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Key Points:

- We tested the hypothesis that tree groundwater uptake is related to species identity
- Both rooting depths and the ratio of root to water table depths were significant phylogenetic signals
- Isotopic evidence of groundwater uptake showed a significant binary phylogenetic signal

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Phylogenetic Underpinning of Groundwater Use by Trees

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Abstract Root water uptake (RWU) strategies shape climate-vegetation feedbacks and ecosystem productivity. A fundamental relationship between RWU strategies and evolutionary histories (phylogeny) of trees, however, remains poorly understood. Establishing a phylogenetic basis for tree RWU, particularly groundwater use, could improve their representation in terrestrial biosphere models (TBMs) that are crucial for understanding hydrologic and ecosystem responses to climate perturbations. We explored possible phylogenetic bases for tree RWU using two independent data sets: (a) observed root and local groundwater depths representing 502 tree species, and (b) groundwater, soil, and xylem water isotopic evidence for groundwater uptake representing 412 species. Maximum rooting depths (RD_{MAX}), the ratio between RD_{MAX} and mean water table depth (WT) (RD_{MAX}/WT), and isotopic evidence of groundwater uptake showed significant phylogenetic signals, suggesting that tree RWU strategies are more similar among closely related species. Our findings may be used to parameterize species-level RWU in TBMs, particularly for data-poor regions.

Plain Language Summary Transpiration dominates terrestrial evapotranspiration, strongly influencing the movement of water, carbon, nutrients, and pollutants in the landscape. Despite evidence for global variations in water uptake strategies across tree species, the models that simulate water and solute movement through soils and ecosystems mostly neglect this complexity. This is in part because we lack empirical studies to parameterize species-level variations in rooting depth in model code. Our research demonstrates via two independent data sets (observed rooting depths and isotopic evidence of groundwater uptake) that rooting depth has greater degrees of similarity in more closely related species than for distantly related species. Overall, our study finds that phylogenetic relationships of trees could provide reasonable estimates of tree groundwater use, improving global-scale ecosystem models in the absence of empirical studies.

1. Introduction

Transpiration mediates the transfer of water and energy between the land surface and the atmosphere (Fan et al., 2017; Good et al., 2015), impacting the regulation of climate and distribution of vegetation over land (Beerling & Berner, 2005). Trees play a particularly relevant role in water and energy transfer because they exhibit a wide range of maximum rooting depths (RD_{MAX}). This suggests that trees may be able to access groundwater that is not immediately available for evaporation. Root water uptake (RWU) of local soil moisture and groundwater by trees thereby influences the partitioning of precipitation between surface runoff (immediate streamflow), water infiltrating into forest soils (i.e., catchment stored water) and transpiration. Establishing a possible environmental and physiological basis for RD_{MAX} and RWU patterns is specifically important because current ecohydrological models at catchment and continental scales tend to oversimplify RWU strategies (Warren et al., 2015). These simplifications in turn limit model veracity and utility for predicting future global change (Fan et al., 2019; Ferguson et al., 2016; Kennedy et al., 2019; Kleidon & Heimann, 1998).

While the evolution of deep roots and their access to groundwater have been associated with major changes in global hydrological and biogeochemical cycles (Beerling & Berner, 2005; Beerling et al., 1998; Ibarra et al., 2019), we cannot yet adequately explain all variations in observed rooting strategies and their ecosystem function (Pierret et al., 2016). Specifically, the degree to which vegetation connects the water table to the atmosphere via RWU of groundwater, as opposed to uptake and transpiration of moisture held under

tension in smaller soil pores (Fan, 2015) remains unclear. On the one hand, some trees may gain an energy advantage either by relying on recently infiltrated precipitation in shallow soils or via hydraulic redistribution (Hafner et al., 2017; Sun et al., 2018) of deeper water from neighboring species. On the other hand, trees that invest in the growth and maintenance of deeper rooting systems to access more stable water sources may gain a competitive advantage during periods of drought. A conceptual model of rooting strategies and empirical observations is presented in Figure S1.

