Global community-level coordination of fine root traits and their environmental drivers

Hui Guo[1], XiaoYu Meng[2,3], Yun Zhao[4], Lei Wang[1], Liang Kou[5]

[1]School of Environmental Science and Engineering, Xiamen University of Technology, Xiamen, 361024, China

[2]Key Research Institute of Yellow River Civilization and Sustainable Development, Henan University, Kaifeng, 475001, China

[3]Faculty of Geographical Science and Engineering, Henan University, Zhengzhou, 450046, China

[4]Graduate Program in Environmental Science, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA

[5]Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;

Author for correspondence:

Liang Kou

Email: koul@igsnrr.ac.cn

Summary

- Trait-based root economics space (RES) is important for understanding species-level belowground strategies. Yet, how trait coordination scales from species to community levels and its environmental drivers remain largely unknown.
- We compiled global fine-root trait data from 301 natural plant communities and employed the plant trait network (PTN) method to map community-level trait covariation and explore the potential environmental drivers.
- The PTN segregated root traits into two independent modules: a morphological module dominated by root diameter and specific root length, and a module dominated by root chemical traits and root tissue density, supporting the bi-dimensionality of the species-level RES. The morphological module reflects shifts in belowground strategies along a soil fertility gradient: nutrient-rich soils favor roots with greater specific root length for direct uptake, while nutrient-poor soils promote thicker roots with higher reliance on mycorrhizal fungi. Unlike the species-level coupling between root tissue

density and root nitrogen concentration, however, these two traits decoupled at the community level, possibly because they were shaped by contrasting environmental factors.

- This study underscores that the species-level RES is difficult to extend to the community level and provides new insights into vegetation dynamics modeling under global change.

Keywords: community-level, root traits, environmental factors, nutrient acquisition strategies, root economics space.

Introduction

Functional trait analyses at the community level are pivotal in ecology because they unite species' traits, abundances, and intraspecific variation to explain how communities assemble and function (Dubuis et al., 2013; Walker et al., 2022). Central to this effort is trait economics—understanding how plants allocate resources among growth, maintenance, and reproduction—since these trade-offs determine ecological strategies across environments (Augusto & Boča, 2022). While species-level frameworks reveal individual plant strategies, ecosystem processes arise from the collective trait composition of coexisting species, rather than those of single taxa (Bardgett et al., 2014; Bruelheide et al., 2018). Therefore, extending trait-economic theory to the community level is critical for uncovering how plant trait coordination responds to environmental gradients and governs ecosystem functioning.

Root traits play a pivotal role in the belowground resource acquisition of plants. The root economics space (RES) framework offers a conceptual model for organizing fine-root traits—including root diameter (RD), specific root length (SRL), root tissue density (RTD), and root nitrogen (RN) concentration—along two main axes: a fast–slow conservation gradient (dominated by RTD and RN) and a collaboration gradient (dominated by RD and SRL) (Bergmann et al., 2020). The RES has been linked to plant resource-use strategies and ecosystem functions such as nutrient cycling and soil carbon dynamics (Freschet et al., 2021). However, community-level tests of the RES are scarce and yield inconsistent results: across 129 communities, RD, SRL, and RN converge on a single axis, with RTD forming a separate axis (Li et al., 2019), while in 20 communities, RN varies independently of RD and SRL (Prieto et al., 2016). These discrepancies

underscore the crucial need for comprehensive, global-scale analyses that utilize direct community-level trait measurements to validate the RES framework's scalability and capture the full diversity of fine-root functional strategies.

Community-level fine-root trait patterns reflect environmental filtering and niche differentiation. Environmental filtering imposes constraints through climate and soil properties, selecting for traits suited to prevailing conditions. For example, species-level studies show that increased precipitation reduces RTD and SRL, enhancing resource uptake in wetter environments (Chen et al., 2013; Freschet et al., 2017), while warmer temperatures decrease root phosphorus (RP) concentration and the N:P ratio, reflecting phosphorus (P) limitation in tropical systems (Vitousek et al., 2010). Nutrient-rich soils promote roots with high SRL for direct uptake, whereas nutrient-poor soils favor thicker, mycorrhizal-dependent roots (Ma et al., 2018; Liu et al., 2022). Soil pH also modulates these relationships by altering nutrient availability and microbial communities (Guo et al., 2024). Conversely, niche differentiation fosters coexistence of diverse strategies, dampening trait differences across biomes through resource partitioning (MacArthur & Levins, 1967). Understanding these mechanisms globally is therefore essential for predicting plant community responses to environmental change (Suding et al., 2008).

