically regulate resource acquisition and ecosystem nutrient cycling. Despite their importance as integrated indicators of plant responses to environmental shifts, community-level adaptations of fine root traits to global climate and soil nutrient gradients remain poorly understood. This study synthesizes data from 301 natural communities worldwide to examine the mechanisms driving fine root trait variation across different community types. Our findings demonstrate distinct regulatory pathways: precipitation negatively correlates with root tissue density, reflecting optimized resource capture in humid environments, whereas in arid regions, higher root tissue density enhances resilience by increasing structural stability and

prolonging root lifespan to cope with resource scarcity. Additionally, temperature-driven phosphorus limitation reduces root phosphorus content. Soil nutrient enrichment promotes thinner roots and elevated specific root length, indicative of autonomous nutrient acquisition strategies, while nutrient scarcity favors thicker roots and reduced specific root length, signifying increased mycorrhizal dependence. The divergent patterns of root nitrogen content in relation to soil nitrogen between grasslands and forests suggest that grasslands employ an "acquisitive" nutrient acquisition strategy, while forests adopt a more "conservative" approach. Principal component analysis reveals coordinated variation in community-level root traits, challenging the universality of the species-level root economics space. This study emphasizes the integrated responses of community-level root traits, offering new insights into plant resource economics in the context of global environmental change.

Keywords: Plant community, fine root traits, environmental factors, nutrient acquisition strategies, root economic space

Introduction

Fine roots serve as the primary organs for underground resource acquisition and play a pivotal role in regulating carbon allocation patterns and nutrient uptake efficiency, fundamentally influencing the productivity and material cycling of forest ecosystems (Jackson et al., 1997; Hou et al., 2024). While much research has explored species- or individual-level adaptations of root traits (Carmona et al., 2021; Laughlin et al., 2021), ecosystem functions emerge from integrated multispecies interactions and environmental filtering at the community level (Pasari et al., 2013). Unlike species-level trait variation, coordinated trait divergence at the community scale better reflects the holistic response of plant functional groups to heterogeneous environments (Bruelheide et al., 2018). Particularly under global climate change and soil nutrient restructuring, elucidating environmental drivers of community-level root traits provides critical parameters for predicting ecosystem cascading effects (Riva et al., 2023).

Climate and soil nutrients drive the adaptive evolution of root traits through dual pathways. Among climate factors, precipitation and temperature influence root construction strategies by regulating soil water availability: in warm, moist climates, plants increase root and vessel diameters while reducing specific root length (SRL) to enhance water and nutrient uptake (Chen et al., 2013; Kong et al., 2021); in arid regions, high root tissue density (RTD) extends lifespan to withstand stress (Gu et al., 2014; Valverde-Barrantes et al., 2017; Laughlin et al., 2021); and in cold environments, finer roots with higher SRL expand soil exploration (Zadworny et al.,

2017; Guo et al., 2024). Temperature further influences root chemistry by affecting metabolic rates, with low temperatures elevating root nitrogen content (RNC) to sustain enzyme activity and high temperatures reducing phosphorus content due to enhanced soil leaching (Yuan et al., 2011).

Soil nutrient availability—nitrogen, phosphorus, their forms (e.g., ammonium, available phosphorus), and pH—directly affects root morphology and chemical traits. In high-nutrient environments, RD decreases while SRL increases to facilitate the production of more root length per unit resource investment (Fort & Freschet, 2020), with elevated nutrient levels also enhancing RNC and root phosphorus content (RPC) to boosts metabolic efficiency—a strategy reflecting “self-reliant rapid resource acquisition” under resource-rich conditions (Ding et al., 2020; Yan et al., 2022). While phosphorus limitation reduces RPC, increases the N/P ratio, and promotes thicker roots and higher SRL to enhance mycorrhizal associations (Kong et al., 2014; Addo-Danso et al., 2020). Soil pH further indirectly influences root traits by regulating nutrient form transformations (e.g., inhibiting nitrification) and microbial activity (Liu et al., 2022).

