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Fine roots of plants growing in organic soils occupy a distinct niche within the Root Economics Space

Kathleen Renee Coffman

kcoffma6@vols.utk.edu

UT Knoxville: The University of Tennessee Knoxville https://orcid.org/0000-0003-3149-8967

Jitendra Kumar
Colleen Iversen
Stephanie Kivlin
Kellie Walters
Verity Salmon

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Abstract

Aims

Linking belowground plant traits and soil properties is critical to better understand and predict global biogeochemical cycling. While most soils across the world have low amounts of carbon, high-latitude soils are often highly organic and dominated by plant communities adapted to cold, wet, nutrient-limited conditions that limit decomposition. These ecosystems are also vulnerable to rapid warming and disturbance, requiring improved understanding of belowground dynamics to predict global patterns of plant allocation and resource acquisition.

Methods

We present a synthesis exploring the interface between plants and soils by examining how fine-root trait relationships vary with soil organic C (SOC), especially in highly organic soils. We examined species-level fine-root traits by combining the GRooT root trait database with SOC maps from SoilGrids 2.0 and grouping soils into organic or mineral categories based on a breakpoint analysis of SOC concentration.

Results

The traits analyzed (fine-root nitrogen (N), diameter (D), tissue density (RTD), and specific root length (SRL), reflect key aspects of root function related to metabolism, uptake strategy, structure, and efficiency. We found that the Root Economics Space (RES) differs between organic and mineral soils and is influenced by soil type, plant functional type (PFT), and mycorrhizal associations.

Conclusion

Our synthesis highlights the need for more data from species rooted in organic soils to understand belowground dynamic responses to environmental change in C-rich, nutrient-poor ecosystems.

Introduction

The distribution and accumulation of soil organic matter vary substantially across the terrestrial biosphere (Jenny *et al*., 2011). Persistent water saturation, low oxygen availability, and/or cold temperatures – conditions often found in peatlands and other wetlands, boreal forests, and in tundra ecosystems– lead to the accumulation of partially decomposed plant material over time (Silva Neto et al., 2023; Farnham and Finney, 1965; Paustian et al., 2019). Thus, extensive areas of biomes located in northern latitudes and along the coast are underlain by highly organic soils (Crowther et al., 2019). Soil organic carbon (SOC; i.e., the C content of soil organic matter), plays a crucial role in soil fertility, water retention, ecosystem resilience, and biogeochemical cycling (Korneef *et al.*, 2024), particularly in cold,

acidic, and waterlogged environments (Yang et al., 2023b). Importantly, organic soils exist along a continuum, with some soils having intermediate SOC levels due to varying drainage, climate, and vegetation inputs (Köchy et al., 2015).

Narrow diameter, fine roots of plants serve as the primary interface for water and nutrient uptake from surrounding soil (Epstein, 1977). However, roots vary in their anatomy, morphology, chemistry, and physiology, particularly among species and across spatial scales, soil conditions, environments, and through time (Ryan et al., 2016; Freschet et al., 2017; Freschet et al., 2021). Fine roots, usually defined as < 2 mm in diameter, contribute heavily to ecosystem C, water, and nutrient cycling, and microbial community dynamics via resource acquisition, respiration, root exudation, and turnover throughout the soil profile (Bardgett et al., 2014; Wang et al., 2014; Iversen et al., 2017; Saha et al., 2023). Shifting species dominance in warming northern ecosystems can alter root traits and resource-use strategies, with important consequences for soil C dynamics (Iversen *et al.*, 2014; Parker *et al.*,2021).

Plant species that root in highly organic soils have evolved to tolerate relatively extreme conditions that include low oxygen availability, high acidity, and nutrient limitations (Sorrell *et al.*, 2013). Many of these species, including sedges (*Carex* and *Eriophorum* spp.), ericaceous shrubs (*Vaccinium* and *Rhododendron* spp.), and coniferous trees (*Pinus* and *Picea* spp.) possess specialized root traits. These specialized traits include anatomical and morphological adaptations that enhance resource acquisition in nutrient-poor soils (Iversen et al., 2018; Read *et al.*, 2003). In addition, many plants form symbiotic relationships with mycorrhizal fungi (e.g., arbuscular, ectomycorrhizal, and ericoid types) to improve phosphorus (P) and nitrogen (N) uptake, compensating for slow decomposition and limited nutrient availability in highly organic soils (Fig. 1; Read *et al.*, 2004). Plant species can be grouped into plant functional types (PFTs) such as shrubs, trees, graminoids, and herbs that reflect above- and belowground phylogenies and resource acquisition strategies (Wullschleger *et al.*, 2014; Weber and Iversen, 2023).

Our current understanding of belowground strategies is laid out in the Root Economics Space (RES), which describes orthogonal, coordinated axes of fine-root trait variation related to resource acquisition and conservation strategies based on the four most commonly measured fine-root traits (Bergmann et al., 2020). These traits reflect core aspects of root function: root N concentration is related to metabolic activity and decomposition, diameter (D) relates to resource uptake strategy, root tissue density (RTD) reflects structural investment and longevity, and specific root length (SRL) captures efficiency in soil exploration and nutrient acquisition. Bergmann et al. (2020) described the RES as encompassing a collaboration gradient ranging from a ‘do-it-yourself strategy’ (higher SRL) to an ‘outsourcing’ strategy (higher D and cortex fraction for mycorrhizal association) that is orthogonal to a conservation gradient ranging from ‘fast’ (higher N concentration) to ‘slow’ (higher RTD) life history strategies for return on investments of C and nutrients (Fig. 1 in Bergmann et al. 2020). These importance of these axes are supported by other literature: roots with higher N concentrations typically have faster metabolism and respiration rates based on data from 74 species including graminoids and herbaceous and dwarf shrubs (Roumet et al., 2016), and temperate tree roots with higher N concentrations had shorter lifespans (McCormack et al., 2012). Roots with shorter lifespans also typically had lower RTD (Ryser, 1996:

McCormack et al. 2012). Identifying where and why these trait-tradeoffs break down is essential for understanding the boundaries of their applicability across ecosystems. The root traits of plants growing in highly organic soils, however, may not fit neatly into the RES spectrum.