To address these gaps, we compiled a global dataset of fine-root trait measurements from 301 natural plant communities across forests, grasslands, and shrublands. We employed the plant trait network (PTN) method to partition root trait covariation into distinct functional modules (He et al., 2020). Subsequently, we associated each module with site-level climate and soil properties to identify dominant environmental drivers. In doing so, we measured six key fine-root traits (RD, SRL, RTD, RN, RP, and the root N:P ratio) that can well reflect root nutrient economy and soil nutrient limitation type. Specifically, we aimed to address two key questions: (i) Do community-level fine-root trait trade-offs follow the dual-axis structure of the species-level RES? (ii) How do climate and soil variables shape the root functional modules and thus the RES at the community level?

Methods

Data collection

To compile a comprehensive global dataset of community-level fine root traits, we conducted a systematic literature review across three major databases: Web of Science,

Google Scholar, and the China National Knowledge Infrastructure (CNKI). The search, covering publications up to December 2024, employed a combination of keywords in English and Chinese, including: “fine roots”, “root diameter”, “specific root length”, “root tissue density”, “root nitrogen concentration”, “root phosphorus concentration”, “community root traits”, and “belowground plant strategies”.

Studies were included based on the following criteria: (1) Field-based data: Only studies reporting observational data collected in natural plant communities were considered. We excluded studies conducted in greenhouses, pots, hydroponic setups, or heavily disturbed/restored sites. (2) The majority of included studies defined fine roots as those with diameters < 2 mm, consistent with common morphological criteria. A few studies instead classified fine roots based on developmental order, typically including only first- to third-order roots. (3) Trait values had to be reported at the community level, using methods such as bulk sampling through soil cores, root growth cores, or soil pits. Studies presenting species-level values, species-weighted means, or species averages were excluded. (4) Trait completeness: Each included study must report at least one of the following traits: RD, SRL, RTD, RN, RP and N:P ratio. (5) Environmental data: Geographic coordinates or location descriptors had to be provided, along with corresponding climate variables (mean annual temperature and precipitation) and soil nutrient properties derived from shallow soil layers (no deeper than 0–20 cm), including total nitrogen (N) and P, ammonium N (NH_4^+), nitrate N (NO_3^-), available P, and soil pH. (6) Use of control data: For studies based on experimental designs, only trait values from untreated control plots were used to avoid confounding treatment effects.

Following this selection process, we compiled data from 101 peer-reviewed articles, covering 301 natural plant communities globally. These included forests (n = 194), grasslands (n = 95), and shrublands (n = 12). The distribution of sampling sites across biomes is illustrated in Fig. S1.

Biome stratification and trait comparisons

To explore ecological variability across vegetation types, forests and grasslands were further classified into distinct biomes based on geographic and climatic contexts. Forests were grouped into three biomes (tropical rainforest, temperate deciduous forest, and boreal forest); grasslands into three biomes (tropical grasslands, temperate grasslands,

and tundra). We applied one-way analysis of variance (ANOVA) with Tukey's honest significant difference (HSD) post-hoc tests to compare trait values across biomes. This analysis allowed us to identify functional divergence and convergence among communities occupying different environmental niches.

Multivariate analysis of trait coordination

To meet the assumption of normality and homoscedasticity, root trait data were log-transformed before statistical analysis. For each site, trait values were treated as community-level means representing aggregate functional properties of local vegetation.

Considering extensive missing values in our root trait matrix, list-wise deletion was impractical for principal component analysis. We therefore used the PTN framework to assess root trait covariation patterns (He et al., 2020). This approach groups plant traits into functional modules based on pairwise connectivity, analogous to principal component-derived axes commonly used in plant trait classification. We standardized all traits to zero mean and unit variance, then computed pairwise Spearman rank correlations across communities. Only significant correlations ($|\rho| > 0.2$, $p < 0.1$) were retained as edges in an undirected weighted network, with edge thickness reflecting correlation strength. To mitigate algorithm-specific biases, we applied seven community-detection methods in R's igraph package—Louvain, Walktrap, Infomap, Fast-Greedy, Edge-Betweenness, Spinglass, and Leading-Eigenvector—each executed 100 times. For each method, partitions were compared using the Rand index, and the run with the highest average similarity was selected as the "most stable" solution. The consensus partition, supported by the majority of algorithms, defined the final modules, with the corresponding modularity score reported. All PTN construction, stability assessments, and network visualization were conducted in R using igraph, wgcna, and ggraph packages.

Results

Biome-level differentiation of root traits

At the biome scale, fine-root traits varied markedly among communities (Fig. 1). RD was narrowly distributed in biomes with constrained trait distributions—tropical grasslands (0.2–0.3 mm), tundras (0.35–0.5 mm), arid-region shrubs (≈0.5 mm) and boreal forests (0.45–0.7 mm) (Fig. 1a). In contrast, tropical forests, temperate forests and temperate

grasslands exhibited broader ranges in RD (0.2–1 mm, Fig. 1a). SRL peaked in tropical grasslands and tundras (50–150 m g^{-1}; Fig. 1b), whereas tropical forests, temperate forests, boreal forests and shrubs clustered at 5–50 m g^{-1} and temperate grasslands spanned 1–150 m g^{-1}. RTD overlapped across biomes: tundras centred on 0.15–0.25 g cm^{-3}, shrubs ranged from 0.15 to 1 g cm^{-3}, and other biomes centred on 0.2–0.5 g cm^{-3} (Fig. 1c). Finally, RN in boreal forests and tundras was constrained to 10–17 mg g^{-1}, while other biomes ranged from 5 to 30 mg g^{-1} (Fig. 1d).

