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Contrasting Depth Dependencies of Plant Root Presence and Mass Across Biomes Underscore Prolific Root-Regolith Interactions

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Abstract Root distributions are typically based on root mass per soil volume. This plant-focused approach masks the biogeochemical influence of fine roots, which weigh little. We assert that centimeter-scale root presence-absence data from soil profiles provide a more soil-focused approach for probing depth distributions of root-regolith interfaces, where microsite-scale processes drive whole-ecosystem functioning. In 75 soil pits across the continental USA, Puerto Rico, and the Alps, we quantified fine and coarse root presence as deep as 2 m. In 70 of these pits we estimated root mass and created standardized metrics of both data sets to compare their depth distributions. We addressed whether: (a) depth distributions of root presence-absence data differ from root mass data, thus implying different degrees of root-regolith interactions with depth; and (b) if root presence or any depth-dependent differences between these data sets vary predictably with environmental conditions. Presence of fine roots exhibited diverse depth-dependent patterns; root mass generally declined with depth. In B and C horizons, standardized root presence was greater than standardized root mass; random forest analyses suggest these discrepancies are greater in B horizons with increasing mean annual precipitation and in C horizons with increasing mean annual temperature. Our work suggests that deep in the subsurface, biogeochemical and reactive transport processes result from more numerous root-regolith interfaces than mass data suggest. We present a new paradigm for discerning patterns in depth distributions of root-regolith interfaces across multiple biomes and land uses that promotes understanding of the roles of those interfaces in driving key critical zone processes.

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Key Points:

- Fine and coarse root presence or absence measurements in 75 deep soil profiles open an illuminating way to characterize root distributions
- Root presence depth distributions contrast with root mass, underscoring distinct hydrologic and biogeochemical roles of fine and coarse roots
- Discrepancies in depth profiles of root presence vs. root mass are driven by distinct ecosystem features at different depths

Supporting Information:

Supporting Information may be found in the online version of this article.

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Plain Language Summary Understanding how plant roots are distributed throughout soil layers is important for predicting where plants promote transformations of soil carbon, generate soil and redistribute nutrients, and modify water flows. All these processes affect climate by regulating how well plants take in atmospheric CO_2. In 75 soil pits across the US and the Alps, we quantified fine and coarse root presence as deep as 2 m. In 70 of these we estimated root mass, permitting comparison of these data sets' variation with depth. Fine root presence exhibited especially great variation with depth compared to root mass. Differences between the data sets were greatest in B and C horizons and reflect numerous fine roots that weigh little. Discrepancies between total root presence and mass were linked to mean annual precipitation (MAP) in B horizons and mean annual temperature (MAT) in C horizons, with the root presence metric increasingly dwarfing root mass in these horizons as MAP and MAT increases. We illuminate how, deep in the subsurface, plant-mediated carbon, water, and nutrient transformations emerge from more numerous root-soil interfaces than mass data suggest. Our work presents a new paradigm for discerning depth-dependent patterns of the root-soil interactions that drive the ecosystem functions that sustain life.

1. Introduction

The extent to which Earth's regolith (Merrill, 1897; Richter et al., 2020) is rooted determines critical ecosystem functions. Roots and their growth and death shape the belowground arrangement of soil particles and thus the pores that surround them (Angers & Caron, 1998; Barley, 1953; Clark et al., 2003; Guthrie et al., 2025; Hinsinger et al., 2009; Oades, 1984; Rillig et al., 2015), modulating fluid and solute flows and associated ecosystem productivity (Sullivan et al., 2022). The volume of rooted regolith helps define the volume throughout which organic carbon (C)—whether from root tissue itself, root exudates, or microbes in the rhizosphere—is distributed belowground (Callesen et al., 2016; Dietzel et al., 2017; Jobbágy & Jackson, 2000; Kravchenko et al., 2019; Poeplau et al., 2021). Rooted regolith volume further determines the water and nutrients potentially available to vegetation, though the depths at which roots may derive water and macro- and micro-nutrients often are incongruent.

Roots, and particularly fine roots, can serve different purposes across depths. For example, in grasslands, the majority of root water uptake appears to be derived from near-surface soil layers, though fine roots persist at great depths in these systems (Asbjornsen et al., 2007; Nippert & Knapp, 2007; O'Keefe & Nippert, 2017). In other ecosystems, rooting depths are linked to the depths at which regolith water is stored (Y. Fan et al., 2017), with even deep, rock-derived moisture contributing to forest water balance (Rempe & Dietrich, 2018). Moreover, within a given depth interval, roots function differently to access varied abundances of organic matter- and mineral- or rock-bound nutrients (Hauser et al., 2023; Newman et al., 2020). Organic matter-bound nutrients tend to proliferate near the soil surface, while deeper roots tend to experience greater exposure to mineral- and rock-bound nutrients. The differential depth distribution of organic and mineral nutrient sources of many terrestrial ecosystems requires contrasting exudates for nutrient liberation (i.e., enzyme- vs. acid-based), drives nutrient uplift, and feeds back to the distribution of roots throughout the regolith (Hauser et al., 2020; Jobbágy & Jackson, 2004; Soper et al., 2018).

Root abundance is often examined in a way that reflects plant-focused research questions (Figure 1a). Estimates of rooting depth distributions are often based on root mass or root C per unit volume of soil (Freschet et al., 2021); depth distributions of root specific length per unit volume of soil are less frequently reported (cf. Ostonen et al., 2007) due to the more time-consuming nature of such assays. The root mass approach reveals general declines in root mass with depth in a diversity of biomes that imply a decline with depth in root-regolith interactions, here defined as the interplay of belowground, microsite-scale biological, physical, and chemical processes that drives whole-ecosystem functioning. These declines in root mass with depth are often approximated using some form of an exponential decline function such as:

$$Y = A \cdot e^{-\beta \cdot d}$$

where Y is root mass, A is root mass at the soil surface, d is soil depth, and β is a modeled parameter defining the steepness of root mass decline with depth. In this formulation, β approximates the negative natural log of β

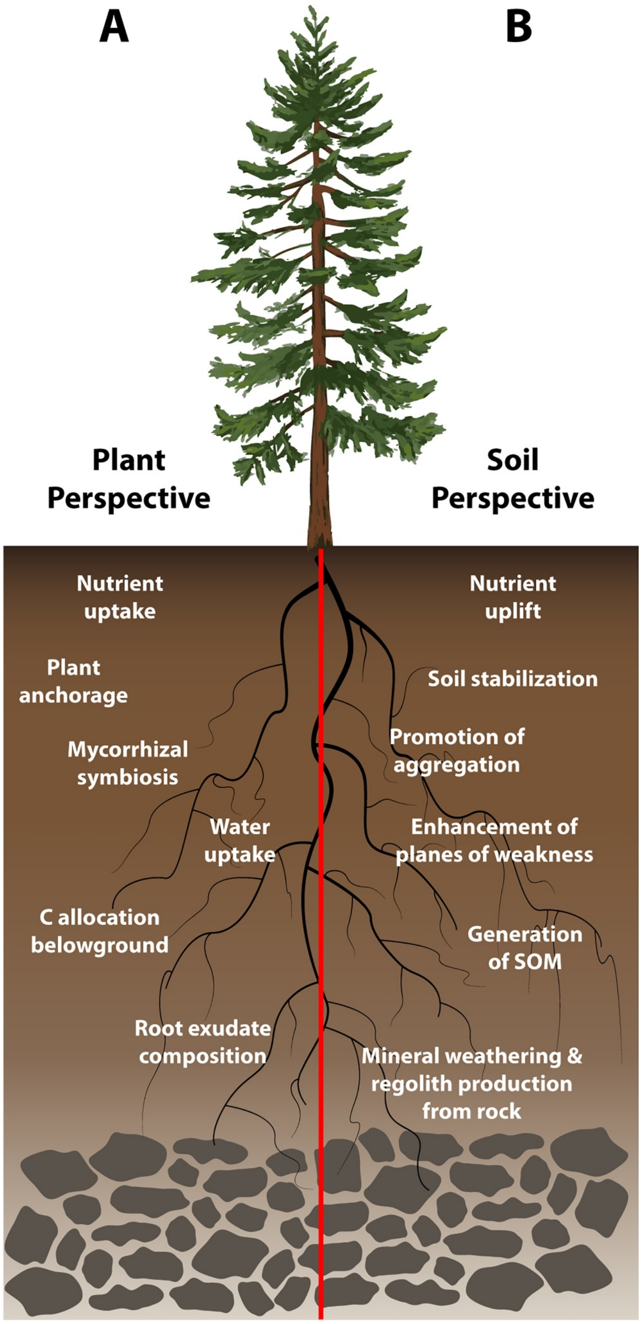

Figure 1. Contrasting targets of research of plant- (a) and soil- (b) focused researchers who investigate root functions in the soil they inhabit. SOM, soil organic matter.

presented in Jackson et al. (1996), who model the cumulative fraction of root mass with depth. Though roots can exhibit bimodal mass distributions in some ecosystems (M. Lu et al., 2025), exponential decline functions have proven useful for categorizing rooting depth distributions by biome, projecting how humans modify rooting depths at regional and global scales, and revealing global-scale variation in belowground plant investments (Hauser et al., 2022; Jackson et al., 1996; Tumber-Dávila et al., 2022; Zeng, 2001). The β values also are leveraged in a variety of hydrologic and land surface models, some of which represent global terrestrial water, energy, and C land-atmosphere exchange in Earth system models (ESMs). For example, in the Community Land Model version 5 (CLM5), β values emerging from inferred exponential declines of root mass with depth help define soil water and C fluxes and soil water removed from each soil layer, and indirectly control the partitioning of precipitation into runoff and transpiration by influencing near-surface moisture (Lawrence et al., 2019). The shape of root mass-derived rooting depth distributions thus has important implications for ESM projections of water, C, and energy exchanges between the land surface and atmosphere, and inferences about belowground plant investments and root-regolith interactions—those biological, physical, and chemical processes that intersect to drive ecosystem functioning.

In spite of the utility of plant-focused approaches for multiple research questions about root distributions, root mass measurements present a key challenge if we seek a predictive understanding of the influence of roots on the subsurface and the more soil-derived ecosystem functions that emerge from root-regolith interactions. Indeed, the extent of root-regolith interfaces is difficult to represent using root mass values, which are dominated by coarse roots. Fine roots generally exhibit relatively low mass but higher surface area per unit mass than coarser roots (Freschet et al., 2021). Compared to relatively coarse roots, fine roots thus respire more rapidly (Makita et al., 2012; Paradiso et al., 2019), can promote greater accrual of soil organic C (SOC; Malhotra et al., 2025), generate more root exudates (Guyonnet et al., 2018; Meier et al., 2020; Sun et al., 2020), grow faster (Eissenstat, 1991), support larger rhizosphere microbial communities (L. Wang et al., 2020), and exhibit greater turnover (Hou et al., 2024; McCormack et al., 2012) and acquisition of both water (Bachofen et al., 2024) and nutrients (Cochavi et al., 2020). As a result, fine roots play an outsized role in many ecosystem processes given their relatively meager mass and that root and rhizosphere volumes are dwarfed by whole-soil volume in many systems (e.g., Schlüter et al., 2018; Stevenson, 1967; Wiersum, 1961). Such mismatches between root mass and the extent of root-regolith interactions are likely to be particularly acute deep in soil profiles. Deep in the subsurface, the tendency of roots to extend into pore spaces with diameters greater than themselves (Wiersum, 1957) means that coarse roots have fewer spaces available to them than fine roots and must make room for their growth, a process that requires an increase in the density of the surrounding soil (Martinez et al., 2021). Thus, fine root growth tends to dominate over coarser roots in relatively deep soil (e.g., J. Fan et al., 2016). This, combined with the high process rates promoted by relatively fine compared to coarse roots, suggests that mass-derived rooting-depth distributions likely underestimate the deep root-regolith interactions that define many ecosystem functions.