The species-level "root economics space" hypothesis posits trade-offs between rapid acquisition (higher RNC, lower RTD) and conservative storage (lower RNC, higher RTD), and between mycorrhizal dependence (smaller RD, lower SRL) and autonomous absorption (larger RD, higher SRL) (Bergmann et al., 2020). However, community-level trait integration may diverge from this framework (Bruelheide et al., 2018; Luo et al., 2021). The limiting similarity hypothesis suggests coexisting species

differentiate traits to reduce competition (MacArthur & Levins, 1967), while the habitat filtering hypothesis predicts trait convergence in harsh environments (Westoby & Wright, 2006). Thus, understanding community-scale integrated traits at the community level can clarify how species interactions and environmental pressures shape plant resource economics.

This study integrates data from 301 natural communities worldwide to address two questions: (1) How do climate and soil nutrients influence fine root traits at community-level? (2) Do community-level trait trade-offs align with the species-level root economics space? By analyzing responses to climate-soil gradients, we aim to characterize community-level root economics and inform ecological modeling and adaptation predictions.

Methods

We systematically searched Web of Science, Google Scholar, and China National Knowledge Infrastructure (CNKI) databases for studies on fine root traits published up to December 2024, using keywords like "fine roots," "root diameter," "specific root length," "root tissue density," "root nitrogen content," "root phosphorus content," and their Chinese equivalents. Studies were selected based on: (1) field-based observational data from natural communities, excluding greenhouse, pot, or heavily disturbed sites; (2) fine roots (diameter ≤2 mm) sampled at the community level via soil cores, root growth cores, or soil pits, not species-weighted means; (3) inclusion of at least one morphological or chemical trait; (4) reported geographic, community,

climate, and soil nutrient data; and (5) use of control data only from experimental studies. This yielded 301 sites from 101 papers, spanning forests (n=194), shrubs (n=12), and grasslands (n=95) (Figure S1).

Trait data were log-transformed to ensure normality. We applied analysis of variance (ANOVA) with Tukey's test to assess trait differences across community types, subdividing forests and grasslands into biomes (e.g., tropical rainforest, temperate forest, boreal forest; tropical grassland, temperate grassland, tundra) for divergence analysis. Correlation and regression models evaluated the effects of climate (temperature, precipitation) and soil nutrients (nitrogen, phosphorus, pH) on traits. Principal component analysis (PCA) explored community-level root economics space using diameter, specific root length, tissue density, and nitrogen content. Analyses were conducted in R 4.3.1.

Results

Community-level fine root trait differentiation

Fine root traits varied significantly across vegetation types. Root diameter (RD) ranged from 0.25–0.90 mm (forests), 0.40–0.60 mm (shrubs), and 0.15–0.50 mm (grasslands); specific root length (SRL) from 5–50 $m \cdot g^{-1}$, 10–25 $m \cdot g^{-1}$, and 5–100 $m \cdot g^{-1}$; and root tissue density (RTD) from 0.15–0.60 $g \cdot cm^{-3}$, 0.15–0.70 $g \cdot cm^{-3}$, and 0.10–0.50 $g \cdot cm^{-3}$, respectively (Figures 1a–c). Grasslands had smaller RD and higher SRL than forests and shrubs, with no significant differences in RTD.

Root nitrogen content (RNC) ranged from 5–15 $mg \cdot g^{-1}$ across vegetation types,

while root phosphorus content (RPC) ranged from 230–1000 $mg \cdot kg^{-1}$ (forests), 350–450 $mg \cdot kg^{-1}$ (shrubs), and 350–600 $mg \cdot kg^{-1}$ (grasslands). The N/P ratio was higher in forests (10–40) than grasslands (5–15), with shrubs intermediate (Figures 1d–f).