Modular independence of root morphological and chemical-density traits

With five of seven algorithms consistently partitioning the six traits into two modules (Table S1), PTN method partitioned six fine-root traits into two largely independent functional modules: a morphological module (RD and SRL) and chemical-density module (RN, RP, N:P ratio and RTD) (Fig. 2a). Within-module associations were strong: RD and SRL were negatively correlated (r = −0.59, p < 0.001), while RTD correlated positively with N:P ratio (r = 0.50, p < 0.05), RN covaried positively with RP (r = 0.43, p < 0.01) and with N:P ratio (r = 0.67, p < 0.001), and RP was inversely related to N:P ratio (r = −0.35, p < 0.05). Cross-module links were minimal: RD, serving as the central hub, linked to RN (r = 0.43, p < 0.05) and N:P ratio (r = 0.6, p < 0.001), whereas SRL exhibited only a weak connection to RTD (r = −0.23, p < 0.05) (Fig. 2b).

Climate and soil nutrients effects on root traits

Climate factors primarily influenced RTD, RP, and N:P ratios (Fig. 3). Specifically, higher precipitation significantly reduced RTD (r^2 = 0.15, p < 0.001), a pattern consistently observed in 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). Higher temperatures reduced RP in forests (r^2 = 0.18, p < 0.01; Fig. 4a), concurrently lowering N:P ratios (r^2 = 0.56; p < 0.01; Fig. 4b). Besides, precipitation negatively affected RD in grasslands (r^2 = 0.17, p < 0.05) (Fig. S2a), temperature significantly reduced RTD in shrubs (r^2 = 0.57, p < 0.05; Fig. S2b) and RNC in grasslands (r^2 = 0.26, p < 0.01; Fig. S2c).

Soil nutrient availability and pH significantly influenced root morphological traits, with distinct patterns across ecosystems (Fig. 5). Globally, higher soil ammonium N (NH_4^+) content was associated with thinner roots, as evidenced by an inverse correlation with RD (r^2 = 0.51, p < 0.01) (Fig. 5a). This trend was particularly pronounced in forests,

where RD decreased with total P content (r^2 = 0.25, p < 0.05) (Fig. 5b). In forests, SRL increased with both soil total N (r^2 = 0.14, p < 0.01) and available P content (r^2 = 0.39, p < 0.05) (Fig. 5c–d). In contrast, grasslands exhibited a positive correlation between RD and soil pH (r^2 = 0.31, p < 0.01) (Fig. S3).

RN and RP showed inconsistent relationships with soil nutrients, depending on ecosystem type (Fig. 6). RN negatively correlated with soil total N in forests (r^2 = 0.27, p < 0.01), while positively in grasslands (r^2 = 0.32, p < 0.01), yielding no global correlation (Fig. 6a–c). RP increased with soil P (global: r^2 = 0.46, p < 0.01) and N content (global: r^2 = 0.23, p < 0.05; forests: r^2 = 0.25, p < 0.05) (Fig. 6d–f). The N:P ratio decreased with soil N (r^2 = 0.22, p < 0.05) and P content (r^2 = 0.31, p < 0.01) but increased with soil N:P ratio (r^2 = 0.65, p < 0.05) (Fig. 6g–i). Besides, soil pH negatively correlated with RN globally (r^2 = 0.17, p < 0.01) and in forests (r^2 = 0.22, p < 0.01) (Fig. S4).

Discussion

The PTN method reveals that community-level fine-root trait relationships exhibit modular independence, mirroring the bi-dimensionality of the species-level RES (Bergmann et al., 2020). Fine-root traits cluster into two functional modules: a root morphological module dominated by RD and SRL, and a root chemical-density module comprising RN, RP, the N:P ratio, and RTD (Fig. 2a). However, key internal trait relationships, notably the RTD–RN axis, are decoupled at the community level (Fig. 2b). This decoupling indicates that, while the broad two-dimensional RES structure is overall retained, its specific trait interactions do not fully extend to the community level. Consequently, community-level root trait syndromes require independent assessment rather than reliance on species-level frameworks (De-La Riva et al., 2023; Matthus et al., 2025). This insight calls for further research to elucidate how community-level trait dynamics shape ecosystem processes under diverse environmental conditions.