Trait combinations expressed by plant species dominating highly organic soils may occupy a unique and underrepresented region of the root trait space because of their adaptations to distinct physical and chemical soil environments. A divergence would not be surprising given that the RES was primarily developed from species associated with AMF (Bergmann et al., 2020), which differ markedly from species with other mycorrhizal strategies or those that lack fungal associations altogether (Averill *et al.*, 2014). In peat-rich environments, plants may prioritize structural or physiological adaptations, such as aerenchyma formation or low-density tissue, over traits traditionally linked to nutrient acquisition efficiency (Freschet et al., 2020). For example, aerenchymous graminoids, which dominate many organic soil systems, exhibit large-diameter, low-density roots that support internal oxygen diffusion but are typically non-mycorrhizal (NM; Michelson *et al*., 1998). This trait pattern deviates from the RES expectation that larger root diameter indicates increased fungal collaboration. Conversely, ericaceous shrubs rooted in highly organic soils combine high SRL with strong ErM associations, confounding the predicted 'collaboration' tradeoff where fine roots with a high SRL are less dependent on mycorrhizal fungi (Wurzberger *et al.*, 2009). Yet not all observations conflict with the RES; for example, graminoids in tundra ecosystems often exhibit high root N concentrations and low RTD (Iversen et al., 2015). These cases highlight the importance of recognizing functional tradeoffs that are context-dependent, particularly when assessing plant contributions to soil C cycling and nutrient dynamics in organic-rich ecosystems (Jungkunst et al., 2022; Lu et al., 2024).

One of the biggest challenges in root ecology is the global variation in root traits within and among species (Bardgett et al., 2014; Iversen et al., 2017). Standardizing root trait measurements remains difficult due to limited data availability (Freschet et al., 2021). The Fine-Root Ecology Database (FRED; Iversen et al., 2017) has helped advance understanding of root traits and ecosystem functioning (McCormack et al., 2015, 2018). Studies using FRED have examined root morphology, allocation patterns, and trait covariation across PFTs and biomes (An et al., 2022; McCormack et al., 2020; Wang et al., 2023). GRooT (Guerrero-Ramirez *et al.*, 2020) leveraged FRED by combining species-specific data from FRED to create a limited, species-specific dataset emphasizing the most commonly measured root traits to develop the RES concept (Bergmann et al., 2020). Given our species-specific focus, we used GRooT in the following analyses.

We conducted a systematic review and synthesis of findings from multiple studies (i.e., a narrative synthesis) by pairing geolocated root trait observations from GRooT with SOC concentration from SoilGrids 2.0 (Poggio et al., 2021). SoilGrids 2.0 is a system for digital spatial soil mapping at the global scale maintained by the International Soil Reference and Information Center (ISRIC). It includes 250-m resolution soil properties such as bulk density, soil N content, SOC, and others, at several standard depth intervals. We tested the following hypotheses: (1) Most fine-root trait observations used to build the current RES have been from species rooted in mineral soils, (2) the root trait space occupied by roots of

species in biomes with highly organic soils is different from those in mineral soils, and (3) root traits are best predicted not only by PFT and mycorrhizal type, but also by soil type. We expect roots growing in organic soils may align with the global RES in two ways: lower root N and higher root RTD may position these roots toward the “slow” end of the conservation gradient, or a higher D and lower SRL may place them on the “outsourcing” end of the collaboration gradient, favoring nutrient acquisition via mycorrhizal partners (Bergmann et al., 2020).

Materials and Methods

Though our analyses of the most commonly measured fine-root traits (N, D, RTD, and SRL) rely on established global databases rather than new observations, it is valuable to consider how these traits are generally measured. Most studies, including those in global trait databases, focus on distal fine roots ≤ 2 mm in diameter (Pregitzer et al., 2002). Fine-root N is typically quantified using an elemental analyzer where dried, homogenized root tissues are combusted. D and SRL are derived from scanned images of fresh roots processed with software such as WinRHIZO or RhizoVision Explorer (Seethepalli et al., 2021), and RTD is calculated as dry mass per unit root volume (Birouste et al., 2013). These standardized methods enable consistent comparisons across studies, plant species, and locations.

To pair fine-root traits in the GRooT database with SOC values, we overlaid georeferenced root trait observations with ISRIC’s SoilGrids 2.0 map. This map product is derived from the full ISRIC soil observation database (with data inputs from WoSIS- World Soil Information Service) that is comprised of almost 200,000 georeferenced profiles from 173 countries which represent more than 800,000 soil horizons (Poggio et al., 2021). While the SoilGrids2.0 map provides global coverage, its accuracy is more uncertain (range between 5th and 95th percentiles of predictions at each grid cell) in areas with high SOC and in high-latitude regions due to sparsity of soil profile data (Poggio et al., 2021). SOC concentrations (mg/g) for 0–1 m soil depth were calculated as depth weighted average using five soil layers (0–5 cm, 5–15 cm, 15–30 cm, 30–60 cm, 60-100cm). We paired root trait observations with associated GPS coordinates with ISRIC SoilGrids 2.0 to determine SOC concentrations at root sampling locations. We then calculated species averages for the fine-root traits (N, D, RTD, and SRL) and averaged SOC concentration associated with root sampling locations for each species. This resulted in 375 species-level, paired root trait and SOC observations that are the basis of the presented analyses. SOC values exhibited a non-normal distribution, which ruled out regression-based analyses for comparing root traits directly to SOC concentrations. Consequently, we categorized soils into ‘organic’ and ‘mineral’ groupings based on their SOC concentration from 0- 100 cm. The 1m depth increment was considered so that the organic category represents locations with high organic content throughout the rooting zone rather than just in a shallow organic horizon. We determined the cutoff between organic and mineral soils by performing a breakpoint analysis on SOC versus rank order using average SOC values by plant species location. This yielded three break points: 3.7, 19.6, and 50.5 mg C/g. When applied to the species-level root data, these three breakpoints would have resulted in 23%, 76%, or 87% of the observations being associated with plants growing in mineral soils. We chose the middle value (19.6 mg C/g) for differentiating organic from mineral soils because the lowest breakpoint identified (3.7 mg C/g)