Root presence-absence data offer a different way of conceptualizing how root-regolith interactions, and thus how many ecosystem functions, vary with depth and drive multiple critical zone processes. Historically, various forms of root presence-absence data have been generated during root mapping efforts in the field (e.g., Dauer et al., 2007; Dauer et al., 2009; van Noordwijk et al., 2000; Weaver & Bruner, 1927). Assessments of root presence or absence on an areal basis, when conducted at an appropriate spatial scale, enable us to estimate volumes of soil intimately affected by root presence and activities. Quantifying root presence or absence within a soil profile at the centimeter scale, for example, allows for detailed, spatially-explicit estimates of depth-varying root-regolith interactions (Billings et al., 2018; Hauser et al., 2020; Jarecke et al., 2024; Souza et al., 2023; L. Wang et al., 2025). Such an approach shifts the focus from the depth-varying, belowground C investments and resource uptake of the plants to the soil, and showcases the depth-dependent volume of soil occupied by, and thus interacting with and modified by, roots.

Given that roots push soil profiles along developmental trajectories that thicken the volume of material available for rooting (Alban, 1982; Hauser et al., 2023; Jobbágy & Jackson, 2001; Stone, 1975; Sullivan et al., 2019), we advocate that it is of equal importance to consider a soil-centered (Figure 1b) approach to root distributions. This approach considers the volume of soil immediately surrounding roots and thus most intimately influenced by them. It is particularly helpful when investigating the influence of plants on belowground processes and consequently their role in governing water and C fluxes to the atmosphere and in driving soil development. Global-scale evidence is mounting that the depths to which roots extend into the regolith, and thus the volume of rooted regolith, is changing via multiple mechanisms (Billings, Sullivan, et al., 2024; Hauser et al., 2022). However, such root mass-derived estimates do not explicitly capture the volume of soil most immediately impacted by roots. As such, understanding the role of roots from a soil-centered approach seems especially important. While the gold standard for quantifying root-regolith interactions is arguably best accomplished through the quantification of root surface area or, perhaps, root length density (Bardgett et al., 2014; Gregory, 2006; Guerrero-Ramírez et al., 2021; Jackson et al., 1997), these studies require *ex situ* measurements and are typically conducted at few locations due to the labor-intensive nature of the work (Wiersum, 1961). However, depth distributions of root presence-absence data, obtained in situ with far less labor than root surface area and root length density measurements, may provide a proxy for understanding variation across depth in root-regolith interactions given robust, positive correlations between root counts and root length density (Dauer et al., 2009).

Here, we compare root presence-absence and root mass data from a diversity of ecosystems. To our knowledge, this is the first comparison of depth distributions of root mass with root presence-absence data that applies consistent methodologies across a wide array of vegetation and soil types. We address two questions: (a) How do depth distributions of root presence-absence data and root mass data differ? and (b) What are the environmental conditions that drive root presence and depth-dependent differences between these types of data? We present depth distributions of root presence for two root size classes derived from 75 soil pits. We estimated the soil volume influenced at the 1-cm spatial scale by these root size classes. For most of these pedons, we compared presence-absence-derived depth distributions with root mass data obtained from the same soil pits. We demonstrate how root presence-absence data present a contrasting view of the degree to which root-regolith interactions vary with depth, and offer a pathway to greater understanding of the mechanisms by which vegetation transforms the biological, chemical, and physical character of the subsurface. Our work offers a way forward for testing key belowground parameters in hydrologic models and in ESMs used to project land-atmospheric coupling and ecosystem functioning. Finally, it provides benchmark values of regolith volumes closely influenced by roots to which we can compare future estimates as climate and land cover continue to change in the Anthropocene.

2. Methods

2.1. Root Presence-Absence Quantification and Assumptions

We estimated the soil influenced by roots at the 1-cm scale by excavating 75 soil pits in multiple ecosystems representing a range of different climate conditions, vegetation and soil types, lithologies, and land-use histories (Table S1 in Supporting Information S1, Figure 2). Most soil pits were excavated to either the depth at which digging became unfeasible ("depth of refusal") or ~2 m, whichever was shallower. Most soil pits (52) were characterized by USDA Natural Resource Conservation Service (NRCS) staff scientists. Twenty-three pits were characterized by soil scientists trained in pit characterization using NRCS methods; all of these individuals have substantial experience in pedology. In each pit, we ensured the pit profile was cleaned of debris and took photographs of the pit face, onto which we placed measuring tapes for scale. We ensured that each photo was taken with the line of sight perpendicular to the vertical pit face, and that the area photographed was broadly representative of visible soil features and root abundance across the pit face area. Wherever possible, pits were dug so

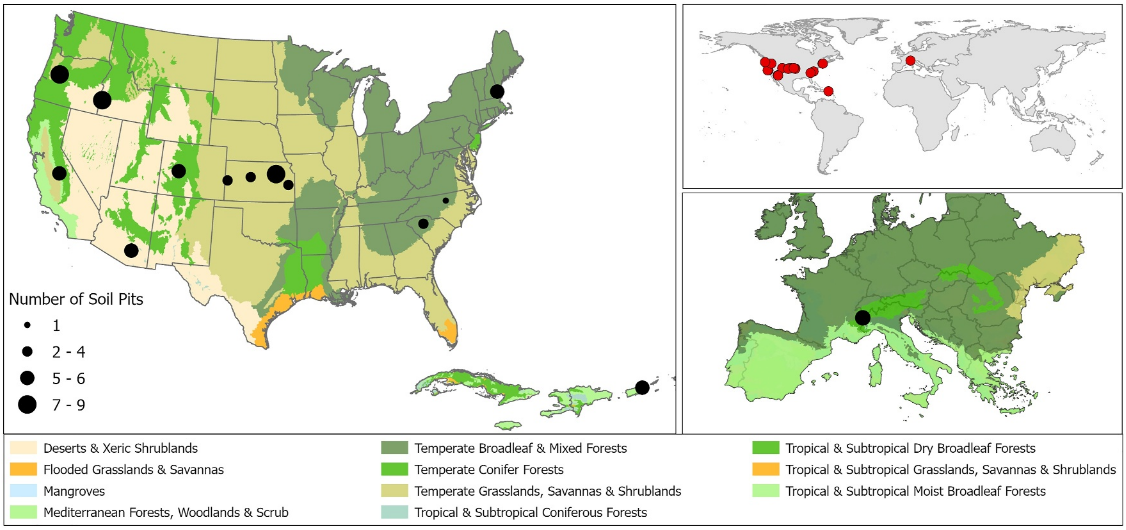

Figure 2. Map of soil pits excavated in the continental US, Puerto Rico, and the Italian Alps for this study. Regions are colored by the specified bioclimatic regions; symbol size reflects number of soil pits in a location.

that the working pit face did not face the afternoon sun, slowing soil moisture loss to evaporation; this approach often helped us capture photos in which roots and soil had sharper color contrasts. In croplands, this approach often also meant that the pit face ran perpendicular to north-to-south-running rows of vegetation, ensuring that soil pit faces included roots from crop rows and row interspaces. We typically photographed pit profiles ∼40 cm wide, though in several pits this was not possible. Photos of adjacent depths captured overlapping areas, resulting in multiple shots of the same pit face area that were useful for checking for root presence or absence in any photo for which there was a question during analysis.

To quantify the presence or absence of roots across each soil pit face, we overlaid each image with a 1 × 1 cm grid in the analysis software ImageJ (Schneider et al., 2012). This approach is broadly similar to manual approaches of observing roots within pits or trenches in situ with a pre-made grid, but relies instead on photographs and a finer-scale grid than typically employed (Freschet et al., 2021; Schuurman & Goedewaagen, 1971; van Noordwijk et al., 2000). Following the methodology first presented in Billings et al. (2018), we assigned each grid cell in the photo a corresponding cell in a spreadsheet, into which we recorded the presence or absence of a root (Figure S1 in Supporting Information S1). Roots less than 1 mm in diameter were scored as fine roots and roots greater than or equal to 1 mm in diameter were scored as coarse. Many studies set an operational definition for fine roots as those with diameters less than 2 mm; however, no strict diameter thresholds for root functioning can be appropriately applied across all vegetation types, depths, and environmental conditions (Freschet et al., 2021). We set the threshold for our fine root category at 1 mm so we could be more confident that roots classified as "fine" are active in root-resource acquisition and exudation than a threshold of 2 mm might allow, though we cannot know with certainty if this was the case. Because our focus is the soil volume at the 1-cm scale containing—and thus under close influence of—roots, only root presence or absence in each grid cell was recorded, not the number of roots nor any root morphological characteristics. We could not reliably distinguish between living or dead roots and thus made no attempt to do so; our discussion of root presence therefore assumes that any dead roots were functioning in the recent past (i.e., over a timescale of months). If a grid cell contained both fine and coarse roots, we recorded that cell as containing a coarse root only (explained below); for brevity, these data are described as "coarse." To ensure consistency in root scoring across personnel, individuals learning how to score root data had their root data from randomly selected soil pits re-scored by the most experienced team member; any discrepancies were highlighted and explained to the trainee. Root data generated by all personnel were periodically checked by others, and all personnel consulted with other lab members when they encountered questionable grid cells. Finally, for each 1-cm thick layer in each soil profile, we computed the fraction of that layer's area containing fine roots, coarse roots (which potentially represents coarse plus fine), and the sum of these two categories.

There are several features of this approach that must be considered when interpreting the data. Data derived from this approach necessarily reflect that the abundance of roots exposed on a soil pit face represents biases. Any pit excavation necessarily results in the cleaving along planes of weakness that may expose root abundances different from what whole-soil volumes experience. Variation in blade sharpness during pit face excavation and clearing also may induce variation in root severing that would influence our data. Further, roots growing perpendicular to the pit face versus those growing parallel to it may be represented to different degrees (van Noordwijk et al., 2000).