Biome-level analyses further demonstrated that tropical rainforests exhibited larger RD than temperate grasslands, whereas tropical grasslands and tundra showed greater SRL than temperate grasslands and forests. Boreal forests also had higher RNC than temperate forests and grasslands (Figure S2).

Climate and nutrient effects on root morphological traits

Climate and soil nutrients influenced root morphology distinctly. Higher precipitation reduced RTD globally (R^2=0.15, $p<0.001$) and across forests (R^2=0.12, $p<0.01$), grasslands (R^2=0.33, $p<0.01$), and shrubs (R^2=0.55, $p<0.05$) (Figures 2a–d), with grasslands RD negatively correlated with precipitation (R^2=0.17, $p<0.05$) (Figure S3a). Temperature negatively affected RTD only in shrubs (R^2=0.57, p<0.05) (Figure S3b).

Soil ammonium nitrogen (NH_4^+) content inversely correlated with global RD (R^2=0.51, $p<0.01$), and forests RD decreased with total phosphorus content (R^2=0.25, $p<0.05$) (Figures 3a–b). Forests SRL increased with soil nitrogen (R^2=0.14, $p<0.01$) and available phosphorus content (R^2=0.39, $p<0.05$) (Figures 3c–d), while grasslands RD rose with soil pH (R^2=0.31, $p<0.01$) (Figure S4).

Climate and nutrient effects on root chemical traits

Higher temperatures reduced fine RPC globally (R^2 = 0.20, $p < 0.01$) and in

forests (R^2 = 0.18, $p < 0.01$; Figures 4a–b), concurrently lowering N/P ratios (global: R^2 = 0.28; forests: R^2 = 0.56; $p < 0.01$; Figures 4c–d). Besides, grasslands RNC decreased with temperature (R^2=0.26, $p<0.01$) (Figure S5).

Forests RNC inversely correlated with soil nitrogen (R^2=0.27, $p<0.01$), while grasslands RNC rose (R^2=0.32, $p<0.01$), yielding no global correlation (Figures 5a–c). global RPC increased with soil phosphorus (global: R^2=0.46, $p<0.01$) and nitrogen content (global: R^2=0.23, $p<0.05$; forests: R^2=0.25, $p<0.05$) (Figures 5d–f). The N/P ratio decreased with soil nitrogen (R^2=0.22, $p<0.05$) and phosphorus content (R^2=0.31, $p<0.01$) but increased with soil N/P (R^2=0.65, $p<0.05$) (Figures 5g–i). Soil pH negatively influenced global (R^2 = 0.17, $p < 0.01$) and forest (R^2 = 0.22, $p < 0.01$) RNC (Figure S6).

Coordinated variation of fine root traits

At the community scale, morphological and chemical traits showed coordinated variation. RD inversely correlated with SRL (r = −0.59, $p < 0.001$) and RTD (r = −0.23, $p < 0.05$; Figure 6a). RNC positively correlated with RPC (r = 0.43, p < 0.01) but negatively with N/P ratio (r = −0.35, $p < 0.05$), while RPC also inversely related to N/P ratio (r = −0.35, $p < 0.05$). Morpho-chemical linkages included RD's negative correlation with RNC (r = −0.60, $p < 0.001$) and positive correlation with N/P ratio (r = 0.43, $p < 0.05$), alongside RTD's positive relationship with N/P ratio (r = 0.50, $p < 0.05$). Principal component analysis (PCA) revealed community-level traits diverged from species-level root economics space: PC1 (48% variance) loaded on RD, RTD, and RNC, while PC2 (25%) linked SRL and RNC (Figure 6b).

Discussion

Climate and nutrient-driven adaptive strategies

Precipitation and temperature differentially shape fine root traits. Increased precipitation reduced root tissue density (RTD) globally and across vegetation types (Figure 2), likely due to looser root structures in wet environments enhancing resource uptake (Chen et al., 2013; Gu et al., 2014; Kong et al., 2014). In arid regions, higher RTD bolsters resilience (Laughlin et al., 2021). Grassland root diameter (RD) decreased with precipitation (Figure S3a), unlike the species-level trend (Freschet et al., 2017; Ding et al., 2020, 2023), possibly reflecting larger diameters in drier conditions for hydraulic safety (O'Keefe et al., 2022).