was deemed too low to represent the minimum SOC of organic soil profiles and the upper value (50.5 mg C/g) would have resulted too many high-end SOC values in our database being categorized as mineral (see Fig. 2 & Fig S3). After categorizing observations with SOC greater than 19.6 mg C/g as organic and categorizing the remainder of observations as mineral, we determined how species-specific root traits and their RES relationships differ between organic versus mineral soils by conducting Principal Component Analyses (PCA) on species-averaged root traits. PCAs were performed on our entire dataset (n = 375 observations), mineral soils only (n = 284 observations), and organic soils only (n = 91 observations). We calculate correlations between unique pairs of the four fine-root traits for both organic and mineral soil types and the statistical significance of these correlations was determined by a Pearson test ($\alpha = 0.05$). We also conducted three phylogenetically corrected PCAs on our entire dataset, mineral soils, and organic soils to determine how shared evolutionary history might impact our results.

We performed two- and three-way ANOVAs to investigate how species-specific root traits may be shaped by varying levels of SOC, mycorrhizal association, and PFT. Mycorrhizal fungal association types (ErM, AM, ECM, and NM) were appointed within GRooT (Guerrero-Ramirez, 2021) based on the FungalRoot global database (Soudzilovskaia et al., 2020). To normalize root trait observations, N was square-root transformed, while D, RTD, and SRL were log-transformed. For some PFTs and mycorrhizal associations, only a few datapoints existed or observations spanned only one soil type, which led to an imbalanced statistical design. To address this, we removed ErM (52 observations only in mineral soils) from the mycorrhizal analysis and removed ferns (12 observations) and sub-shrubs (2 observations) from the PFT analysis. Differences between root trait observation means for organic versus mineral soils were evaluated with two-way ANOVAs and post-hoc tests. Analyses and graphing were completed in R version 4.4.0 (R Core Team 2024).

Results

Of the fine-root observations included in GRooT, 76% were made on plant species growing in mineral soils as defined by our breakpoint analysis (Fig. 2); this species-specific pattern held for individual fine-root trait observations (N, D, RTD, and SRL). Interestingly, all four mean trait values differed between organic and mineral soils (Table S1, Figure S4). Species-level observations for plants growing in organic soils had, on average, 29% lower root N ($p < 0.0001$), 1.8% larger D ($p = 0.001$), 69.1% lower SRL ($p < 0.0001$), and 14.2% greater RTD ($p < 0.0001$) (Fig. 2).

The PCA of the entire GRooT dataset indicated the same axes of variation as the RES laid out by Bergmann et al. (2020) (Fig. 3A, Table S2). However, when we separated GRooT observations into organic versus mineral soils, the RES axes became skewed. PCAs performed on species rooted in mineral soils (Fig. 3B, Table S3) tended to resemble the PCA from the entire GRooT dataset, while the PCA performed on species rooted in organic soils showed a positive correlation between root N and root D (Fig. 3C, Table S4). All three PCAs captured a similar cumulative portion of variation within the first two axes (0.72–0.75, Table S4). The phylogenetically corrected PCA (Figure S4) yielded similar patterns: it also revealed altered trait tradeoffs between organic and mineral soils. Fine root N correlates with D in

the uncorrected PCA while it correlates with RTD in the phylogenetically corrected analysis. Because our goal was to examine the RES framework as developed in Bergmann et al. (2020), which is based on uncorrected PCA axes, we focus our discussion on the regular PCA results.

Further information about trait-trait tradeoffs for mineral versus organic soils can be gleaned by examining correlations between individual traits (Table S5). Plant species rooted in organic soils had root traits with a positive relationship between N and D, but mineral soils did not. In turn, the relationship between N and SRL was negative for organic soils but positive for mineral soils. D and RTD in organic soils had a negative relationship, but mineral soils did not. The relationship between RTD and SRL was not significant in organic soils but was negative in mineral soils. The phylogenetically corrected PCA showed the same trait relationships exist regardless of phylogeny in mineral soils, but the relationships changed in organic soils (Figure S4). Instead of a positive relationship between N and D, the phylogenetically corrected PCA showed a positive relationship between N and RTD, suggesting N's covariation with other traits differs depending on phylogenetic relatedness for plants growing in organic soils.

When we investigated variation within fine-root N, D, RTD, and SRL observations, we found that PFT, mycorrhizal type (MT), and soil type (ST) were important predictors (Table 1). PFT consistently emerged as a dominant predictor for all root traits. Interactions between PFT and mycorrhizal fungal association type influenced D and SRL, while the interaction between PFT and soil type also impacted all fine root traits except RTD. All three contextual variables were together crucial for predicting the location of roots observations within the RES.

Table 1 Three-way **ANOVA for discerning influence of PFT, mycorrhizal association type, and soil type on fine-root traits** (N: square root transformed [√]; SRL, RTD and D: log transformed [$\log_e$]), where * denotes significant impacts. PFT: plant functional type; Df: degrees of freedom; F value: strength of signal compared to noise.