There also are features specific to our presence-absence scoring approach important to consider when interpreting the data and our transformations of them. First, grid cells hosting more than one root of either size class are represented in the data set in the same way as those hosting only one. Particularly in shallow horizons where grid cells hosting more than one root were more common, this approach results in a data set that differs from that produced by efforts that might report counts (not just presence or absence) of visible roots. The approach is designed to permit assessment of whether soil is or is not directly influenced by (i.e., is within 1 cm of) a root. Second, fine roots are not recorded when they occur in the same grid cell as coarse roots. This approach, prompted in part by the need to reduce root size class information into a dichotomous variable, results in presence data for fine roots being more conservative than coarse roots and thus establishing a known underestimation of fine roots, especially near the surface. Our estimates of soil closely influenced by fine root presence, then, are also conservative. This approach might have greater implications in forest ecosystems, where coarse and fine roots likely intermingle to a greater extent than in grass-dominated systems. Third, the data presented are most appropriately interpreted in the context and at the scale of the 1-cm grid. If the overlaid grid cells had been smaller (e.g., 0.5 × 0.5 cm), the values of our metric could not have increased but may have decreased. Thus the degree to which the reported metric is conservative depends on the spatial scale at which it is assessed, and our results must be interpreted in that context. Fourth, our approach ignores the length of individual roots. Our method of scoring root presence therefore does not differentiate between multiple, distinct roots present in multiple grid cells, or single roots extending through multiple grid cells. Such differentiation is difficult to achieve when working with pit faces, but our focus is on root presence, not counts. Further, if a single root traversed through multiple grid cells, we cannot know the degree to which root function remains constant throughout its length, a limitation that constrains any inference about a root's influence on the surrounding soil.

Finally, we consider the fraction of each layer's area containing roots to represent a conservative estimate of the minimum fraction of soil volume in each 1-cm thick layer extending 1 cm into the pit face that contains roots. Though using two-dimensional root data to make inferences about three-dimensional space can be problematic (van Noordwijk et al., 2000), our approach allows for this if we accept that any such volume-based estimation of root presence or absence is conservative, given that grid cells not displaying a root on the pit face are scored as such (i.e., not present) in spite of any invisible root just beyond the soil pit wall. We thus estimated the volume of soil within 1 cm^3 of each root at each sampled site using the photo-derived, presence-absence data from each 1-cm thick soil layer and assuming these data were representative of the soil layers comprising a 1 m × 1 m column extending to the deepest depth excavated for each soil pit. With the understanding that pit excavation may introduce biases, and that our estimates of especially fine root presence are conservative, our grid-cell-based approach allows us to approximate depth distributions of soil in contact with or very near roots at the 1-cm scale, and provides us with a means of estimating soil volumes most directly influenced by roots throughout soil profiles.

2.2. Root Mass Quantification

For 70 of the 75 soil pits we were able to quantify root mass per unit volume of soil (we could not obtain both root mass and bulk density measures for the same soil depths in the remaining five pits). Bulk soil samples (>1 kg) were collected during pit excavation, either from each genetic horizon or at regular depth intervals. Upon return to the laboratory, representative subsamples (~50–75 g) were air-dried, frozen, or oven-dried at 60°C for at least 48 hr. Prior to subsampling, each soil sample was homogenized within the bag by hand (after thawing for frozen samples). Any rocks >2 mm were removed from the subsample prior to recording its weight. We then hand-picked roots from each subsample using forceps. For some clay-poor soils, excess soil easily was separated from roots. However, for most soils, roots required gentle washing over a fine-mesh sieve (212 μm) to remove soil. Root samples were then oven-dried at 60°C for at least 48 hr, with the exception of roots from sites with soils regulated by the United States Department of Agriculture. For those sites, we dried roots at 110°C > 24 hr. We then recorded the dry root mass. Because root mass was collected either at 10-cm intervals or by soil horizon, depending on the soil profile, these data reflect lower depth resolution than the 1-cm-scale, photo-derived presence-absence data.

For each air-dried or fresh-frozen soil sample, another subsample was collected to determine soil moisture content. For these samples, we sub-sampled ∼5 g, oven-dried this sub-sample at 105°C for at least 24 hr, and then re-weighed. We calculated the dry-soil fraction for each sample and used these values to calculate dry soil mass to generate root mass metrics per g dry soil. We then used bulk density collected for each horizon or 10-cm depth intervals at the time of excavation to transform our root mass values into root mass per unit soil volume. Bulk density values for "fines" (i.e., with soil particles <2 mm in diameter) were obtained using the oven-dried mass <2 mm in diameter extracted from soil pits with a core of known volume (Lang et al., 2025). Because soil subsamples were subjected to oven- or air-drying prior to root removal and root volume shrinks differentially upon drying across size classes, we were unable to reliably classify roots into size classes. We thus present total root mass for each soil depth interval within a soil pit. We also note that, as for root presence assays, we could not reliably distinguish between roots that were living or dead at the time of sampling. Accordingly, we use the term "mass" instead of "biomass" to acknowledge this uncertainty.

2.3. Additional Site Information

During pit excavation, we recorded basic ecosystem features like the dominant vegetation classification (*DomVeg*, the coarsest vegetation category used), specific cover type (*Landcover*, a more specific descriptor of the site's vegetation), the dominant soil formation process, and the underlying lithology (Table S1 in Supporting Information S1). For each site, we obtained mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET), actual evapotranspiration (AET), and net primary productivity (NPP) estimates (Table S1 in Supporting Information S1) from NASA's Application for Extracting and Exploring Analysis Ready Samples (AppEEARS) portal at appeears.earthdatacloud.nasa.gov. We also quantified soil organic C (SOC) and clay concentration (Table S1 in Supporting Information S1). We obtained SOC data by oven-drying soil subsamples, grinding them to a fine powder, and combusting them in an elemental analyzer at the stable isotope laboratory at Kansas State University or, for the Alps samples, at the National Research Council of Italy's Institute of Geosciences and Earth Resources. We added drops of 1 N HCl to samples suspected of containing carbonates to determine carbonate presence; no sample exhibited signs of needing acid treatment prior to measurement. Clay concentrations were obtained via sedimentation cylinders following NRCS protocols (Soil Survey Staff, 2022a) or a laser diffraction approach as described in Rauscher et al. (2018).

As with all ecosystem studies necessitating soil excavation, site selection and soil pit location at each site are two of the most important decisions made by the investigator. Three features of sites selected for this study deserve special mention. First, in all ecosystems, we tried to situate soil pits in locations that represented the site well. However, we cannot know the extent to which we succeeded in doing so without accessing an unknown, larger number of pits in each ecosystem. We also cannot claim that the sampled locations are accurate examples of their broader ecosystem type. For example, our "tropical hardwood" sites all occur in Puerto Rico and our "alpine meadow" sites all occur in Italy, though these ecosystem types exist in diverse locations. Further, our sites are not necessarily representative of key dominant traits often observed in their soil order. For example, soils at the desert sites do not contain carbonates, a key feature in most Aridisols that can influence root architecture in many aridlands, especially if a caliche layer is present. Thus, we emphasize that our site descriptors are intended only to help the reader envision the site, and not as an indication that any one site's data represent that ecosystem type globally. Second, we also must consider a key difference between grass-dominated systems and those with a greater fraction of interspace at the soil surface (i.e., the space between dominant vegetation in forests, shrublands, deserts, and croplands). Investigators can readily dig soil pits in grass-dominated systems and observe grass roots that support the vegetation growing immediately at the surface of the pit face. In other systems, this is more difficult. For example, forest soil pits are nearly always between and only rarely directly under trees. Thus, data from grassland soil pits may represent root presence at grassland sites, while data from forest, shrubland, and cropland pits necessarily represent the interspace. Third, our study does not include sites containing permafrost, and thus permafrost's physical constraints on root depth are not considered here. With proper consideration of these constraints, our sampling efforts allow us to explore root abundance measures in a diversity of ecosystem types.

2.4. Scaling and Statistical Approaches

We scaled data by dividing each value by its maximum value within each pit to permit direct comparisons of total root presence-absence (i.e., the sum of the two size classes' data) and total root mass data within each soil pit. We tested for differences across scaled metric values in each pedon's major diagnostic horizons (A, B, C). Because the distributions of the scaled metrics were not normally distributed and the homogeneity of variances was violated for parametric approaches, we performed a Wilcoxon signed-rank test to assess differences in median values between presence- and mass-derived metrics within each of the three major horizons. Because of the increased risk of observing a Type I error (i.e., a false positive) when testing for significant differences within three horizons, we applied a Holm-Bonferroni correction to our p values. Given the challenges of obtaining relatively deep root mass or presence-absence data, we also assessed whether the average of either metric in a given horizon could be used to estimate that metric's value in a deeper horizon (e.g., if the average of the scaled presence-absence metric in all A horizons was a useful predictor of the average scaled presence-absence metric in all B horizons). To do this, we assessed relationships between each metric's mean value across each of the major horizons (A, B, C) using linear models to predict that metric's mean value in another major horizon, across all the soils. If the data violated assumptions of homogeneity of variance or normality, we recalculated p values based on Huber-White robust standard errors (Huber, 1967; MacKinnon & White, 1985; White, 1980).

We used random forest models within each major horizon designation (A, B, C) to estimate the most robust predictor of fine and coarse root presence. We also used random forest models to estimate predictors of the discrepancy between the scaled total presence-absence root metric and the scaled root mass metric, which we calculated as the ratio of the scaled metrics ($R_{p/m}$) for each major horizon. This ratio allows us to identify the pedons in which the root presence-absence and root mass approaches differed the most. Random forest models leverage a machine-learning algorithm to build multiple decision trees from random subsets of the data with replacement (Breiman, 2001). For each of the three major horizons separately, we bootstrapped ($n = 100$) random forest models using the *cforest* function in the R package "party," which can handle missing predictor values and work well on relatively small data sets (Hothorn et al., 2008; Hothorn, Bühlmann, et al., 2006; Hothorn, Hornik, & Zeileis, 2006; Strobl et al., 2007, 2008; Zeileis et al., 2008). Our random forest models contained 500 individual decision trees that the model aggregated to make its predictions. The *cforest* function is based on conditional inference trees, and predictions of fine and coarse root presence as well as $R_{p/m}$ emerge based on the mean of all trees. The models retained observations with missing predictor variables by routing them fractionally, in proportion to the observed split distribution, avoiding the loss of a whole observation if just one predictor variable was missing for that case. These models are more protected from overfitting than other methods, and the approach works with continuous (e.g., climate data) and categorical (e.g., underlying lithology) predictor variables in the same model.

Potential predictor variables included the continuous variables *MAT*, *MAP*, *PET*, *AET*, a dryness index (*DI,* defined as $PET\ MAP^{-1}$), *NPP*, *SOC*, and percent clay (*Clay*; Table S1 in Supporting Information S1). Categorical variables included each site's *Landcover*, *DomVeg*, underlying lithology (*Lithology*), and soil-formation type (*SoilFormation*; Table S1 in Supporting Information S1). Note that all predictor variables have the same value for each individual pedon's A, B, and C horizons except *SOC* and *Clay*, for which we used the horizon-averaged values.