Temperature mainly affected chemical traits, reducing root phosphorus content (RPC) and N/P ratios globally and in forests (Figure 4) due to leaching-induced phosphorus limitation in warm climates (Du et al., 2020), where plants prioritize phosphorus allocation to metabolic processes (e.g., ATP synthesis) over storage (Vitousek et al., 2010). Grassland root nitrogen content (RNC) declined with temperature (Figure S5), possibly due to increased microbial nitrogen availability, while colder environments elevated nitrogen for physiological efficiency (Yuan et al., 2011). Biome comparisons showed larger RD in tropical rainforests and higher specific root length (SRL) in tundra versus temperate forests (Figure S2), reflecting cold-adapted nutrient uptake strategies. Biome-specific adaptations are evident: tropical rainforests' thicker roots and tundra's thinner roots (Figure 1) reflect

divergent strategies for nutrient acquisition—thicker roots for mycorrhizal cooperation vs. longer roots for expanded soil exploration (Zadworny et al., 2017; Guo et al., 2024).

Soil nutrient gradients drive coordinated morphological-chemical adaptations. High nutrient availability promotes thinner roots and higher SRL (Figure 3), indicating a shift toward autonomous nutrient acquisition via reduced mycorrhizal dependence (Kong et al., 2014; Ma et al., 2018). Conversely, nutrient depletion led to thicker roots and lower SRL, indicating greater dependence on mycorrhizal fungi (Kong et al., 2014; Ma et al., 2018). Grassland RD increased with soil pH (Figure S4), possibly linked to thicker roots in arid, high-pH soils coping with nutrient stress (Lambers et al., 2008).

Contrasting RNC responses between forests and grasslands (Figure 5b–c) underscore fundamental strategy differences: Grasslands' "fast acquisition" (positive soil N correlation) aligns with rapid nutrient exploitation in competitive environments, while forests' "conservative" strategy (negative soil N correlation) suggests metabolic optimization under variable nitrogen availability (Freschet et al., 2017). Global RPC's positive correlation with soil nitrogen and phosphorus content (Figures 5d–f) supports the nutrient synergy hypothesis, where nitrogen enrichment enhances phosphorus mineralization via microbial phosphatase activity (Harpole et al., 2011). Lower soil pH correlated with higher RNC (Figure S6), reflecting mycorrhizal reliance in acidic, ammonium-rich soils (Smith & Read, 2010).

Vegetation-Type differentiation

Significant differences in fine root traits between forests and grasslands reflect divergent survival strategies. Grasslands' "acquisitive" strategy (thinner roots, higher SRL and RNC; Figure 1) enables rapid resource exploitation in nutrient-poor or disturbed environments through short root lifespans and high turnover (Freschet et al., 2017). For example, tundra grasslands' high SRL and RNC enhance cold-region nutrient acquisition while avoiding significant resource losses during winter' falling (Wang et al., 2019). In contrast, forests' "conservative" strategy (thicker roots, lower SRL and RNC; Figure 1) ensures long-term persistence and promotes stronger mycorrhizal fungal cooperation in competitive environments (Ma et al., 2018). Moreover, the higher N/P ratios observed in forests (Figure 1f) underscore a stronger phosphorus limitation in woody ecosystems (Vitousek et al., 2010). Finally, the intermediate traits of shrubs (Figure 1) likely reflect their transitional ecological niche, balancing the rapid resource exploitation of herbaceous species with the long-term survival of woody species—a hypothesis that warrants further validation with larger shrub datasets (Eldridge et al., 2011).