Trait	Term	Df	Sum Sq	Mean Sq	F value	p-value	Significance
N √	**PFT**	**7**	**68.79**	**9.827**	**11.077**	**<0.0001**	***
	Mycorrhizal fungal association type	**6**	**28.32**	**4.719**	**5.32**	**<0.0001**	***
	Soil type	1	2.53	2.535	2.857	0.092	
	PFT × Mycorrhizal association type	9	8.89	0.987	1.113	0.353	
	PFT × Soil type	**4**	**11.75**	**2.938**	**3.312**	**0.011**	*
	Mycorrhizal association type × Soil type	2	3.42	1.711	1.928	0.147	
	Mycorrhizal association type × PFT × Soil type	3	0.39	0.129	0.145	0.933	
	Residuals	306	271.47	0.887			
RTD $\log_e$	**PFT**	**7**	**84.1**	**12.014**	**30.78**	**<0.0001**	***
	Mycorrhizal association type	**6**	**5.74**	**0.956**	**2.458**	**0.025**	*
	Soil type	1	1.37	1.368	3.516	0.062	
	PFT × Mycorrhizal association type	9	5.8	0.644	1.655	0.099	
	PFT × Soil type	4	0.98	0.245	0.629	0.642	
	Mycorrhizal association type × Soil type	2	0.15	0.073	0.189	0.828	
	Mycorrhizal association type × PFT × Soil type	3	0.51	0.171	0.438	0.726	
	Residuals	306	119.09	0.389			
D $\log_e$	**PFT**	**7**	**23.66**	**3.38**	**24.592**	**<0.0001**	***
	Mycorrhizal association type	**6**	**1.41**	0.235	1.712	0.118	
	Soil type	1	**0.02**	0.022	0.16	0.69	
	PFT × Mycorrhizal association type	**9**	**3.41**	**0.378**	**2.754**	**0.004**	**
	PFT × Soil type	**4**	**1.65**	**0.413**	**3.006**	**0.019**	*
	Mycorrhizal association type × Soil type	**2**	**0.94**	**0.472**	**3.431**	**0.034**	*
	Mycorrhizal association type × PFT × Soil type	3	0.002	0.007	0.048	0.986	
	Residuals	306	42.05	0.137			
SRL $\log_e$	**PFT**	**7**	**350.5**	**50.07**	**71.368**	**<0.0001**	***
	Mycorrhizal association type	**6**	**18.2**	**3.04**	**4.331**	**<0.001**	***
	Soil type	1	0.35	0.351	0.493	0.483	
	PFT × Mycorrhizal association type	**9**	**17.92**	**1.99**	**2.832**	**0.003**	**
	PFT × Soil type	**4**	**9.71**	**2.432**	**3.463**	**0.008**	**
	Mycorrhizal association type × Soil type	2	2.4	1.211	1.718	0.181	
	Mycorrhizal association type × PFT × Soil type	3	1.6	0.543	0.768	0.513	
	Residuals	306	214.7	0.7			

Across root traits, soil type was a predictor on its own and/or showed interactions with PFT and mycorrhizal type (Table 1). To better understand the complex interactions between soil type and PFT as well as soil type and mycorrhizal type, we performed two-way ANOVAs with soil type and each of these variables separately (Figs. 4 and 5; Tables S9 & S11). When examining the relationship between PFT and soil type, we saw both variables significantly impacted fine-root N (panel A, p = < 0.0001, p = 0.001 respectively) and their interaction was also (p = < 0.002) (Fig. 4, Tables S8 and S9). PFT impacted fine-root D (panel B, p < 0.0001) though soil type does not (p = 0.601), but their interaction was more significant (panel B, p = 0.011). Both PFT and soil type influenced RTD (p < 0.0001, p = 0.044), as did their interaction (panel C, p < 0.0001). SRL is affected by PFT, soil type, and their interaction as well (panel D, p < 0.0001, p = 0.004, p = 0.025, respectively).

In contrast, root traits showed weaker separation by mycorrhizal association types and soil type (Fig. 5; Table S10). Mycorrhizal type and soil type both significantly affected all four root traits examined. The

interaction between mycorrhizal type and soil type was only significant for fine-root N concentration and RTD (Fig. 5, panel A, p = 0.020; p = 0.003).

Discussion

Root Trait Observations are Biased Toward Mineral Soils

We found that the foundational RES as outlined by Bergmann et al. (2020) heavily reflected observations from mineral soils, supporting our first hypothesis (H1). The original RES gradients (i.e., the conservation gradient between fine-root N and RTD and the collaboration gradient between fine-root D and SRL) were still present in our PCA when root trait observations were narrowed down to only include plant species occupying mineral soils (Fig. 3b). While the dominance of mineral-soil observations in the GRooT database likely reflects a historical sampling bias toward temperate and agricultural systems, it may also reflect a biological reality: organic soils are unique environments that impose physiological constraints such as anoxia and high acidity which limit the pool of specialized species capable of surviving there. Therefore, the "missing" data are both a research gap and a reflection of intense edaphic specialization (Blume-Werry et al., 2019; Hewitt et al., 2018; Iversen et al., 2010; Weber and Iversen, 2023).

Plant Species Rooted in Organic Soils Have Distinct Root Trait Tradeoffs

Our analyses also supported our second hypothesis (H2), revealing that fine-root traits of species rooted in organic soils occupied areas of the RES that differed from those rooted in mineral soils. Notably, fine-root N and D were positively correlated in organic soils, diverging from the patterns observed in mineral soils. The phylogenetically corrected PCA revealed a subtly different pattern (Figure S4): root N was more strongly aligned with RTD, and the N-D relationship weakened.