The morphological module reflects a trade-off between direct root foraging and mycorrhizal-mediated nutrient acquisition. In nutrient-rich environments, communities develop roots with high SRL to maximize soil contact and minimize construction costs (Fig. 5), enhancing rapid uptake of N and P (Kong et al., 2014; Ma et al., 2018). This strategy optimizes resource capture in fertile soils where competition for nutrients is intense, allowing plants to allocate surplus resources to growth or reproduction (Yan et al., 2022). In nutrient-poor soils, thicker roots provide structural longevity and support

mycorrhizal symbiosis, improving nutrient acquisition under scarcity (Addo-Danso et al., 2020; Yan et al., 2022). This adaptation is critical in oligotrophic ecosystems, where reliance on fungal partnerships compensates for limited soil resources (Wang et al., 2025). In grasslands, RD decreases with increasing precipitation (Fig. S2a), contrasting with species-level trends of thicker roots in wetter conditions (Zadworny et al., 2017; Fort & Freschet, 2020; Ding et al., 2020). This suggests that mesic grasslands favor thin-rooted species to exploit transient nutrient pulses (O'Keefe et al., 2022), a strategy likely driven by seasonal water availability. Similarly, a positive correlation between soil pH and RD was observed in grasslands (Fig. S3), indicating that thicker roots in alkaline soils may mitigate aluminum toxicity or enhance calcium uptake, bolstering stress tolerance (Lambers et al., 2008).

The chemical-density module expands beyond the traditional RES framework by incorporating RP and the N:P ratio, offering a comprehensive view of ecosystem nutrient limitation type. RP reflects P acquisition and storage, while the N:P ratio signals ecosystem nutrient limitation (Yuan et al., 2011; Du et al., 2020). PTN analysis shows tight covariance among RTD, RN, RP, and the N:P ratio (Fig. 2b), and the N:P ratio serves as a key integrator, coordinating shifts in RTD, RN, and RP. These patterns emphasize an integrated response to N–P co-limitation rather than the species-level "fast–slow" axis (Bergmann et al., 2020), and highlight how community-level interactions amplify stoichiometric constraints, reflecting a collective adaptation to nutrient scarcity. It is worth noting that a positive correlation between the N:P ratio and RTD suggests that under elevated N:P ratios, communities favor denser root tissues, likely to prolong root lifespan and enhance P retention in P-limited conditions (Weemstra et al., 2016). RP and N:P ratio are jointly shaped by both climatic and soil factors. In forests, rising temperatures reduce RP and elevate N:P ratios (Fig. 4), indicating intensified P limitation in warmer and wetter climates (Wang et al., 2020). This trend may exacerbate P leaching, limiting plant growth in tropical systems. At the community level, RP is positively correlated with soil total P (Fig. 6d), reflecting increased P uptake and storage in P-rich soils, likely facilitated by enhanced root metabolic activity and mycorrhizal associations (Vitousek et al., 2010). Conversely, the root N:P ratio is negatively correlated with both soil N and P, but positively correlated with the soil N:P ratio (Fig. 6g–i). These relationships suggest that in nutrient-rich soils, communities tend to reduce the root N:P ratio by increasing RP relative to RN, optimizing nutrient balance for efficient uptake. In

contrast, high soil N:P ratios, indicative of P limitation, drive elevated root N:P ratios, promoting greater reliance on mycorrhizal fungi to enhance P acquisition (Luo et al., 2021). This dynamic adjustment reflects community-level stoichiometric homeostasis, enabling plants to adapt to heterogeneous nutrient landscapes (Wang et al., 2019). Furthermore, a positive correlation between RP and soil total N at both global and forest scales (Fig. 6e–f) supports the concept of nutrient co-limitation (Harpole et al., 2011). In N-rich environments, elevated soil N may enhance the biological demand for P (Du et al., 2020), enabling plants to increase P acquisition and incorporation into roots. This interplay between N and P dynamics suggests that changes in one nutrient, such as those induced by anthropogenic N deposition (Guo et al., 2025), could indirectly affect the uptake of the other, highlighting critical implications for ecosystem nutrient management.