To guide selection of which ecosystem characteristics of the suite to include in the models, we employed Pearson correlation coefficients for continuous variables and Cramer's V for categorical variables. We considered relatively high values (i.e., >0.8) of both statistics as indicators of a variable that could be omitted from the model. This practice limits the problem of distributing variable importance across closely related variables, which can mask the potential importance of those variables. Using these guided, bootstrapped models, we generated variable importance values with which to assess the most robust predictor(s) of $R_{p/m}$ for each horizon. We also computed pseudo-R^2 values to estimate variability of model fits across multiple model runs. All errors presented represent one standard deviation from the mean.

All data processing, plotting, and statistical tests were performed in R 4.5.1 (R Core Team, 2023). Some scripts, particularly ggplot functions, were made more efficient with artificial intelligence (AI). Data displayed in all plots were checked to ensure fidelity with the original input dataframe, whether that plot's ggplot commands were assisted with AI or not.

3. Results

3.1. Distinct Depth Profiles in Presence-Absence and Mass Data

Depth distributions of fine, coarse, and total root abundance derived from presence-absence data exhibited a diversity of patterns, including increasing, decreasing, and highly variable abundance with depth (Figure 3, Figure S2). Coarse root abundance appeared to decline with depth more regularly than fine roots and more closely matched depth distributions of root mass (Figure S3), though this was not universal. Depth trends in total root presence often masked disparate depth trends in fine and coarse root presence. In the top 10 cm of all pedons, a mean of 47 ± 25% of soil pit face area contained fine roots, 21 ± 16% contained coarse roots, and 67 ± 25% contained coarse plus fine roots (i.e., the sum of coarse and fine categories). In the bottom 10 cm of all pedons, these values were 36 ± 28%, 7 ± 13%, and 41 ± 30%, respectively. Mean root presence thus declined from the top 10 cm to the bottom 10 cm by 24%, 66%, and 39% for fine, coarse, and total roots, respectively. The fraction of soil volume directly influenced by fine roots (i.e., at the 1-cm scale) ranged from 0.04 to 0.95 for fine roots, 0 to 0.77 for coarse roots, and 0.08 to 1 for total roots (Figure S4).

Depth distributions of root mass reveal general declines in mass with depth, though this pattern was not observed in mixed conifer and white fir forests, some Douglas fir and spruce forests, and one desert and one crop site (Figure 3, Figure S3). The shallowest and deepest values of root mass exhibited high variation across all pits, with root mass nearest the soil surface averaging 4.2 ± 7.4 mg cm^{-3}, and 0.08 ± 1.6 mg cm^{-3} at the deepest available depths. This represents an average decline with depth of 82%.

3.2. Scaled Data Highlight Horizon-Specific Differences Between Root Presence and Mass Data

Scaled values of total presence-absence and root mass data permit direct comparison of these metrics' depth distributions (Figure 3, Figure S5). Of the 70 pedons for which we had both presence-absence and root mass data available, all had A horizons, 68 had B horizons, and 33 had C horizons. The Wilcoxon signed-rank test revealed no difference in medians between the two scaled metrics in A horizons ($p = 0.994$) and significant differences in B ($p < 0.001$) and C ($p < 0.001$) horizons (Figure 4).

Root mass in any of the three major horizons was an inconsistent predictor of mass in other horizons. We observed a significant, negative relationship between mean scaled root mass metric values in A and B horizons with low explanatory power ($p = 0.010$, adj. $r^2 = 0.09$; Figure 5a) and a significant, positive relationship with more explanatory power between B and C horizons ($p = 0.049$, adj. $r^2 = 0.32$; Figure 5b). The relationship for mass metrics between A and C horizons was not significant (Figure 5c). We observed significant, positive relationships of presence-absence root data across all horizon pairings (i.e., A vs. B, B vs. C, and A vs. C horizons; Figures 5d–5f). Presence-absence root-abundance data in A horizons effectively predicted those in B horizons ($p < 0.001$, adj. $r^2 = 0.55$) and C horizons ($p = 0.038$, adj. $r^2 = 0.17$). Presence-absence root abundance data in B horizons also were effective predictors of those in C horizons ($p = 0.002$, adj. $r^2 = 0.44$). Congruent with observed differences between scaled root metrics in B and C horizons (Figure 4), the magnitude of discrepancies between scaled presence-absence and scaled mass metrics (i.e., values of $R_{p/m}$) in B and C horizons was greater than those in A horizons (note scaling of X-axes in Figure 6).

3.3. Distinct Drivers at Different Depths Govern Root Presence and Presence-Mass Discrepancies

Relationships among potential predictor variables in the random forest models, as revealed by Pearson's correlation coefficients for continuous variables and Cramer's V for categorical variables, suggest that *AET, NPP* and *Landcover* were closely related to other variables. Thus, the model best able to highlight variable importance values for each major horizon included *MAP, MAT, PET, DI, SOC, Clay, DomVeg, Lithology,* and *SoilFormation* (Table S1 in Supporting Information S1).

Performance of the random forest models in predicting fine and coarse root presence varied among horizons. For fine root presence, mean pseudo-R^2 values were lowest in A horizons (0.32 ± 0.00; Figure S6 in Supporting Information S1), where variable importance values suggest that *DomVeg* was the top predictor (Figure S7 in Supporting Information S1). In B horizons, mean pseudo-R^2 values were 0.54 ± 0.00 (Figure S6 in Supporting Information S1) and *Lithology* was the top predictor (Figure S7 in Supporting Information S1). In C horizons,

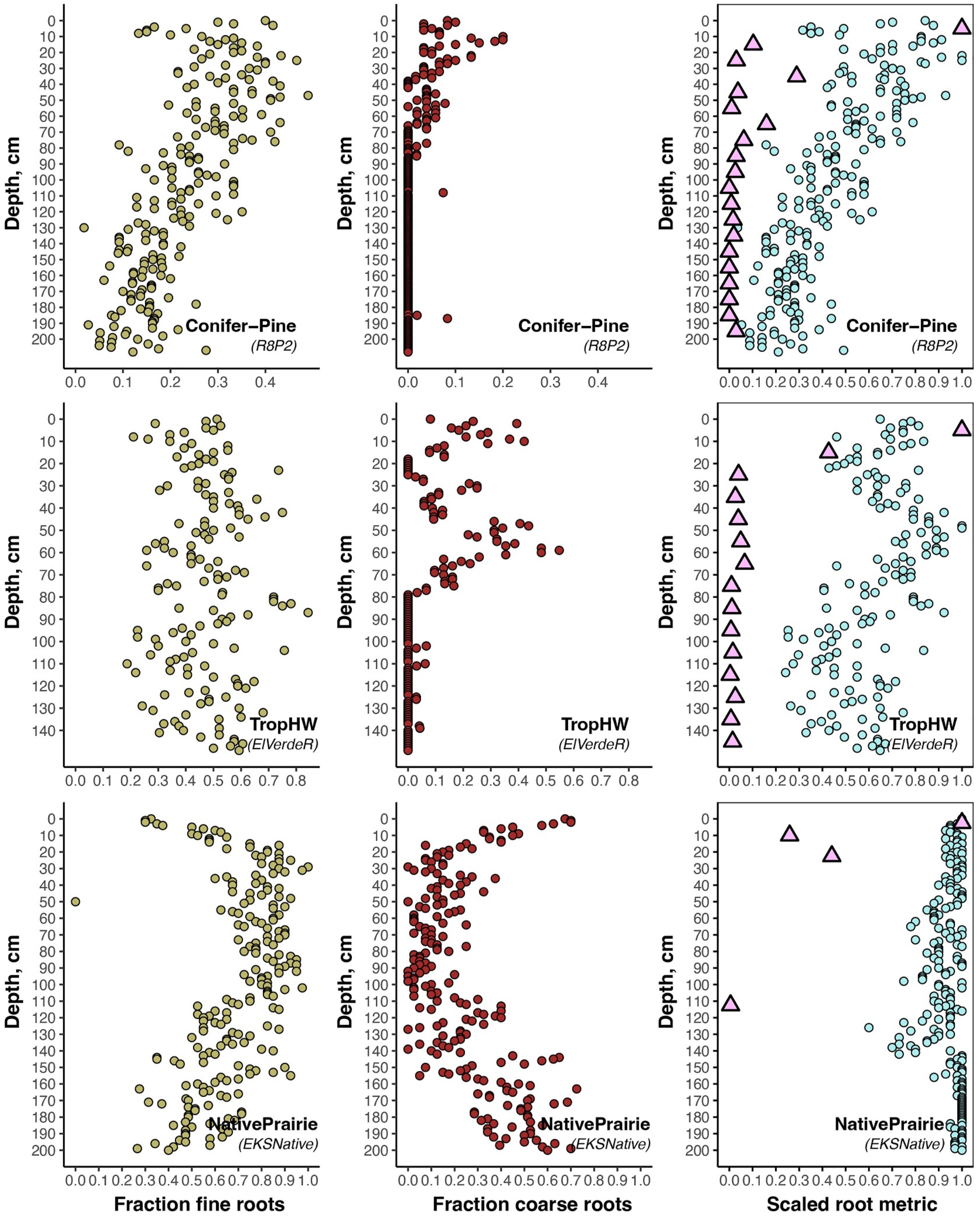

Figure 3. Examples of contrasting depth dependencies of root abundance as revealed by different metrics. Fraction of each 1 cm-thick layer containing fine (<1 mm diam) roots quantified via root presence-absence approach (left column; see Methods for details) exhibits declines (top row), no discernible trend (middle row), and increases (bottom row) with depth across different ecosystems (see Table Sl in Supporting Information S1 for details of each soil pit). Fraction of each 1 cm-thick layer revealing coarse (2 ≥ 1 mm diam.) root presence (middle column) reveals contrasting patterns across ecosystems, and with fine roots within each ecosystem. Bottom row presence-absence data redrawn from Souza et al. (2023). Total root mass (pink triangles, right column) contrasts with total root presence (turquoise circles, right column) in many ecosystems (Figure S5), highlighting greater root-regolith interfaces than root mass data can imply, particularly in deeper horizons.

pseudo-R^2 values were 0.50 ± 0.00 (Figure S6 in Supporting Information S1) and *SoilFormation* was the top predictor (Figure S7 in Supporting Information S1). Partial dependence plots further illuminate the role of model predictors. Greater fine root presence was linked with grass, savanna, and woody-encroached prairie systems in A

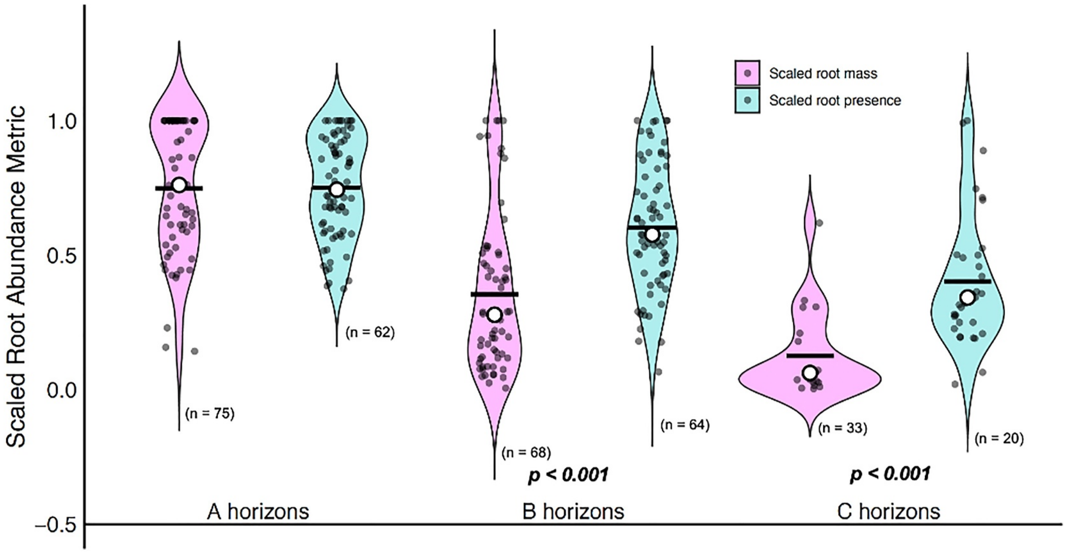

Figure 4. Violin plots depicting mean (black bars), median (white circles), and relative distributions of the scaled total root mass metric (pink) and scaled root presence-absence metric (turquoise) for all A, B, and C horizons in all soil pits assessed. Statistics refer to significant differences between medians of scaled root mass and presence metrics for the specified horizons. See text for details of scaled metrics.

horizons (Figure S8 in Supporting Information S1). In B horizons, the effect of *Lithology* on fine root presence was driven by systems underlain with limestone or glacial till (Figure S8 in Supporting Information S1). Soil formation reflecting mixed colluvium and residuum was linked to fine root presence in C horizons (Figure S8 in Supporting Information S1).