Community-Level root economics

Community-level traits did not mirror species-level root economics space (Figure 6b). Strong trait correlations (Figure 6a) suggest species-level trade-offs do not scale directly (Riva et al., 2023). Limiting similarity may drive convergence of fine root traits in forests—for example, differences among forests' biomes are less pronounced than those seen at the species-specific level (Chen et al., 2013, Ma et al., 2018), while filtering in tundra and tropical grasslands converges traits like high SRL (Figure S2),

highlighting the role of species interactions and environmental pressures (MacArthur & Levins, 1967; Westoby & Wright, 2006).

Conclusion

This study demonstrates that climate and soil nutrients drive community-level fine root traits through distinct pathways, with precipitation enhancing resource capture via lower tissue density and temperature reducing phosphorus content in warm climates. Nutrient-rich soils foster self-reliant strategies, while scarcity enhances mycorrhizal reliance. Grasslands adopt an "acquisitive" approach, contrasting with forests' "conservative" strategy, reflecting evolutionary trade-offs. Community-level traits diverge from species-level economics space, shaped by filtering and limiting similarity. These findings refine our understanding of plant resource economics and inform ecological modeling under global change.

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Author contributions

H.G. conceived the idea and performed the data analysis. H.G. and Y.Z. wrote the manuscript. Y.Z., L.W., and X.Q.C substantially contributed to revisions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Supplementary data to this article can be found online.