Contrary to species-level findings of a strong RTD–RN correlation (Bergmann et al., 2020; Hou et al., 2024), no such coupling exists at the community level. RTD is primarily driven by precipitation (Fig. 3), with wetter conditions reducing tissue density to optimize water and oxygen transport (Chen et al., 2013; Laughlin et al., 2021). This adaptation enhances root resilience in waterlogged soils, a critical factor in flood-prone regions (Dubuis et al., 2013). RN, however, responds to soil pH (Fig. S4), with acidic soils promoting ammonium uptake and alkaline soils favoring nitrate (Guo et al., 2024). This pH-driven shift influences N availability, affecting community-level nutrient strategies. Interestingly, community-level RN shows no global correlation with soil N (Fig. 6a), likely because forest and grassland RN exhibit opposing trends in relation to soil N. In forests, RN decreases with increasing soil N (Fig. 6b), possibly due to allocation to aboveground tissues or microbial partners to reduce metabolic costs (Valverde-Barrantes, 2017), a strategy that may prioritize resources investment elsewhere. Notably, this pattern contrasts with some species-level studies in forests, which reported increased root N with higher soil N supply (Nadelhoffer et al., 1985; Ding et al., 2020; Yan et al., 2022). Cautions are therefore required when extrapolating relationships between species-level root traits and environmental variables to the community level. In contrast, grasslands exhibit higher RN (Fig. 6c), reflecting an acquisitive strategy suited to nutrient pulses and rapid growth (Wang et al., 2019). Furthermore, in grasslands, RN decreases with rising temperatures (Fig. S2c). Elevated temperatures often accelerate the decomposition of soil organic matter and microbial N cycling, potentially reducing the

retention of plant-available N in roots (Liu et al., 2022). The observed decline in RN under warmer conditions may suggest that grassland plants in hot climates either experience increased N limitation or down-regulate root N storage in response to more rapid N supply from microbial activity (Sweeney et al., 2021).

Moreover, despite the largely independent nature of the morphological and chemical-density modules, RD functions as the central hub in the PTN, exhibiting significant positive correlations with RN and root N:P ratio (Fig. 2). This cross-module linkage likely arises because thicker roots, characterized by a more extensive cortex and larger xylem conduits (Kong et al., 2021), provide enhanced capacity for nutrient storage and transport, thereby promoting N accumulation. Additionally, under high N:P conditions that indicate relative P limitation, plants tend to develop thicker roots to enhance mycorrhizal associations (Fig.5) (Ma et al., 2018), which explains the positive relationship between RD and the N:P ratio.

At the biome scale, fine root traits exhibit convergence in some environments, such as constrained RD and SRL ranges in tundra, arid shrublands, and boreal forests (Fig. 1a-b). However, traits like RTD and RN show minimal differentiation across biomes (Fig. 1c-d), indicating weak environmental filtering at the community level. This contrasts with species-level biome-specific trait syndromes (Freschet et al., 2017; Ma et al., 2018), highlighting the role of niche differentiation in community assembly. Heterogeneous environments facilitate species coexistence through complementary trait combinations, which may mitigate large-scale trait divergence (MacArthur & Levins, 1967; Bruelheide et al., 2018).

Conclusion

This study synthesizes fine-root trait data from 301 global plant communities and employs the PTN method to evaluate the RES framework at the community level. Six key traits—RD, SRL, RTD, RN, RP, and the N:P ratio—cluster into two distinct and largely independent modules: a morphological module (RD and SRL) and a chemical-density module (RN, RP, N:P ratio, and RTD). Each module exhibits strong internal coordination but limited inter-module coupling, reflecting divergent adaptive strategies shaped by environmental constraints. The morphological module represents a continuum from root foraging (high SRL, small RD) to mycorrhizal symbiosis (low SRL, large RD) along soil fertility gradients. The chemical-density module, which includes RP and the N:P

ratio, highlights stoichiometric regulation under N–P co-limitation, with temperature and soil nutrient availability primarily influencing RP and N:P dynamics. At the community level, RN and RTD are decoupled, driven by distinct environmental filters: RN is primarily governed by soil pH, while RTD is strongly influenced by precipitation. Taken together, these findings demonstrate that while community-level root traits display a bi-dimensional structure, they diverge from species-level RES patterns due to the decoupling of RN and RTD. This highlights the importance of developing a community-level RES framework to better understand plant adaptation and nutrient cycling across diverse ecosystems.

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Competing interests

None declared.

Author contributions

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

Data availability

All data supporting the findings of this study can be accessed in Dryad database.

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Figure legend

Figure 1. Density distributions of root traits among global biomes

Figure 2. Community-level root traits network and correlation analysis

Figure 3. Relationship between precipitation and root tissue density

Figure 4. Relationship between temperature and root phosphorus concentration and N: P ratio in forests

Figure 5. Relationship between soil nutrients content and root morphological traits