Crucially, both PCA approaches suggest a fundamental shift in root economic strategies in organic soils. This context appears to decouple traits that are typically linked within a PFT-driven framework. In high-C, low-nutrient environments, the metabolic cost of nutrient acquisition may force a re-weighting of orthogonal tradeoffs. For example, the weaker relationship between RTD and SRL in organic soils suggests that the trade-offs central to the RES operate differently in fluffy, low bulk density substrate, allowing roots to possess higher SRL. The lower N of roots in organic soils aligns with lower N availability, placing these roots on the “slow” end of the conservation gradient (Bergmann et al., 2020). Though the RES for all observations might have orthogonal axes, it doesn’t mean that a given species has to employ a strategy on one axis or another. For example, plants are not pursuing either a conservation gradient or collaboration gradient and only moving along one axis. All plants are negotiating both axes simultaneously. The relative strength of the collaboration versus conservation tradeoffs in these systems warrants further investigation into ErM-associated species, which are critical players in organic soils but have a limited number of observations.

Root Traits Vary with Soil Type, Mycorrhizal Association, and Plant Functional Type

We found support for our third hypothesis (H3): the influence of PFT and mycorrhizal association on fine-root traits is significantly modulated by SOC, shifting the coordination space of the RES in organic-rich environments. Roots growing in organic soils did not align with the global RES but rather had lower SRL and higher D, emphasizing reliance on nutrient acquisition via mycorrhizal partners. While PFT emerged as the strongest overall predictor of root traits, consistent with established patterns where trees exhibit greater fine-root D and graminoids possess lower RTD, the presence of significant PFT: Soil Type interactions for N, D, and SRL demonstrates that these patterns are contingent upon the soil context. While PFT classifications remain a robust tool for inferring belowground variation (Yang et al., 2023a), the high-SOC environment acts as a critical environmental filter that alters the magnitude and slope of trait expression, likely due to the presence or absence of plant species with a given set of highly-adapted traits.

Mycorrhizal colonization is traditionally mapped onto the RES collaboration axis as a positive correlation with root D (Bergmann et al., 2020), a relationship largely defined by AMF association. However, the significant positive interaction between mycorrhizal association and soil type for root D ($p = 0.034$) indicates that these collaboration rules may be fundamentally restructured in high-SOC systems. Given that ErM fungi can function both as symbionts and saprotrophs, they occupy a unique niche in acidic, nutrient-poor soils that may decouple traditional D-dependency trade-offs (Reed, 1989).

Our findings indicate that the collaboration continuum is not fixed but is instead re-weighted at the ends of what constitutes mineral and organic soils. Specifically, the distinctive trait distributions of ECM and ErM plants in organic soils compared to AMF-associated species in mineral soils underscore recent calls for a more nuanced, context-dependent representation of mycorrhizal strategies (Phillips et al., 2019). Fine root traits are dynamic and challenging to predict as well as interpret. The soil that species grow in provides important context for trait tradeoffs and rooting strategies.

Implications for Predicting Root Impacts on Biogeochemical Cycling in Highly Organic Soils

Our narrative synthesis highlights the critical need for further research into fine-root traits and nutrient acquisition strategies within organic soils, particularly in the context of their role in C storage, nutrient cycling, and mycorrhizal interactions. Our findings indicate that the RES, as traditionally understood, does not fully capture trait tradeoffs in high-C environments. This discrepancy is likely driven by the extreme edaphic specialization of plants growing in organic soils, which may host fewer specialized species than mineral soils, a biological reality that is currently confounded by sampling biases within global databases. The observed positive correlation between fine-root N and D in organic soils suggests that functional strategies in these ecosystems operate differently from those in mineral soils, potentially decoupling or restructuring trait relationships that are typically linked within a PFT-driven framework.

Upon investigation, the trees are driving this decoupling (Figure S5). Furthermore, our analysis demonstrates that both mycorrhizal type and PFT significantly shape fine-root traits, with soil type acting as an important secondary modifier that controls these PFT-specific expectations.

Our binary definition of what constitutes ‘organic’ compared with ‘mineral’ soils influenced our results. We could not fit regressions with our unbalanced SOC data, thus we opted to use a breakpoint analysis to differentiate organic from mineral soils. Additionally, while SoilGrids 2.0 is an essential tool, there are still geographic areas of high uncertainty in arid and high latitude soils (Poggio et al., 2021). Subsequent research could look at a more balanced set of root trait observations across a SOC gradient to determine if these environments host inherently fewer specialized species or simply a different suite of trait strategies.

Future research should expand large-scale trait datasets to better represent the upper layers of organic soils, where root activity is most concentrated, and evaluate how different PFTs occupy the RES under contrasting soil conditions. Such efforts will help determine the extent to which RES axis shifts reflect root trait plasticity. Greater inclusion of shrubs, herbs, and especially ErM-associated species will be essential for refining global models of root trait variation. As PFT, mycorrhizal association type, and soil type jointly shape fine root traits and their relationships, understanding how specialized root adaptations respond to high-SOC environments is crucial for predicting the state of these globally significant root C pools.

Declarations

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Competing interests

The authors declare that they have no known conflicts of interest that could have influenced the work reported in this study.

Author contributions

KC, VS, and CMI conceived of analysis, JK assisted in data extraction from SoilGrids2.0. KC performed data analysis and wrote an initial draft of the manuscript. SK assisted with generating supplementary Figs. 1 and 2. All coauthors provided feedback on several manuscript versions.