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Figures

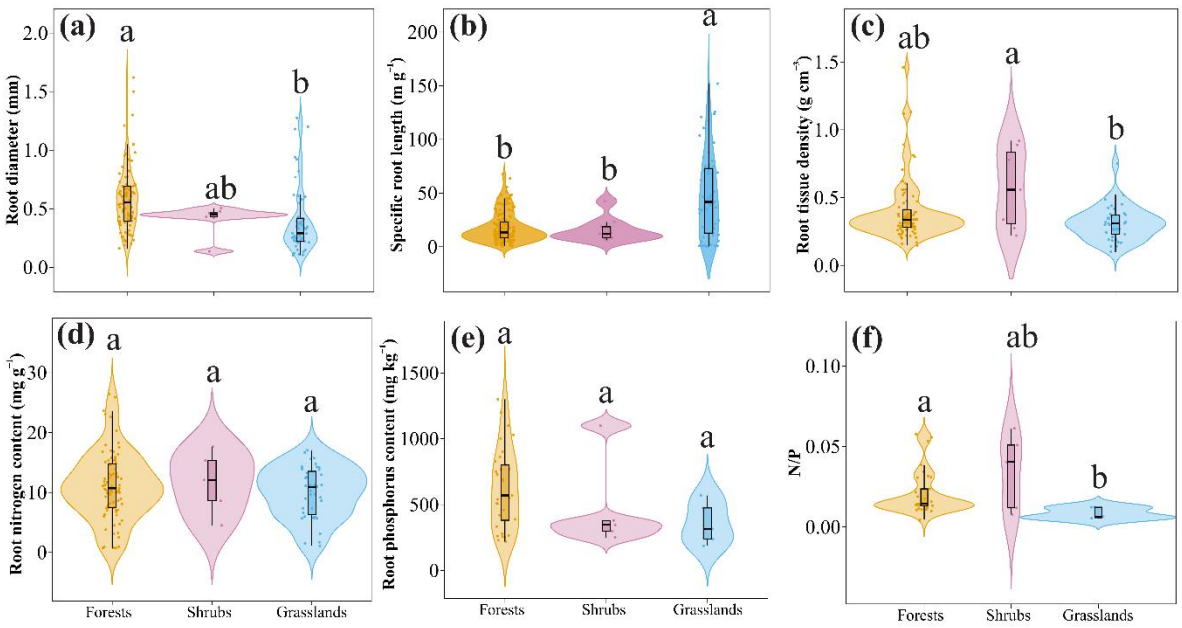

Figure 1 Comparison of fine root traits across different vegetation types

panel (a-c) shows morphological traits, panel (d-f) shows chemical traits

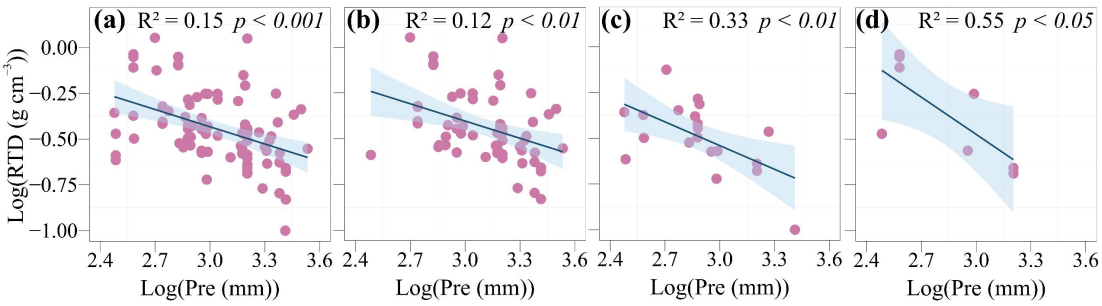

Figure 2 Effects of precipitation (Pre) on fine root tissue density (RTD)

Panel (a) shows Global, (b) Forests, (c) Grasslands, (d) Shrubs, RTD

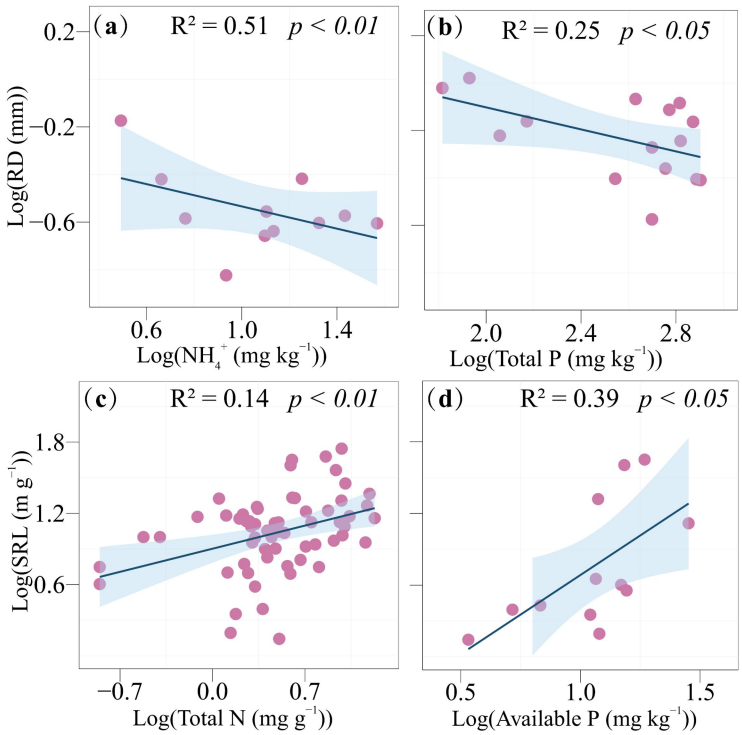

Figure 3 Effects of soil nitrogen and phosphorus on fine root morphological traits

Panel (a) Global NH_4^+ and root diameter (RD), (b) Forest phosphorus content and root diameter, (c) Total nitrogen and forests specific root length (SRL), (d) Available phosphorus and forests specific root length