Figure 6. Relationship between soil nutrients content and root chemical traits

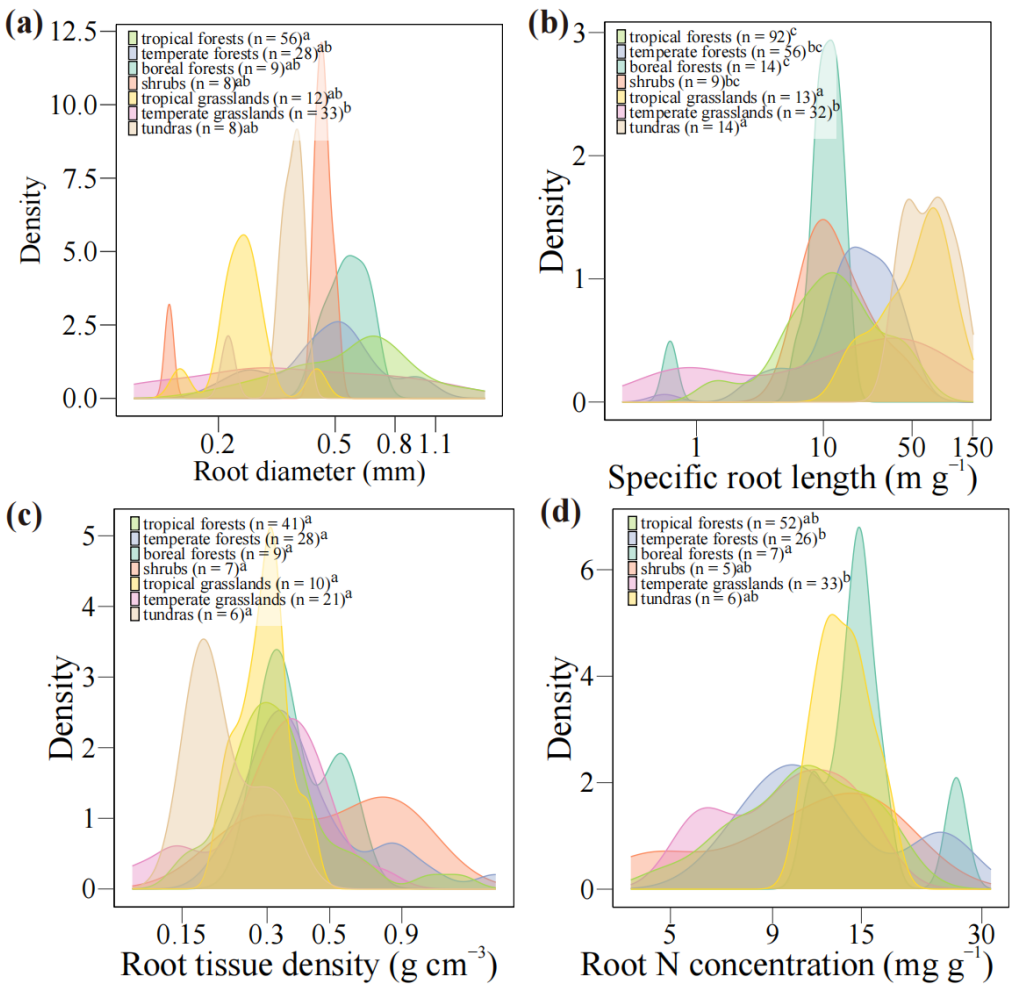

Figure 1 Density distributions of root traits among global biomes

The superscript letters derive from Tukey's HSD post-hoc multiple comparisons following ANOVA. Different letters denote significant differences among groups ($p < 0.05$), while identical letters indicate no significant difference ($p > 0.05$). The root trait data were log-transformed.