A proliferation of studies over the last three decades have used isotopic observations of subsurface waters and tree xylem to provide evidence that some trees are facultative consumers of groundwater (Balugani et al., 2017; Knighton, Conneely, & Walter, 2019; Miller et al., 2010) and others obligate consumers of soil moisture held under tension (Bowling et al., 2017; Evaristo & McDonnell, 2017; Gaines et al., 2016). While local isotopic and sap flux studies have revealed complex RWU strategies in various forest ecosystems (Brum et al., 2019; De Deurwaerder et al., 2018; Gaines et al., 2016; Knighton, Souter-Kline, et al., 2019; Miller et al., 2010; Volkmann et al., 2016), it remains unclear if these empirical observations are climate- and ecosystem-transferable. Given that water is often a limiting resource for plant growth, we would anticipate that RD_{MAX} and the ratio between RD_{MAX} and mean annual water table depth (WT), RD_{MAX}/WT, are traits that relate to RWU strategy and are therefore similar in closely related species.

The environmental and physiological controls on RD_{MAX} and RWU in higher plants are poorly known for several related reasons. One body of knowledge suggests that the realized niche for RWU that trees occupy is determined mainly by local environmental conditions (hereafter *locality hypothesis*), such as soil moisture and topographic positions, regardless of species and life history (Canadell et al., 1996; Evaristo & McDonnell, 2017; Fan et al., 2017, 2019; Hodge, 2004; Schenk & Jackson, 2005). Under this conceptual model, plants are simplified to one monolithic hydrologic functional strategy for RWU that responds to environmental conditions to optimize the water uptake of individual trees. Another body of knowledge suggests that the realized niches for RWU are determined by hydrological niche partitioning in response to neighboring tree species (hereafter *niche segregation hypothesis*). Niche segregation is the partitioning of subsurface water as a resource through different RWU strategies at sufficiently small spatial scales (Silvertown et al., 2015). The deployment of these RWU strategies is determined mainly by species-level competition for the same amount of available water (Brum et al., 2019; Cabal et al., 2020; Gaines et al., 2016; Magh et al., 2020; Volkmann et al., 2016) or complementary hydraulic redistribution that increases total stand productivity (Grossiord et al., 2014; Hafner et al., 2017; Sun et al., 2018). Niche segregation may be the outcome of local soil moisture and topography as well as neighboring species and is a refinement of the *locality* hypothesis. Under this conceptual model, the RWU strategies of individual species cannot be separated from that of the stand (Grossiord, 2020; Grossiord et al., 2014; Knighton, Singh, & Evaristo, 2020).

A third body of knowledge suggests that RWU strategies depend on species identity, with closely related trees exhibiting similar strategies (hereafter *phylogenetics hypothesis*). For example, studies have shown consistent evidence for changes in the sources of RWU used by gymnosperms throughout the growing season (Andrews et al., 2012; Berkelhammer et al., 2020; Mackay et al., 2020) and gymnosperms using different water sources from those of neighboring angiosperms (Knighton, Souter-Kline, et al., 2019; Link et al., 2014; Mackay et al., 2020; Tetzlaff et al., 2021). These studies hint at a fundamental, evolutionary basis for commonalities in RD_{MAX} and RWU strategies. Phylogenetic signals, which describe greater degrees of similarity in more closely related species, could provide a broader context for interpretation of these empirical studies and explain the degree to which taxonomy drives rooting patterns in the presence of external variables such as climate (W. Chen et al., 2013; Kitajima et al., 2010). Root traits have shown consistency among taxonomic classes (Comas & Eissenstat, 2009), as well as significant phylogenetic signals (McCormack et al., 2020; Valverde-Barrantes et al., 2017), though it is unclear if the similarity in traits translates into similar RWU strategy.

We examine tree RWU strategies in the context of a phylogenetic model to address the following hypotheses. H1: there is a significant phylogenetic signal in observed maximum rooting depths, H2: there is a significant phylogenetic signal in the ratio of the maximum rooting depth to the mean annual water table, and H3: there is a significant phylogenetic signal in xylem isotopic evidence of groundwater uptake. We achieve this objective by analyzing two independent global data sets: (a) observed maximum rooting depths (RD_{MAX})

and mean annual water table depths (WT) (Fan et al., 2017; Iversen et al., 2017), and (b) groundwater, soil, and xylem water isotopic evidence of groundwater use (Evaristo & McDonnell, 2017).