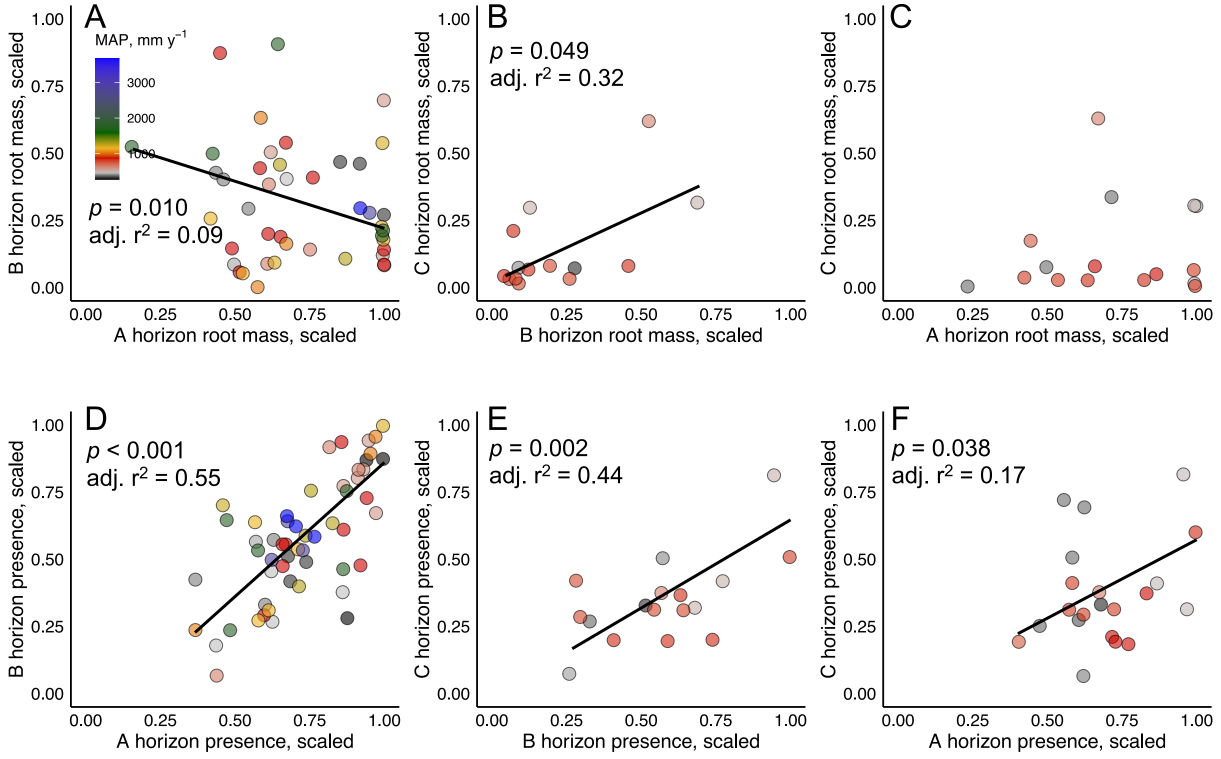

Figure 5. Relationships of scaled root mass metric values between A and B, B and C, and A and C horizons (top row) and scaled root presence-absence metric values between A and B, B and C, and A and C horizon (bottom row). Points are colored by mean annual precipitation (MAP). Significant relationships are depicted with solid regression lines.

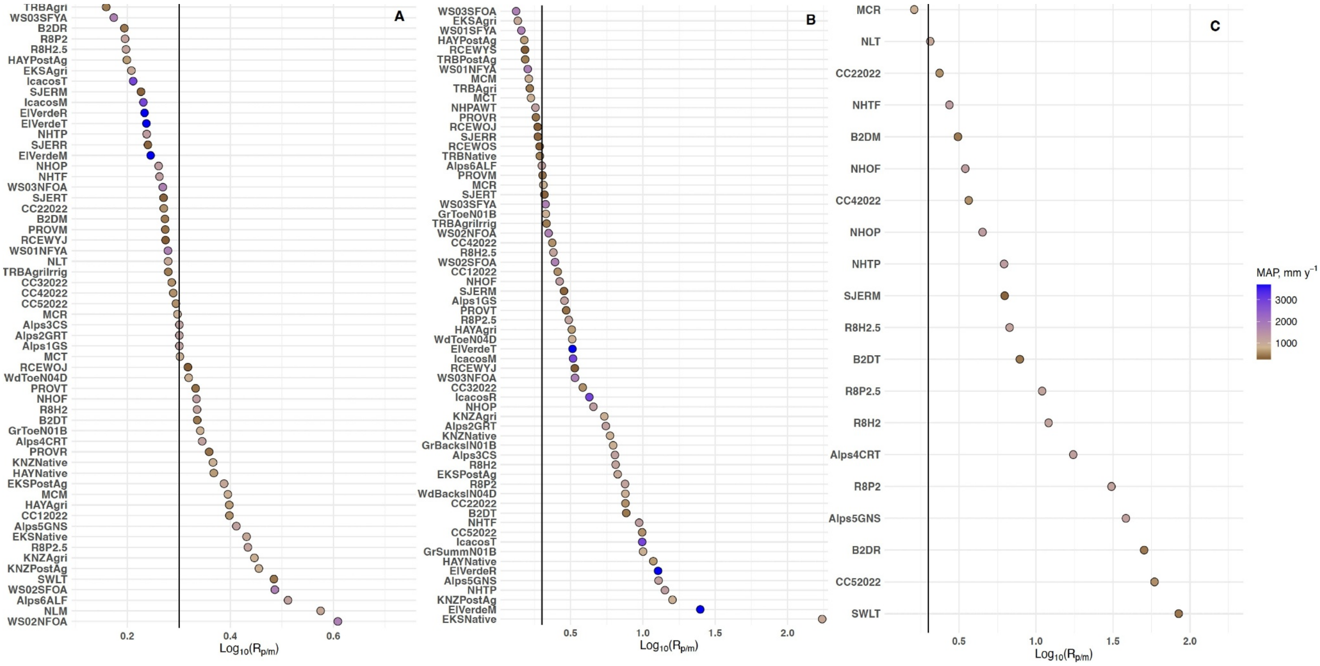

Figure 6. Mean values of the $\log_{10}$ ratio of scaled presence-absence root metric to scaled root mass values ($R_{p/m}$) for each major horizon designation (A, B, C, reflecting their respective horizons) in ascending order and colored by mean annual precipitation (MAP). Vertical line indicates equality of scaled root metrics in log space. Values to the right of the vertical line represent soil pits for which the scaled presence-absence root metric value exceeds the scaled root mass value. The different number of pits across the panels (A horizons = 59, B horizons = 64, C horizons = 20) reflects some pits' lack of root mass in some horizons and the lack of C horizons in some pits. Five pits (WdSummN04D, WS03NFYA, RCEWOC, RCEWYC) are not included in any panel because of their lack of root mass data. See Table Sl in Supporting Information S1 for pit names and characteristics. Note different *X* axis scaling across horizons.

Pseudo-R^2 values in A, B, and C horizons for coarse root presence were 0.31 ± 0.00, 0.51 ± 0.00, and 0.59 ± 0.00, respectively (Figure S9 in Supporting Information S1). Variable importance values suggest *DomVeg* was the most robust predictor of coarse root presence in both A and B horizons (Figure S10 in Supporting Information S1). *Lithology* was the most robust predictor of coarse root presence in C horizons (Figure S10 in Supporting Information S1). Greater coarse root presence was most strongly associated with conifer vegetation in A horizons, with woody-encroached grassland in B horizons, and with limestone-shale lithology in C horizons (Figure S11 in Supporting Information S1).

Random forest model ability to predict $R_{p/m}$ also varied among horizons. Model fit for A horizons generated a mean pseudo-R^2 of 0.26 ± 0.01 across the 500 bootstrapped runs (Figure S12 in Supporting Information S1). Mean pseudo-R^2 values in B and C horizons were 0.27 ± 0.00 and 0.27 ± 0.01, respectively (Figure S12 in Supporting Information S1). Model stability was greatest in B horizons, where the number of observations was greatest and differences between root presence and mass were greatest (Figure S12 in Supporting Information S1, Figure 5). Variable importance values suggest that the top predictor of $R_{p/m}$ in A horizons was *DomVeg* (Figure 7). Especially large increases in this ratio occurred where *DomVeg* was aspen, woody-encroached native prairie, and sagebrush (Figure 8a). In B horizons, the top predictor of $R_{p/m}$ was *MAP*, with $R_{p/m}$ increasing with *MAP* at a threshold of ~1,750 mm y^{-1}, beyond which $R_{p/m}$ increased substantially with a smaller threshold at ~2,800 mm y^{-1} (Figure 8b). In the C horizons, the top predictor was *MAT*; $R_{p/m}$ increased substantially with *MAT* above an apparent threshold at ~10°C (Figure 8c). There was little overlap between variable importance values of the top predictor of $R_{p/m}$ and those of other potential predictors in any horizon.