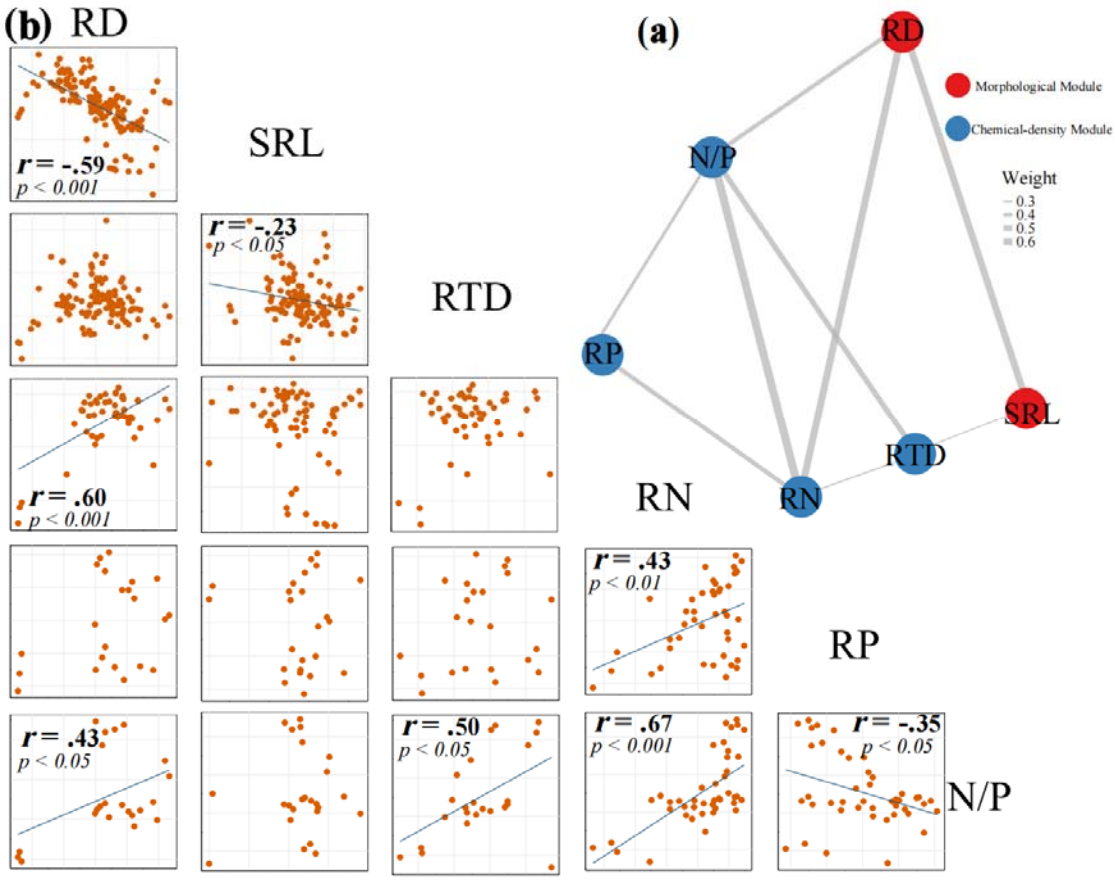

Figure 2 Community-level root traits network (a) and correlation (b) analysis

Trait abbreviations: SRL, specific root length; RD, root diameter; RTD, root tissue density; RN, root nitrogen concentration; RP, root phosphorus concentration; N/P, root nitrogen and phosphorus ratio.

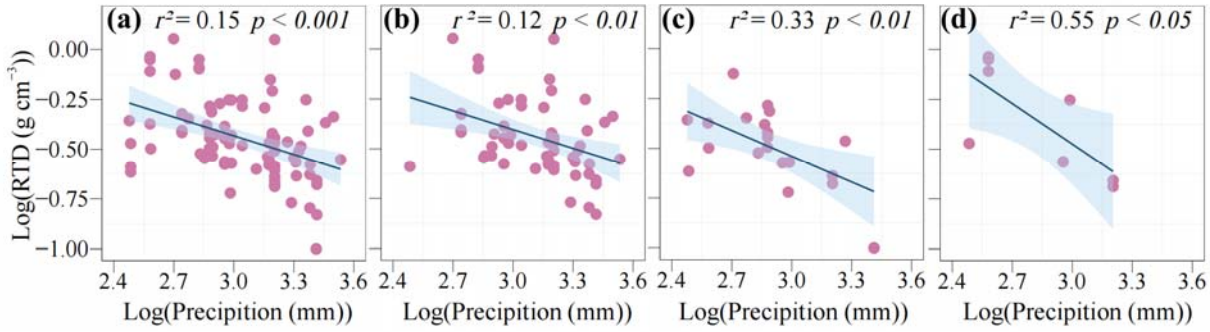

Figure 3 Relationship between precipitation and root tissue density (RTD)

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

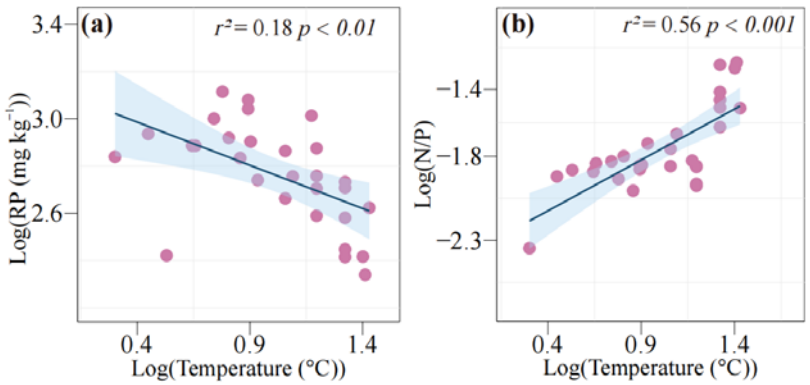

Figure 4 Relationship between temperature and root phosphorus concentration (RP) (a) and N: P ratio (b) in forests