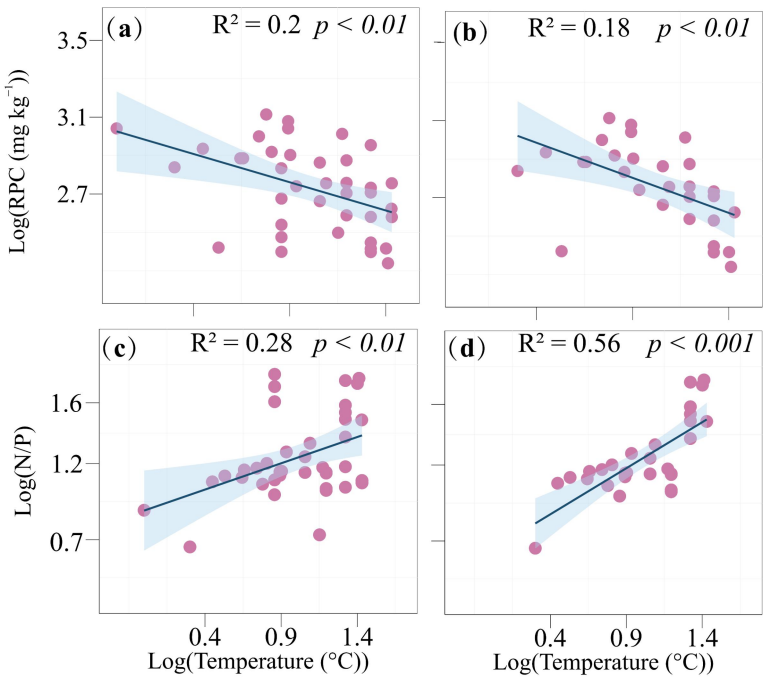

Figure 4 Effects of temperature on fine root phosphorus content and N/P ratio

Panel (a) Global fine root phosphorus content (RPC), (b) Forests fine root phosphorus content, (c) Global fine root N/P ratio, (d) Forests fine root N/P ratio