4. Discussion

Depth distributions of root presence across soil pits located in a diverse array of ecosystems illuminate prolific root-regolith interfaces deep within soil profiles (Figure 3, Figure S2). A key outcome of the discrepancies between depth distributions of root presence and root mass is a clear divergence in interpretation from what often-observed root mass declines with depth may imply (Figure 3; Figures S2 and S3). We also demonstrate that root

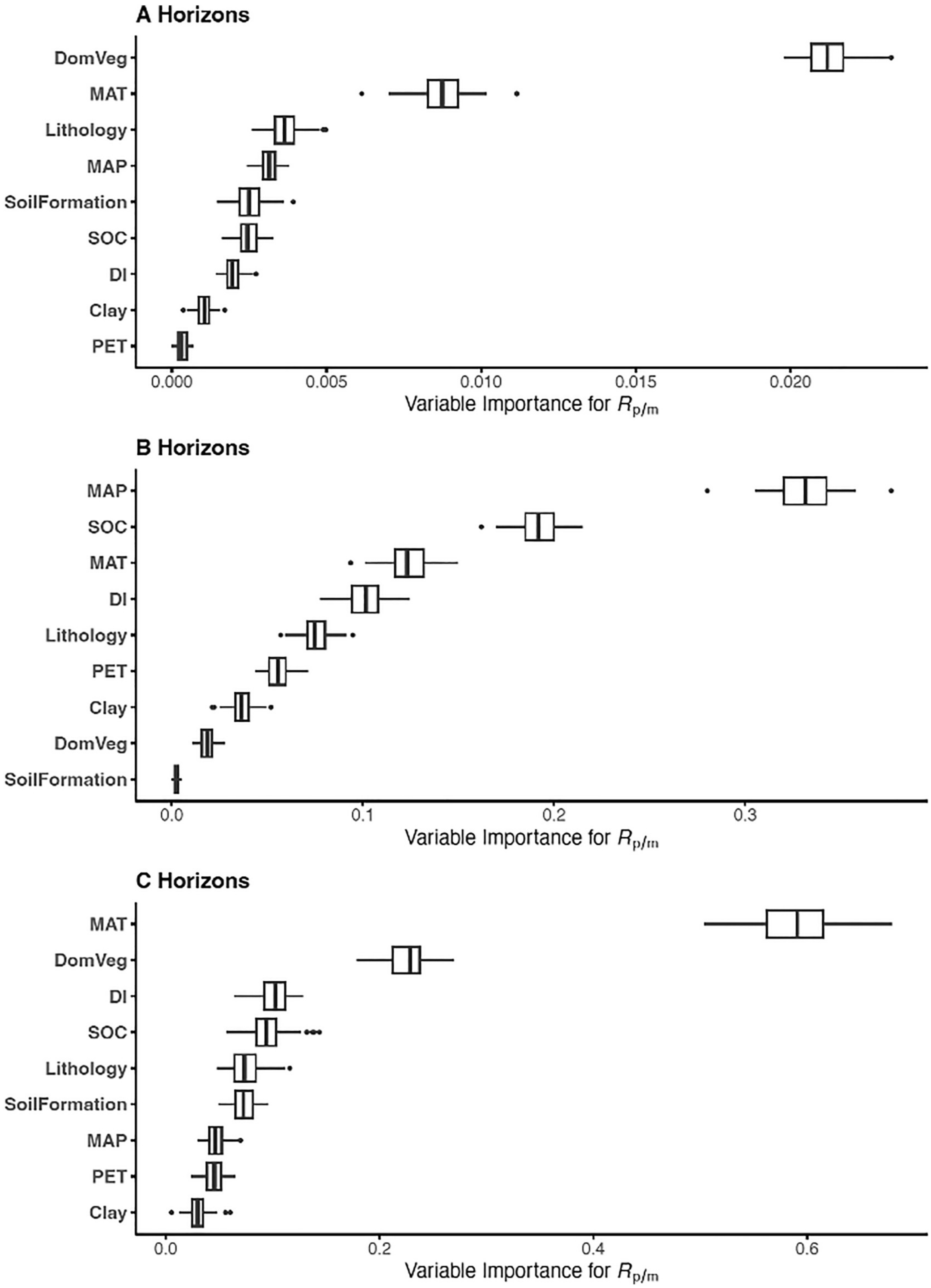

Figure 7. Boxplots of variable importance values ranked in descending order for A (top), B (middle), and C (bottom) horizons derived from horizon-specific random forest models predicting the ratio of scaled presence-absence root metric values to scaled root mass values for A, B, and C horizons of soil pits in a diversity of terrestrial ecosystems. Predictor variables included mean annual precipitation (MAP), mean annual temperature (MAT), potential evapotranspiration (PET), dryness index (PET MAP^{-1}, DI) soil organic C (SOC), clay, dominant vegetation type (Dom Veg), underlying lithology, and soil formation category. Pseudo-R^2 values describing model fits were 0.13, 0.29, and 0.36 for A, B, and C horizons respectively. See text for details of model construction and results.

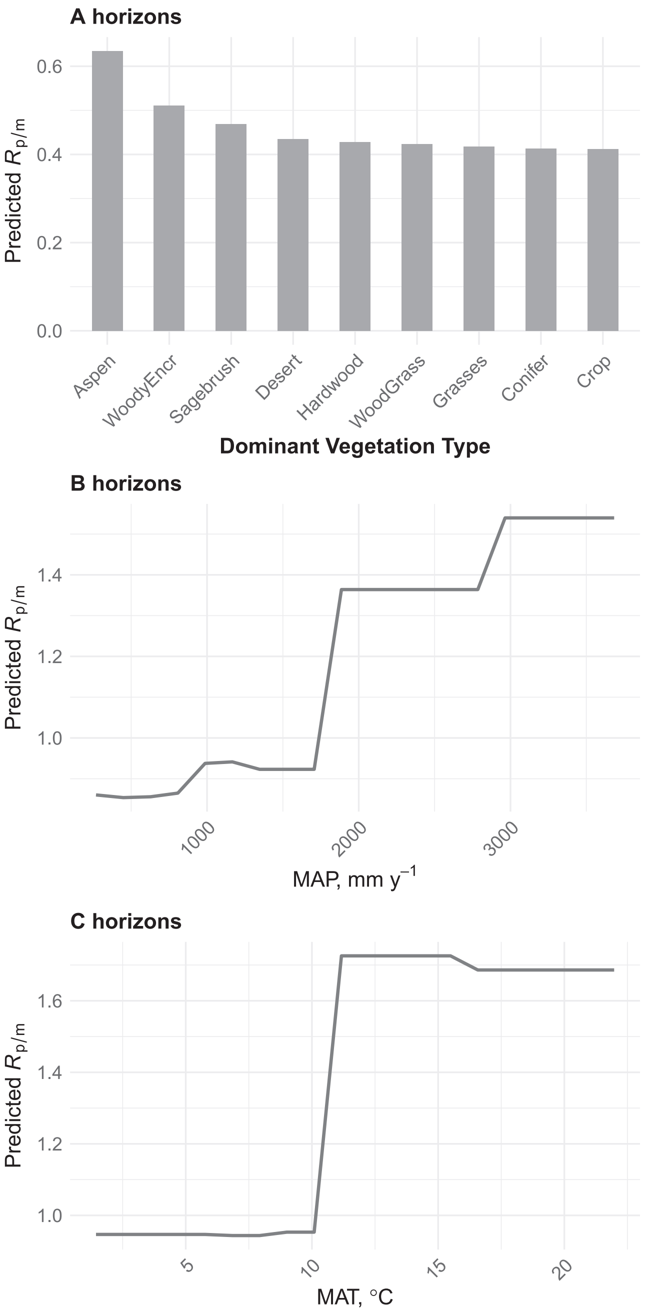

Figure 8. Partial dependence plots revealing how top predictor variables for A (dominant vegetation type, A), B (mean annual precipitation (MAP), B), and C (mean annual temperature (MAT), C) horizons influence the ratio of the scaled presence-absence root metric values to scaled root mass values ($R_{p/m}$). Plots represent horizon-specific random forest models predicting $R_{p/m}$ from a suite of potential predictor variables for 140 observations in 59 soil pits' A horizons, 241 observations in 64 soil pits' B horizons and 73 observations in 20 soil pits' C horizons in a diversity of terrestrial ecosystems. The top predictor variables are those which, when their values are randomly permuted, impose the greatest decline in predictive accuracy of $R_{p/m}$. Predictor variables included MAP, MAT, potential evapotranspiration (PET), dryness index (PET MAP^{-1}), soil organic C, clay, dominant vegetation type, underlying lithology, and soil formation category. See text for details of model construction.

presence in one horizon can be useful for predicting root presence in another (Figure 5), whereas root mass in a given horizon was an unreliable predictor of root mass in other horizons. This may be helpful given the laborious process of quantifying roots deep in the subsurface. Our analyses further highlight depth dependency of controls on $R_{p/m}$, with MAP serving as a key regulator of $R_{p/m}$ in B horizons (Figures 6 and 7) and MAT in C horizons (Figure 7), the two horizons in which root presence and mass indices differed significantly (Figures 4 and 6). We must be particularly cautious when interpreting C horizon random forest predictions, given fewer observations for these horizons. However, if robust, these model results are congruent with less severe declines in root presence compared to root mass with depth in warm, mesic climates.

Although coarse root presence did not always track root mass, coarse root depth distributions appeared qualitatively closer in shape to root mass depth distributions than those of fine roots (compare Figure S2 middle column with Figure S3). The depth-dependent divergence in presence-absence versus mass data thus primarily emerges from the generally small mass of deep, fine roots that can be numerous. Particularly given the growing understanding of changing rooting depths in the Anthropocene (Hauser et al., 2022), the diverse patterns across depth of root presence (Figure 9)—especially fine roots—have implications important to consider for: (a) soil organic C (SOC) production, transformations, and persistence; (b) regolith transformations and formation; (c) water residence time, storage, and fluxes; (d) modeling studies requiring estimates of root abundance.