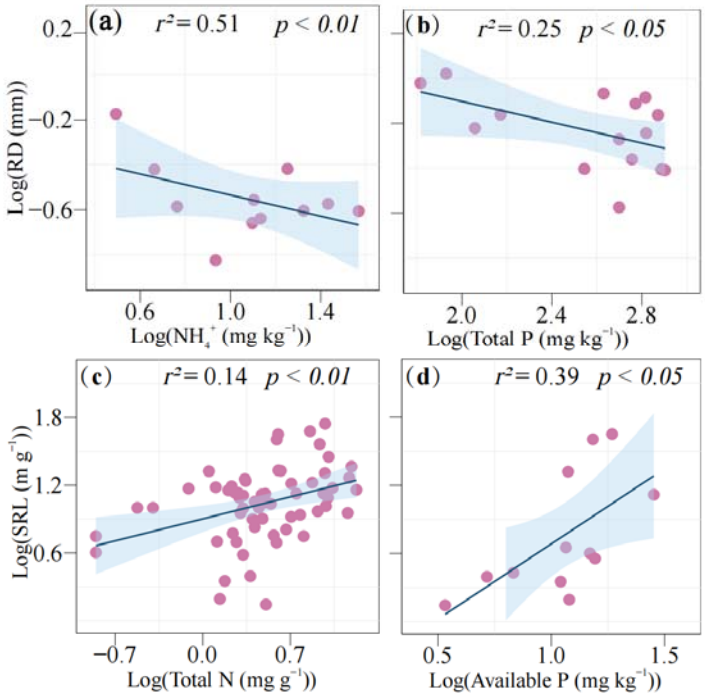

Figure 5 Relationship between soil nutrients content and root morphological traits

Panel (a) Global soil NH_4^+ and root diameter (RD), (b) Forests soil total phosphorus content and root diameter, (c) Forests: soil total nitrogen and specific root length (SRL), (d) Forests: soil available phosphorus and specific root length

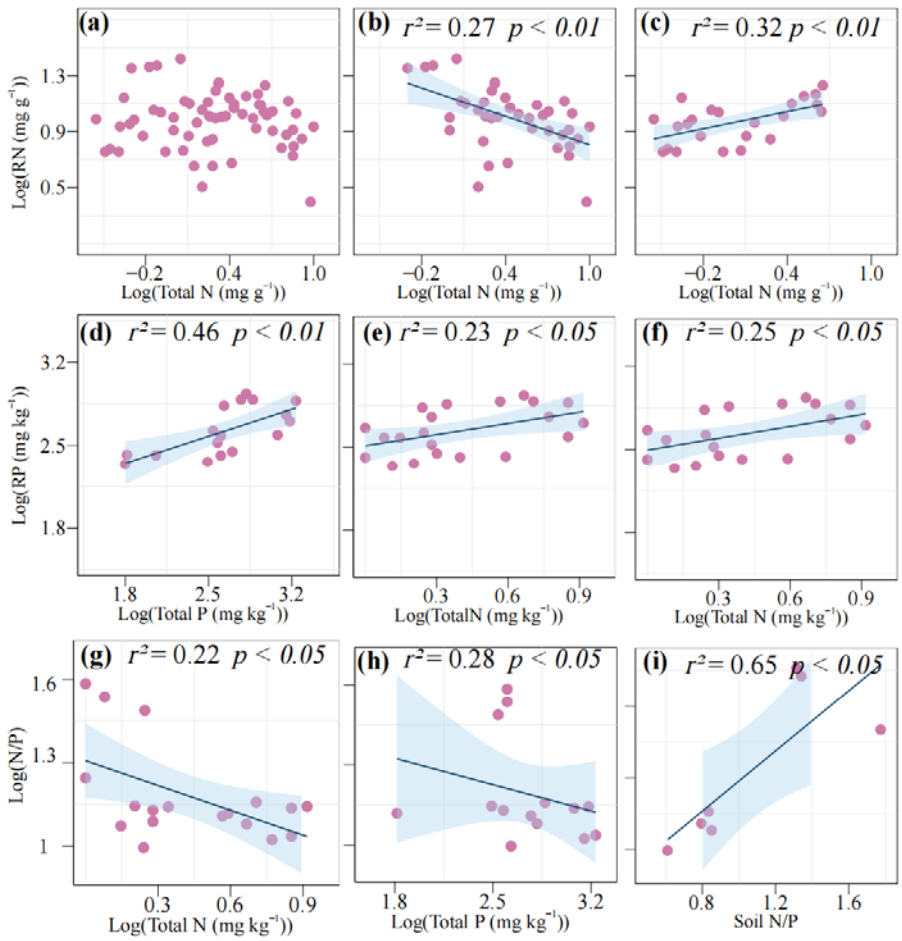

Figure 6 Relationship between soil nutrients content and root chemical traits

Panel (a) Global soil total nitrogen and root nitrogen concentration (RN), (b) Forests: soil total nitrogen and root nitrogen concentration, (c) Grassland: soil total nitrogen and root nitrogen concentration, (d) Forests: soil total phosphorus and root phosphorus concentration (RP), (e) Global soil total nitrogen and root phosphorus concentration, (f) Forests: soil total nitrogen and root phosphorus concentration, (g) Global fine root N:P Ratio and soil total nitrogen, (h) Global fine root N/P ratio and soil total phosphorus, (i) Global fine root N:P ratio and soil N:P ratio