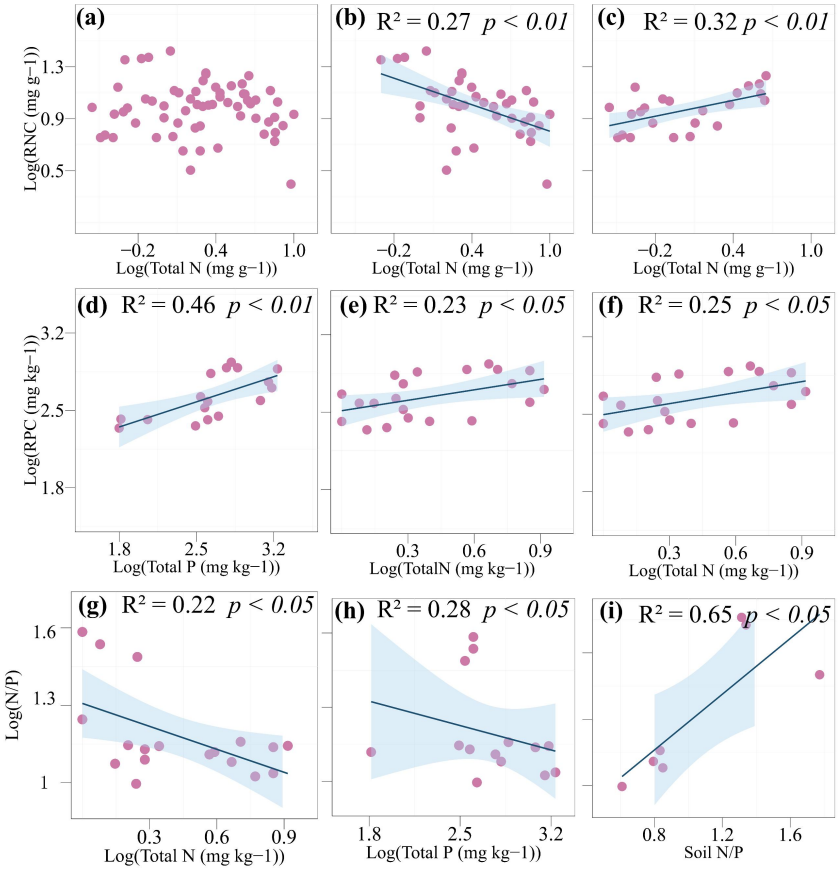

Figure 5 Effects of Soil Nitrogen and Phosphorus on Fine Root Chemical Traits

Panel (a) Global soil nitrogen and fine root nitrogen (RNC), (b) Forest soil nitrogen and fine root nitrogen, (c) Grassland soil nitrogen and fine root nitrogen, (d) Global soil phosphorus and fine root phosphorus content (RPC), (e) Global soil nitrogen and fine root phosphorus, (f) Forest soil nitrogen and fine root phosphorus, (g) Global fine root N/P Ratio and soil nitrogen, (h) Global fine root N/P ratio and soil phosphorus, (i) Global fine root N/P ratio and soil N/P ratio

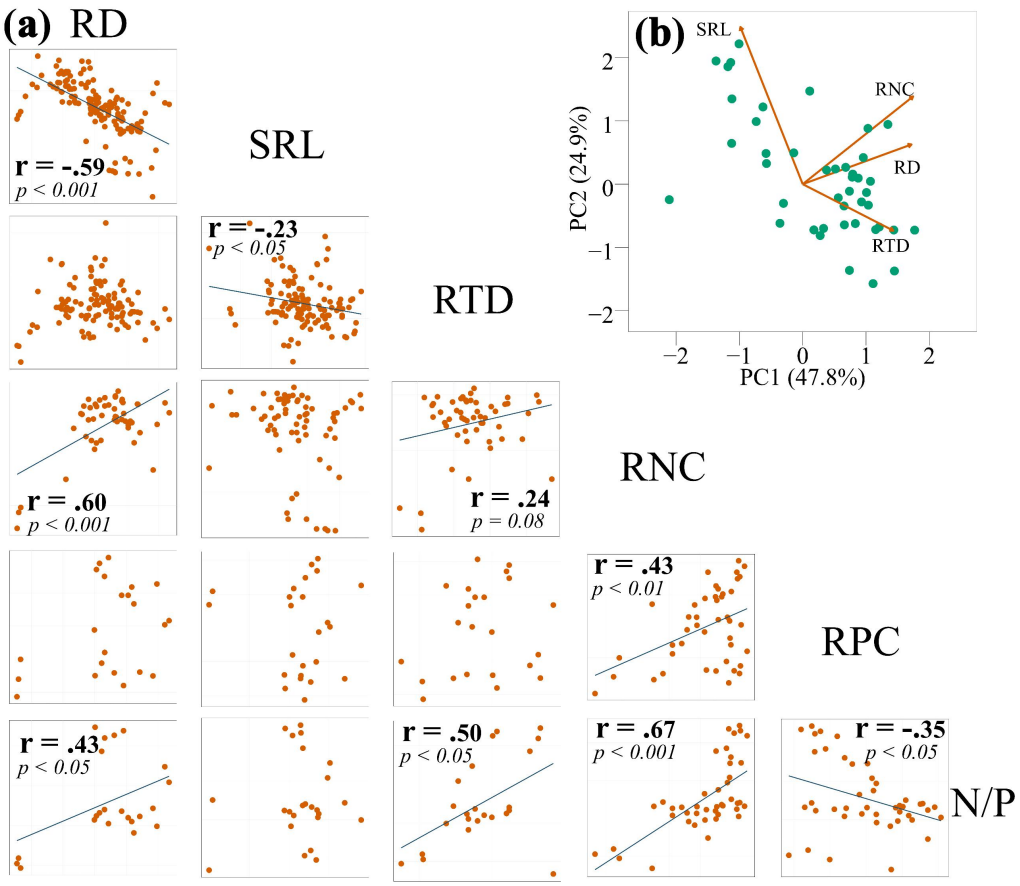

Figure 6 Community-Level fine root trait relationships

Panel (a) Correlations among fine root traits, (b) Principal component analysis of fine root traits. SRL, specific root length; RD, root diameter; RTD, root tissue density; RNC, root nitrogen content, RPC, root phosphorus content; N/P root nitrogen and phosphorus ratio;