4.1. Soil Organic C Production, Transformations and Persistence

Soil organic C accrual in grasslands is linked to mass-derived abundance of roots <2 or 4 mm in diameter (with the metric dependent on site; Malhotra et al., 2025), and indeed we observed in A horizons that grass cover was linked to increasing presence of roots <1 mm in diameter (Figure S8 in Supporting Information S1). We must interpret our results with caution given that we cannot assume our sites are globally representative of their cover type. However, this observation has value given the link between grass cover and SOC stocks. In contrast with mass-derived root data, which are appropriate for probing contributions of root tissue to SOC stocks, root presence-absence data reveal the degree to which root presence throughout soil profiles can influence SOC dynamics by offering insight about the volume of soil in contact with or in close proximity to roots. For example, root exudates and their capacity to promote rhizosphere microbial biomass (Jilling et al., 2021; Yan et al., 2023) can result in microbial priming and associated SOC losses (Dijkstra et al., 2020). The common root exudate oxalic acid can free SOC from mineral protection, promoting its loss (Keiluweit et al., 2015). Countering these mechanisms of SOC loss, root exudate promotion of microbial activity also results in greater production of microbial necromass. Evidence is mounting that microbial necromass contributes to persistent SOC pools (Kallenbach et al., 2015; Liang et al., 2019; Simpson et al., 2007; Sokol et al., 2022), perhaps because of its proclivity to promote soil aggregation and thus SOC physical protection from decay (Jastrow, 1996; Six & Paustian, 2013). Root exudates themselves can also contribute to long-lasting SOC pools. For example, organic acids can become immobilized via mineral adsorption and thus become part of a relatively durable, mineral-associated pool of organic matter (Adeleke et al., 2017; Jones et al., 2003). Thus, high fine root presence relatively deep in soil profiles likely contributes to the

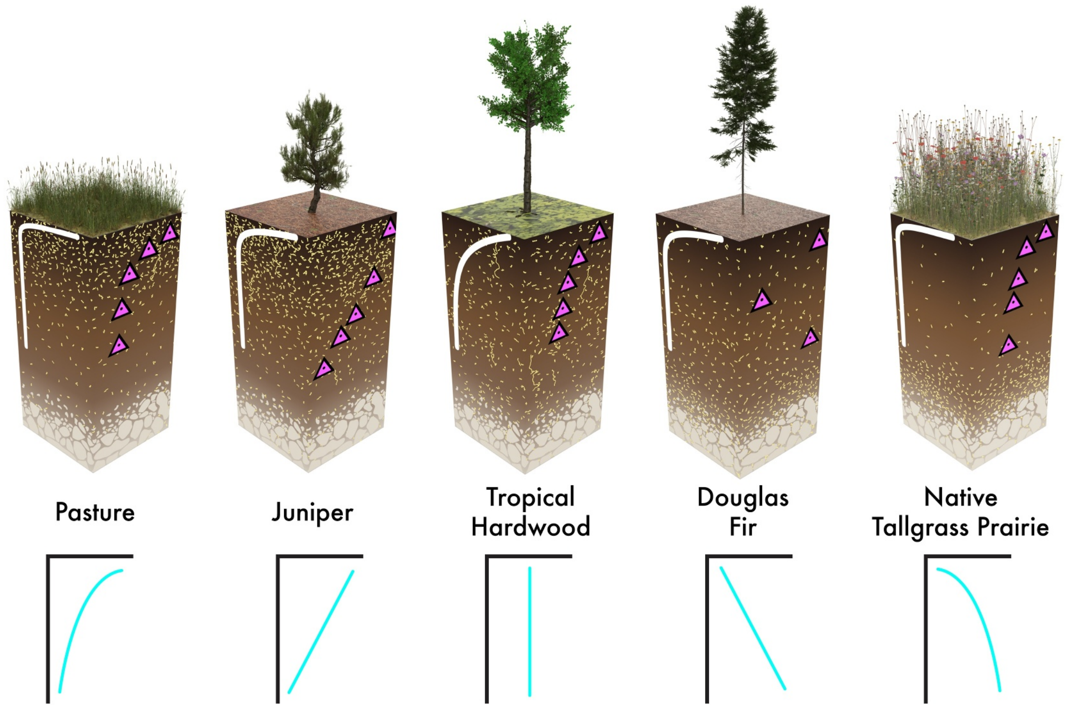

Figure 9. Example profiles depicting the contrasting ways in which depth dependence of root abundance can be conveyed. The pasture, juniper, tropical hardwood, Douglas fir, and native tallgrass prairie systems represented here reflect the range of root presence depth patterns observed in this study, represented by stylized root fragments drawn throughout the profiles and by the simplified turquoise lines below the profiles. These patterns ranged from (1) exponential declines (pasture) to (2) linear declines (juniper) to (3) no trend (tropical hardwood) to (4) linear increases (Douglas fir) to (5) exponential increases (native tallgrass prairie) with depth. In these example profiles, root presence data exhibited distinct depth patterns compared to root mass data, approximated by pink triangles and displayed with depth resolutions often available in the literature. Thick white curves were generated using the β values for exponential declines employed by CLM5 for these plant functional types, and contrast with both root presence data and root mass data. Note that we cannot know if root data derived from these exemplar soil pits represent root behavior of these ecosystem types globally, and that in reality we observed large variation in soil pit depth and soil and bedrock characteristics.

apparent durability of deep SOC stocks by generating (exudates) or promoting (necromass) relatively persistent SOC compounds as well as soil structural characteristics that promote that persistence.

Fine roots play an especially important role in these SOC transactions because it is the specific surface area, not the mass, of roots that governs their capacity to serve as active players in belowground transactions, and thus in SOC dynamics. We cannot compute estimates of specific root surface area or specific root length from presence-absence data, but greater root presence in B and C horizons than might be inferred from mass depth distributions, especially for fine roots (Figure 3, Figure S2), suggests high root surface area in those horizons. Robust, positive correlations between root counts and root length density (Dauer et al., 2009) are consistent with this inference. The general lack of correspondence between fine root presence and root mass depth distributions contrasts with the frequently-matching shape of depth distributions of coarse root presence and root mass; this contrast serves as a powerful reminder of the potential influence of deep fine roots' low mass but relatively high surface area. Indeed, the smaller mean decline of root presence from the surface 10 cm to the deepest-accessible 10 cm (~39% decline for total roots, ~24% for fine roots) than that expressed by total root mass (~82% decline across similar depths) suggests a greater capacity of relatively deep, fine roots to serve as agents of the deep SOC processes described above than root mass estimates might imply. This inference is particularly revealing when considering how SOC depth distributions at a global scale exhibit less-steep declines with depth than corresponding changes in root mass through the top 1 m (Jackson et al., 2000), consistent with global observations of relatively old, deep SOC (Trumbore, 2009). In addition to the transport of dissolved organic C deep into the subsurface (Kaiser & Kalbitz, 2012; Moreland et al., 2021), fine root presence likely serves an important role in providing and promoting C-rich compounds that can become stabilized or that can promote the physical protection of already extant SOC.

4.2. Deep Soil Nutrient Liberation and Regolith Weathering

More variable shapes of depth distributions of root presence compared to those quantified from root mass offer additional insight into chemical and physical transformations of the regolith. The acids that roots and microbes generate create biotic weathering fronts (Brantley et al., 2011, 2014; Drever, 1994; Richter et al., 2007). For example, a fraction of CO_2 from respiration forms carbonic acid, typically considered a relatively weak acid. However, particularly in soils where CO_2 can reach high levels (Hasenmueller et al., 2015; Selker et al., 1999) and even exceed 7% (Billings et al., 2018; Billings, Brecheisen, et al., 2024; Brecheisen, 2018), carbonic acid can serve as a powerful weathering agent (Oh & Richter, 2004). Organic acids like citric, tartaric, and oxalic acids, produced by roots and soil microbes, enhance mineral breakdown and nutrient release, such as potassium and calcium (Bhattacharjee et al., 2023). Siderophores, also from roots and microbes, mobilize iron by forming soluble complexes (Ahmed & Holmström, 2014). The depth variability of root presence across ecosystems revealed here suggests diverse capacities for nutrient release and soil formation at depth, especially near the regolith-bedrock interface. Further, the smaller decline with depth in total root presence compared to that of root mass (39% vs. 82%) and the yet-sharper contrast between depth declines of fine root presence and root mass (24% vs. 82%) suggest a deeper biotic weathering engine (Drever, 1994) than is construed from root mass measurements. We must consider that fine roots are underestimated to some extent by our approach, likely to a greater extent in A horizons. However, combined with the large fraction of soil volume in direct or close contact with roots (Figure S4), this observation illuminates the volume of soil subjected to weathering reactions initiated by nearby roots. If the phenomenon of relatively small declines in rooting presence with depth documented in these pedons is broadly representative of deep root presence globally, these results underscore the vast volumes of soil deep in the subsurface that also experience such conditions.

Beyond their role in fueling weathering reactions, roots also exert control over soil physical erosion rates and thereby soil residence times on the landscape. Specifically, the penetration of roots and their corresponding tensile strength into intact soil profiles reduces erosion rates (Schwarz et al., 2010), whereas root fracture and tree throw can promote pulsed episodes of erosion through bioturbation (Gabet & Mudd, 2010). These root-mediated physical processes combine with root-fueled weathering reactions to drive net rates of soil production (Anderson et al., 2007; Heimsath et al., 1997). The great volumes of relatively deep (i.e., B and C horizons) soil in direct or very close contact with roots (Figure S4) illuminated by the root presence-absence approach suggest the extent to which these root-imposed physical forces can influence Earth's regolith.

To the extent that deep roots are used for uptake of liberated, mineral-bound nutrients, diverse patterns in depth distributions of root presence also suggest variation across ecosystems in vegetation prioritization of deep uptake of mineral-bound nutrients, a feature that may vary with the elemental composition deep in the subsurface. Consistent with this idea, lithology served as the top predictor of B horizon fine root presence (Figure S7 in Supporting Information S1), with limestone and glacial till promoting fine root presence. Fine root presence may be promoted especially where minerals are relatively fresh (e.g., glacial till) or easily succumb to weathering (e.g., limestone). Indeed, others have observed higher specific root length in systems underlain by glacial till (Meier et al., 2020), consistent with our observation of glacial till lithology being associated with greater fine root presence. Biotic transformation of subsurface minerals that liberates nutritive elements fuels the globally observed phenomenon of nutrient uplift, the transfer of deep, rock- and mineral-bound nutrients into biomass more concentrated near the soil surface (Alban, 1982; Jobbágy & Jackson, 2004; Kraepiel et al., 2015; Soper et al., 2018; Sullivan et al., 2019; Switzer & Nelson, 1972). Over millennia this process drives the changing composition and function of subsurface minerals (Brantley & White, 2009; Brantley et al., 2012). The root-presence data reported here hint that vegetation may invest in fine roots where lithology harbors relatively easily-weatherable nutrients, but that biotic capacity to liberate and take up nutrients may not vary with depth in predictable ways. This is particularly true for fine roots, given their more variable depth dependency than coarse roots and highlights the importance of collaborations across disciplines such as ecophysiology and geochemistry for probing these questions.

4.3. Water Residence Times, Storage, and Fluxes

Root mass and presence-absence data also provide complementary insights for understanding depth distributions of water residence times, storage, and fluxes. The steep declines in root mass with depth often observed (Jackson et al., 1996; Schenk & Jackson, 2002) and modeled (Lawrence et al., 2019; Simunek et al., 2016) are consistent with the idea that water uptake from deep within soil profiles is not a large contributor to ecosystem hydrologic budgets. Certainly, plants and especially trees can extend their roots to many tens of meters (Stone & Kalisz, 1991), and intuitively root presence at great depths suggests that some vegetation may use water from these locations (Y. Fan et al., 2017). This idea is bolstered by observations of deep rock water uptake (Dawson et al., 2020; Rempe & Dietrich, 2018), with noted functional significance of deep-water uptake from these locations linked to vegetation survival during drought (Klos et al., 2017; Kuhnhammer et al., 2023; Nepstad et al., 1994). Indeed, we observed an increase with depth in the importance of DI as a predictor of $R_{p/m}$, suggesting that increasing water demand promotes deep root presence (Figure 7).