Data availability

R packages used for analyses:

emmeans, plyr, tidyverse, ggbiplot, grid, agricolae, devtools, Hmisc, ggrepel, ggplot2, viridis, multcompView, patchwork, cowplot, plotly, tibble, adephylo, phylobase, ape, rotl, phangorn, and scales (Lenth, 2024; Wickham *et al.*, 2011; Wickham, 2016; Wickham et al., 2019; Wickham et al., 2022; Wickham et al., 2023; Vu *et al.*, 2024; de Mendiburu, 2023; Harrell, 2024; Iowikowski, 2024; Garnier et al., 2024; Graves et al., 2024; Pedersen, 2024; Wilke, 2024; Sievert, 2020; Müller and Wickham, 2025; Jombart et al., 2010; Paradis et al., 2024; R Hackathon, 2024; Michonneau et al., 2016; Schliep, 2011.

The GRooT database is available here:

Guerrero-Ramírez, N. R., Mommer, L., Freschet, G. T., Iversen, C. M., McCormack, M. L., Kattge, J., Poorter, H., van der Plas, F., Bergmann, J., Kuyper, T. W., York, L. M., Bruelheide, H., Laughlin, D. C., Meier, I. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., Valverde-Barrantes, O. J., … Weigelt, A. (2021). Global root traits (GRooT) database. *Global Ecology and Biogeography*, *30*(1), 25–37. https://doi.org/10.1111/geb.13179.

The SoilGrids 2.0 database is available here:

Poggio, L., de Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., & Rossiter, D. (2021). SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. *SOIL*, *7*(1), 217–240. https://doi.org/10.5194/soil-7-217-2021.

The code supporting the findings of this study are openly available on GitHub at https://github.com/KathleenCoffman/GROOTSG_manuscript

Supplemental materials (separate document)

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Figures

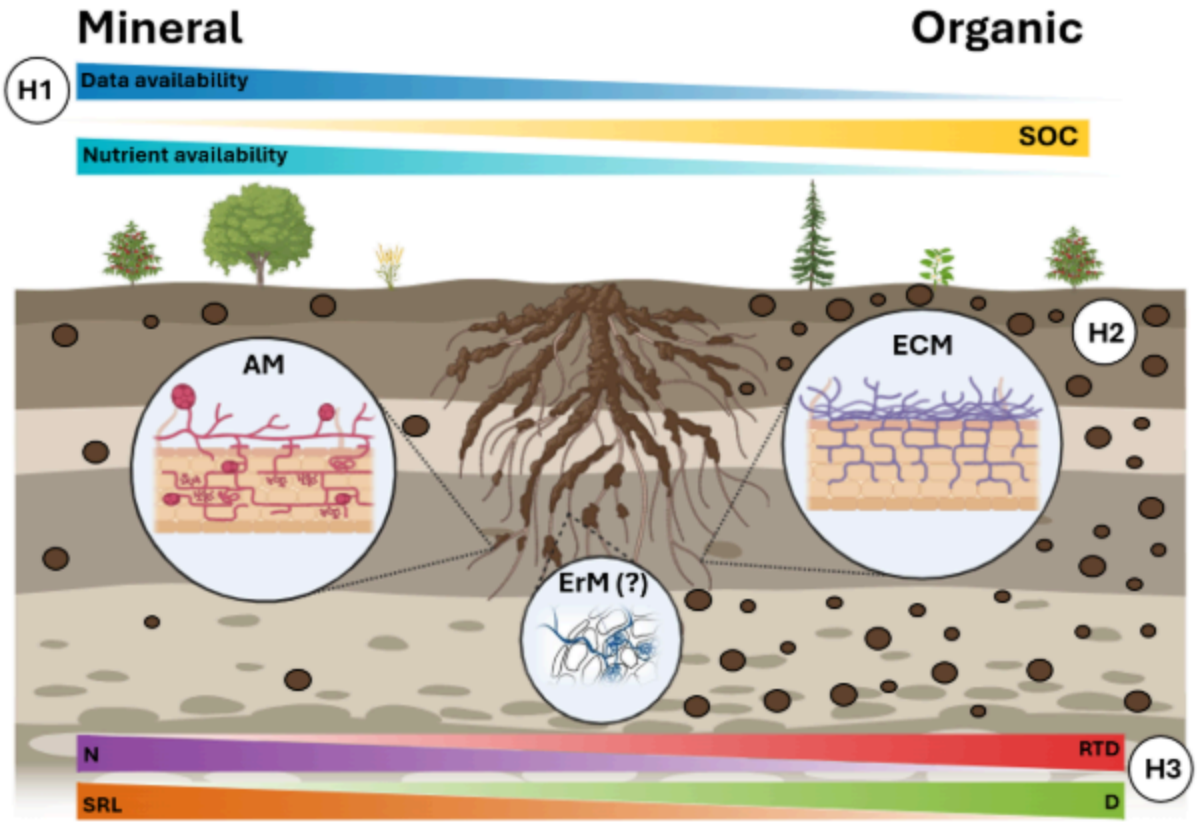


Figure 1

Hypothesized relationships between root traits and SOC and the role of plant functional types and mycorrhizal associations.*H1: Most of the root trait observations used to develop the current RES were from mineral soils. H2: The root trait space occupied by plant species rooted in highly organic soils is different from those rooted in mineral soils. H3: There will be differences in root traits among species, and those differences will be associated with soil type (organic versus mineral), mycorrhizal associations, and PFT groupings. RES (Root economic space of Bergmann et al. 2020); PFT (Plant functional type); AM (Arbuscular mycorrhizal fungi); ECM (ectomycorrhizal fungi); ErM (ericoid mycorrhizal fungi); SRL (Specific root length); N (Root N content); D (root diameter); RTD (Root tissue density). Created in https://BioRender.com*