While there are clear survival benefits of deep root water uptake (Chitra-Tarak et al., 2021; Kuhnhammer et al., 2023; McDowell et al., 2019), most vegetation water uptake appears to derive from relatively shallow depths. This seems particularly true in grassland ecosystems, where 99% of root mass is above 2.4 (tallgrass) or 1.5 m (shortgrass; Zeng, 2001), and ~83% of root mass occurs in the upper 30 cm (Jackson et al., 1996). In these grass-dominated ecosystems, the functional significance of deep roots for water uptake and drought survival may be muted due to limited hydraulic capacity to move water from deep roots (Nippert et al., 2012). This feature may be more exaggerated in grasslands due to a greater capacity of grasses to die back and recover compared to trees. Multiple studies report that deep root water uptake in herbaceous ecosystems does not appear to compose a meaningful fraction of landscape-scale evapotranspiration (Kulmatiski, 2024; O'Keefe et al., 2020). Dominance of shallow water uptake, at least much of the time, may also be a feature in forests. Average water uptake depths of trees are substantially different from their maximum rooting depths, particularly in drier regions (Bachofen et al., 2024). Even during drought, in well-rooted, deep soil layers where moisture is available, root water uptake can be limited (Markewitz et al., 2010). Thus, though evidence exists that even deep rock moisture can be critical for survival for some woody plants during times of moisture shortages (Burns et al., 2023), deep root water uptake may not be a prominent feature of hydrologic budgets for the majority of time in most woody ecosystems. For both woody and herbaceous systems, steep declines in root mass with depth appear consistent with hydrologic partitioning of evapotranspiration that suggests most water uptake occurs in relatively shallow depths.

In contrast with root mass data, root presence-absence data can guide inferences about water fluxes within soil profiles without estimates of hydrologic partitioning. For example, hydraulic redistribution (HR) is likely more closely linked to fine root presence in relatively deep horizons than to deep root mass. In environments where large gradients in soil water potential exist across depths within the soil profile, deep-rooted species can facilitate HR (Bleby et al., 2010; Brooks et al., 2002; Domec et al., 2010; Horton & Hart, 1998; Lee et al., 2005). The occurrence of HR varies by species and ecosystem types, but requires functional deep roots that can move water from depth to other portions of the soil profile. Our mechanistic understanding of HR presumes root functionality that can anatomically regulate reverse flow (from root to soil) down water-potential gradients (Burgess et al., 1998; Neumann & Cardon, 2012). An understudied aspect of this process is the role of fine versus coarse roots at deeper depths to facilitate HR, but the increased specific surface area and smaller conduit diameter of fine relative to coarse roots may facilitate uptake by permitting exploration of greater soil volumes and reducing hydraulic conductivity in vessels. This, in turn, may lead to greater total volumes of water redistributed to shallow soil layers.

Root presence, and less so mass, also plays a fundamental role in shaping soil structure and pore distributions in the subsurface. These physical attributes of a soil profile govern the depths to which infiltrating water recharges the subsurface, the volumes of water that can be stored, and its residence time in the soil profile (Sullivan et al., 2024). For example, dendritic tubular pores have long been recorded during soil profile descriptions and are assumed to result from root growth (Soil Survey Staff, 2022b); some of these pores can be many centimeters in diameter due to coarse root propagation. Such pores decrease in abundance in locations where roots are removed and appear to re-emerge when roots regenerate (Guthrie et al., 2025). Roots also indirectly affect soil structure by their release of organic material, a phenomenon linked especially to fine roots. Their exudates, along with the microbial necromass that results from the microbial activity, promote soil particles binding together, stabilizing aggregates (Attou et al., 1998; Le Bissonnais, 1996; Oades, 1984; Singer et al., 1992). This aggregation can enhance permeability (Denef et al., 2002). Conversely, root growth can obstruct existing pores and break down macroaggregates, reducing permeability. Despite this possibility, roots generally enhance porosity and facilitate water flow rather than restrict it (Sullivan et al., 2022).

Even minor increases in soil macroporosity, such as might be expected with fine root proliferation, can significantly increase saturated hydraulic conductivity (Eck et al., 2016; J. Lu et al., 2020), while water flow along the soil-root boundary can enhance preferential flow to depth (e.g., funnel flow; Johnson & Lehmann, 2006). Through either the creation of biopores or preferential flow paths, these root-generated pores can support the transport of dissolved organic C to depth (Angers & Caron, 1998; Bogner et al., 2010; Chen et al., 1997; Kaiser & Kalbitz, 2012; Lucas et al., 2019; Moreland et al., 2021; Zhang et al., 2015), which can prime microbial activity and influence aggregation processes. That $R_{p/m}$ was particularly great in B horizons where MAP is relatively high suggests the enhanced porosity linked to root proliferation is especially beneficial to vegetation in high rainfall environments; enhanced values of $R_{p/m}$ in C horizons where MAT is relatively high hints that any such benefits may be especially beneficial in warmer environments, where evaporative demand can be great. This idea is consistent with observations of greater porosity and water flow and greater soil drying at deeper depths where deep root abundance increased in a woody-encroached grassland (Jarecke et al., 2024, 2025). By evaluating root presence-absence data, we can begin to unlock the degree to which the entire soil volume is impacted by the ability of roots to sculpt the subsurface. Further, we can explore the ways different horizons within the soil volume interact in functionally different ways with fine and coarse roots, and how both of these categories of processes alter depth distributions of water fluxes and biogeochemical processes. The means by which deep roots can influence water storage and fluxes, then, may not be dominated by quantitative uptake but rather by the ways in which deep roots can modify water redistribution within soil profiles and hydrologic flowpaths.

4.4. Implications of Root Presence Depth Distributions for Modeling

Root presence-absence data suggest that models relying on root mass depth distributions to depict interactions between plants and the subsurface may underestimate the vertical extent of biologically and chemically active soil volumes. Root traits, particularly depth and presence, represent key axes of variability in subsurface biogeochemical processes, with implications for long-term soil development, nutrient cycling, and ecosystem responses to climate and land-use change (Brantley et al., 2017; Hauser et al., 2023; Newman et al., 2020). Developing a more integrated, depth-resolved understanding of root distributions and their functional consequences, particularly through coordinated cross-site studies, will be critical for improving how reactive transport models and ESMs represent critical zone processes and project ecosystem responses to environmental change.

Catchment-scale reactive transport modeling efforts (Kerins et al., 2024; Stewart & Li, 2025) indicate that subsurface respiration may occur at greater depths and at higher rates than traditionally assumed. If so, such results support the idea that fine roots affect a greater soil volume deep in the subsurface than often inferred from root mass measurements to play an important role in biogeochemical processes. Because depth distributions of root presence can regulate water routing and biogeochemical reactions such as SOC transformations and chemical weathering, root presence also shapes water residence times and mineral-water contact. Reactive transport models aptly demonstrate that these hydrologic processes are inseparable from root-mediated C processes. For example, the deepening roots that accompany woody-encroached grasslands can enhance vertical water fluxes (Jarecke et al., 2024) which, in turn, can promote transport of CO_2 produced in shallow soils to greater depths and promote weathering deep in the subsurface (Wen et al., 2021). In this way, roots exert a dual influence, both elevating CO_2 concentrations through respiration and delivering CO_2-rich water to the weathering front that amplifies chemical weathering rates (Anhold et al., 2025), particularly in carbonate terrain (Wen et al., 2021). In contrast with relatively deep roots, soils supporting dense, shallow root networks often promote lateral flow and shallow export of dissolved C while shortening residence time and reducing C mineralization in deeper layers (Wen et al., 2022; Xiao et al., 2021). These findings highlight the central role of the depth distribution of roots in governing not only the production of biogenic CO_2 but also the pathways and magnitude of C and solute transport through the critical zone that reactive transport models represent.

At a larger scale, the implications of our findings are of particular relevance to land models within ESMs like CLM5, given that these models include increasingly sophisticated representations of nutrient cycling, land use change and management, and lateral water flow in the subsurface (R. A. Fisher & Koven, 2020; Swenson et al., 2019). In recent years, for example, CLM5 has been equipped with dynamic, vertically resolved C and N pools in live and dead coarse roots (Koven et al., 2013), a plant hydraulic stress representation that can explicitly represent HR based on simulated gradients of water potential along the soil-root-plant-atmosphere continuum (Kennedy et al., 2019), and fixation and uptake of nitrogen (N) that depends explicitly on the root C density (Brzostek et al., 2014; J. B. Fisher et al., 2010; Shi et al., 2016). At the heart of all these processes lies the assumed exponential vertical distribution of root biomass (Jackson et al., 1996) that is used to allocate root C vertically and distribute water uptake and HR (Figure 9). Although these advances have greatly improved the sophistication of water and nutrient dynamics in the subsurface (Knox et al., 2024; B. Wang et al., 2023), there remains a fundamental constraint on the vertical dynamics of those processes inherent to the assumptions (a) of an exponential distribution of root mass (which this study demonstrates is not always true for a given location; Figure 9), and (b) that the vertical distribution of root mass (and not root specific surface area) controls vertical partitioning of C, N, and water fluxes across the soil-root interface. As currently developed, ESM projections of land-atmosphere exchange of water, C, and energy thus cannot capture the influence of deep, fine-root contributions to SOC-stabilizing processes, their transport of water from deeper horizons to near-surface depths, or their influence on soil structural attributes that dynamically respond to environmental conditions and root growth and decay. These ideas suggest that ESMs may benefit from embracing the idea of greater nuance between the vertical distributions of fine and coarse roots and their corresponding roles within these models (beyond their respective designations as high- and low-turnover pools of C and N) and moving toward representations of roots that are ecosystem-varying and dynamic with depth.

5. Conclusions

We demonstrate that biogeochemical and reactive transport processes deep in the subsurface in many ecosystems result from a greater volume of soil in direct or close contact with roots and more numerous root-regolith interfaces than root mass data may otherwise suggest. These data thus shine a spotlight on the importance of the biotic front as it advances, or retreats, throughout the regolith with varying environmental conditions. At a global scale, changes in root mass-derived rooting depth distributions due to climate and land use change (Hauser et al., 2022) add to uncertainties in projections of vegetation's influence on belowground C, nutrient, and water storage and fluxes. Our work elucidates another source of uncertainty by emphasizing that root mass, while useful for quantifying belowground plant tissue stocks and other plant-centered processes, may not provide the insights needed to understand how soil is transformed by the vegetation it supports across diverse timescales (Figure 1). Instead, we suggest a greater focus on quantifying root-regolith interfaces in a diversity of ecosystems, particularly at depth, to better characterize the volume of regolith in close proximity to roots, which contrasts with assumptions in current ESM efforts (Figure 9). These efforts would be especially valuable in regions not represented in this study, while further work conducted in the ecosystems represented here could help unveil any ecosystem-specific patterns. Fine roots, whose presence is typically underestimated by mass-based approaches, deserve special scrutiny given their status as key biogeochemical agents. The lack of consistent functional form in depth distributions of fine roots renders the use of deterministic functions to describe them difficult. However, our work represents a step forward for discerning patterns in depth distributions of root-regolith interfaces across biomes, land uses, and soil and plant functional types that will be useful for modelers attempting to project critical zone functioning on a changing planet.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The root presence, root mass, and environmental data used for this study (Billings et al., 2025) are available at https://zenodo.org/records/17663627, as are the R scripts that process, plot, and analyze the data.

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