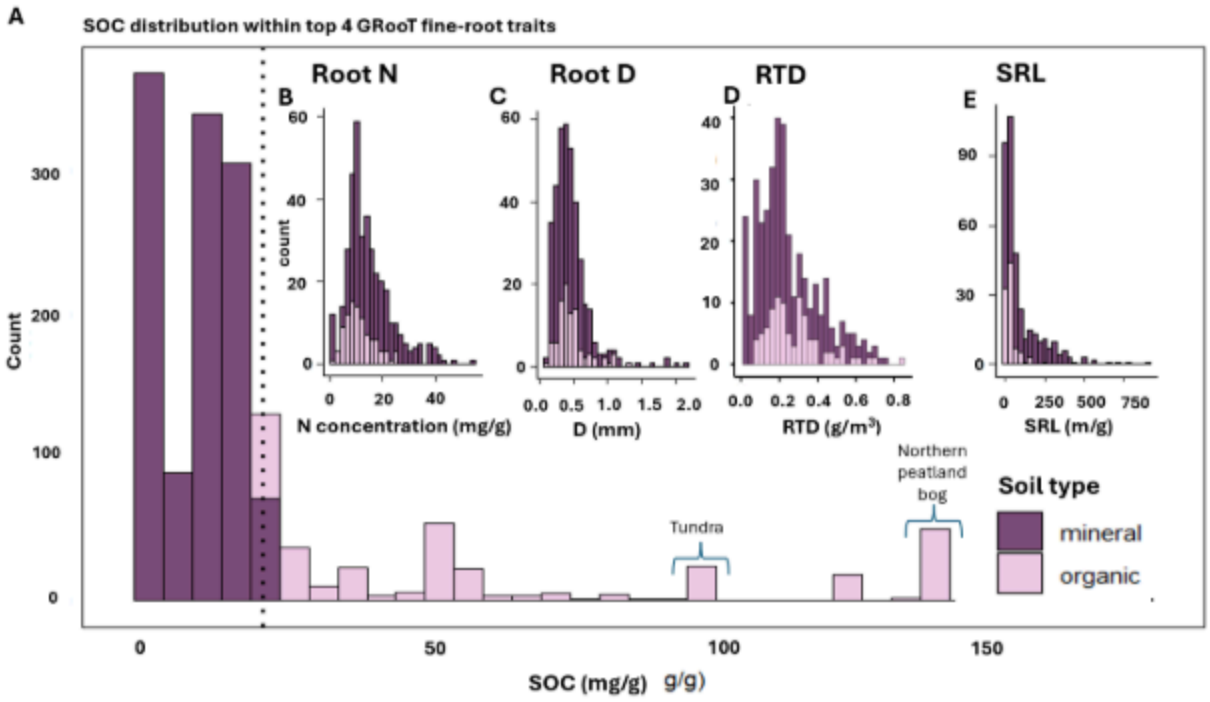


Figure 2

Low representation of fine-root traits within highly organic soils. *Panel A shows observations of fine-root traits nitrogen (N), average diameter (D), root tissue density (RTD), and specific root length (SRL) pooled together from GRooT observations as an average of all traits across an average SOC gradient. Panels B-E show counts of each trait's average values according to soil type. The dotted line in panel A denotes our chosen breakpoint of 19.6 mg/g SOC to categorize mineral and organic soils.*

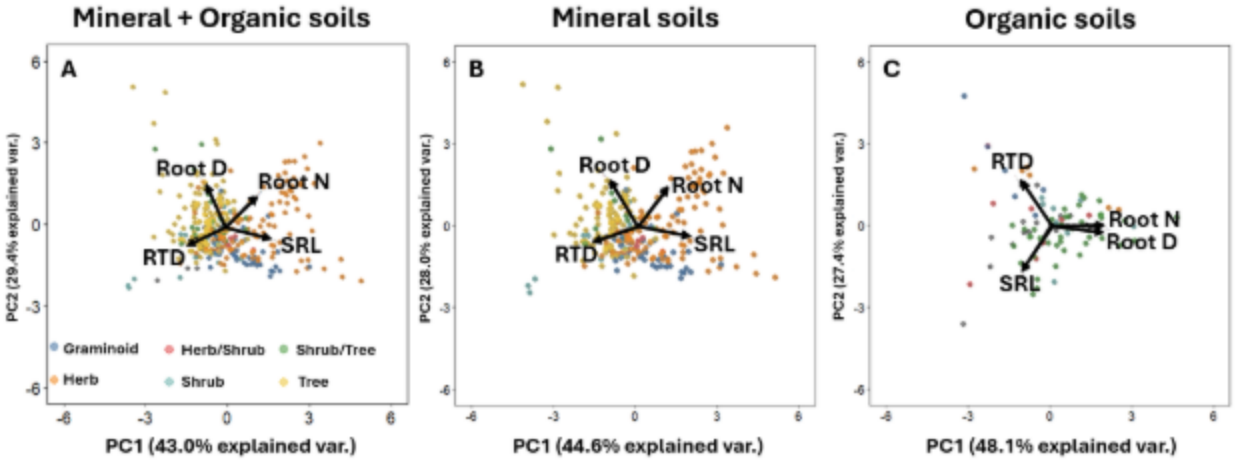


Figure 3

PCAs of all data versus those of species rooted in mineral soils and species rooted in organic soils revealed root trait tradeoffs are dependent on soil type*. Panel A shows the fine-root economics space at the species level (n = 375 species). Panel B shows the fine-root economics space at the species level within mineral soils (n = 284). Panel C shows the fine-root economics space within organic soils (n = 91) and shows a notable shift in trait relationships.*

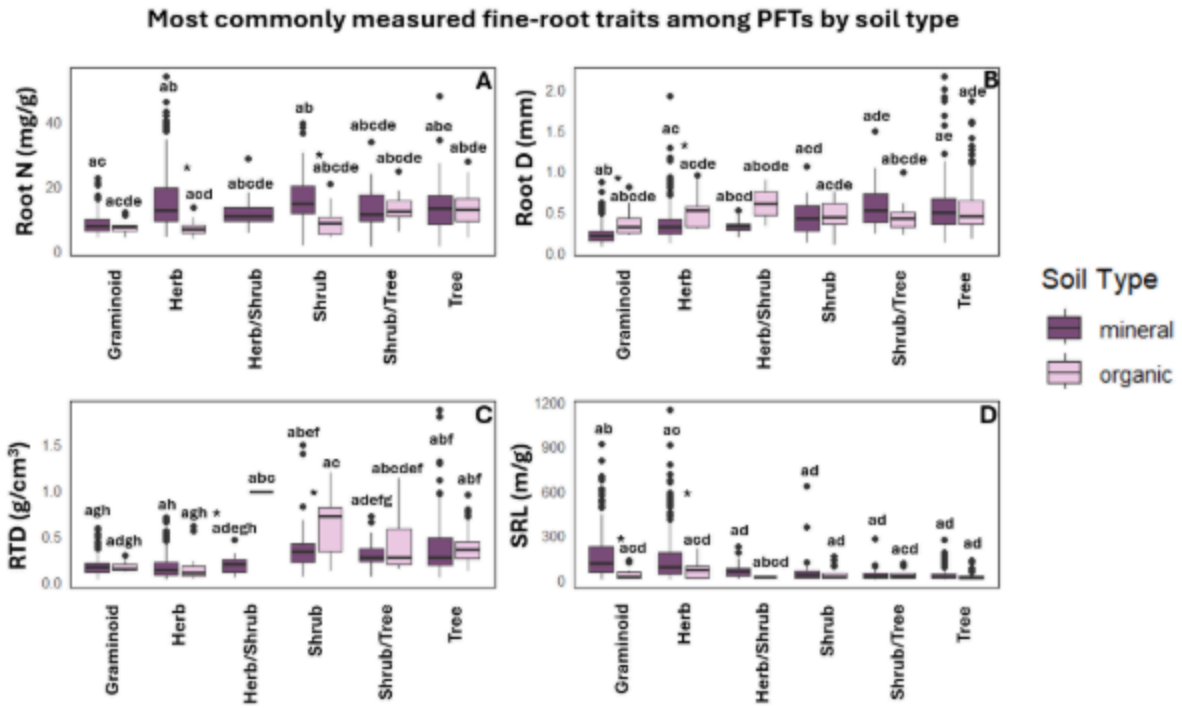


Figure 4

Commonly measured fine-root traits among PFTs and soil types. *Data are grouped by PFT and soil type and were tested for significance with a two-way ANOVA. Asterisks represent significant differences within a given PFT according to soil type while letters represent differences among PFTs.*

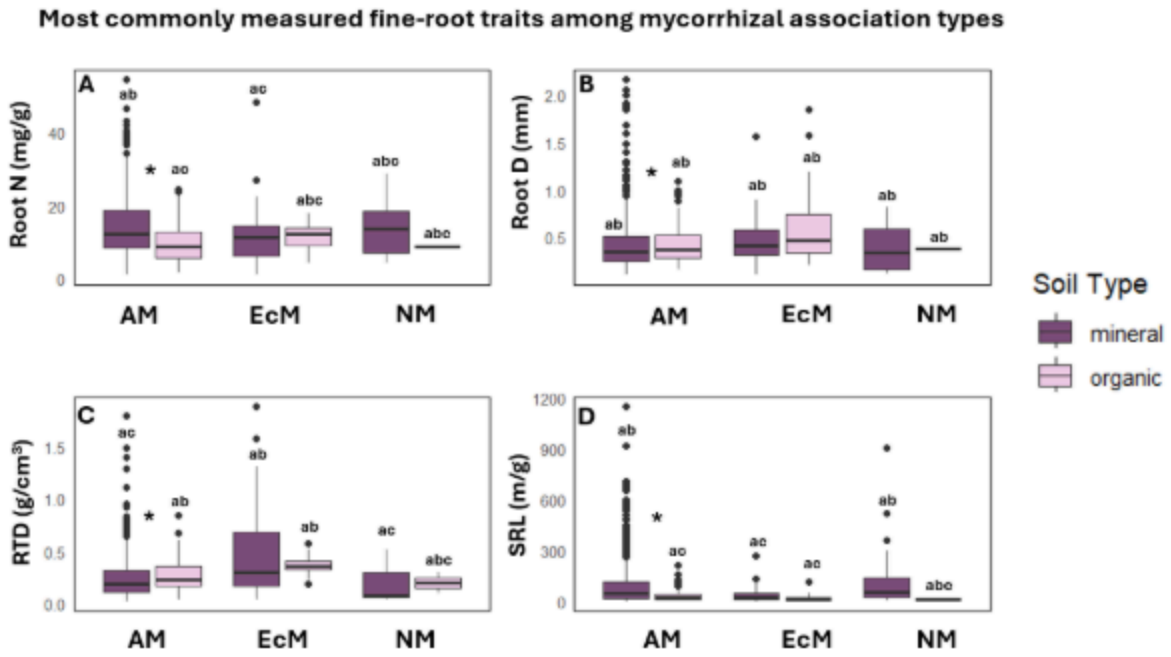


Figure 5

Root trait variation among mycorrhizal types in mineral and organic soils. *Data are grouped by mycorrhizal association type and soil type and were tested for significance with a two-way ANOVA. Asterisks represent significant differences within mycorrhizal type according to soil type while letters represent differences among mycorrhizal types. AM: Arbuscular mycorrhizal fungi; EcM: Ectomycorrhizal fungi; NM: Nonmycorrhizal fungi.*

Supplementary Files

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