2. Materials, Methods, and Data

2.1. Plant Trait and Hydrologic Data Sets and Data Availability

We analyzed two global data sets that aggregate individual measurements of maximum plant rooting depth (RD_{MAX}) and local mean water table depth from a variety of studies (Fan et al., 2017; Iversen et al., 2017). Duplicate records between the databases were removed. We filtered the composite database to retain only records where (a) the study was conducted in a monoculture stand (i.e., only one species was listed in a given study plot), (b) "form/stature" contained the string "tree," (c) records identified trees to species level. This filtering produced a composite database of 1,170 measurements of tree rooting depths covering 641 species. The database contained 304 records covering 268 species with information on both rooting and water table depths.

We examined a second data set based on a meta-analysis that aggregates measurements of soil, groundwater, and tree xylem water isotopic compositions (^{2}H, ^{18}O) collected across ecohydrological studies (Evaristo & McDonnell, 2017) containing 531 observations and 414 unique species. We appended to this database 42 new records published after the original database (see Table S1), increasing the sample size to 573 records and 454 species. The data set includes analysis estimating the proportion of xylem samples for species within each study that presents evidence of groundwater uptake. That is, the number of xylem samples out of a universe of plant samples reported to have groundwater contribution to xylem water. We note that each observation represents a unique study that consists of multiple water isotopic samples of each species.

Each data set (Evaristo & McDonnell, 2017; Fan et al., 2017; Iversen et al., 2017) was validated against The Plant List (TPL), a comprehensive database of accepted plant names (Kalwij, 2012). Records with Latin names that failed to match standardized names in TPL were discarded from analysis ($n_{RDMAX} = 139$ species; $n_{RD/WT} = 108$ species; $n_{isotope} = 2$ species). The databases used for analysis contained 502, 160, and 412 species for analysis of maximum rooting depth (RD_{MAX}), and RD_{MAX}/WT, and isotopic evidence for groundwater uptake, respectively. The databases contain only 53 species with information on rooting depth, water table depth, and isotopic evidence for groundwater uptake, limiting opportunities for comparisons across the data sets. The geographic distribution of database records is presented in Figure S2.

2.2. Establishment of Phylogenetic Relationships for Trees

To define the evolutionary relationships among organisms, we developed phylogenetic dendrograms of both tree databases with V.Phylomaker (Jin & Qian, 2019) using TPL standardized family, genus, and species names within the R scripting environment. Dendrogram structure was established with algorithm Scenario 3, which determines where a new genus tip is bound with consideration for branch length (Jin & Qian, 2019). All subsequent phylogenetic analyses were based on these established dendrograms. R scripts used in phylogenetic analysis are available (https://github.com/jknigh0813/Phylo_GW).

2.3. Regression Analysis of Tree Rooting and Water Table Depths

We compared the spatial distributions of RD_{MAX}, local water table depth (WT), and RD_{MAX}/WT for both angiosperms and gymnosperms. We tested for significant differences in the median latitudes of trees exhibiting isotopic evidence of soil water and groundwater uptake separately for angiosperms and gymnosperms with two-sample Kolmogorov-Smirnov tests. With this and all subsequent hypothesis tests, we evaluated and discuss sensitivity at thresholds for Type 1 errors, α, of 0.1, 0.05, and 0.01.

We examined the relationship between log-transformed RD_{MAX} and WT with both standard major axis (SMA) and phylogenetic least squares (PLS) regression. SMA assumes each database observation is independent whereas PLS accounts for the expected covariance structure of regression residuals based on phylogenetic distance and therefore eliminates the assumption that all records are independent. PLS regressions based on phylogenetic dendrograms require single trait values per species. For each species, we

computed the median of RD_{MAX} and WT where the database contained multiple records for one species. For each regression, we present the best fit linear regression, $\ln(RD) = \beta \times \ln(WT) + \beta_0$, 95% confidence intervals on β, and the adjusted R^2. For PLS, we also present Pagel's λ_P, a measure of the phylogenetic signal strength of regression residuals (Pagel, 1999) (i.e., the degree to which closely related trees show similar deviations from the proposed linear model). We subsequently fitted SMA and PLS to all trees and then separately for angiosperms and gymnosperms. We tested for significant differences in the regression slopes of angiosperms and gymnosperms for both SMA and PLS (Warton et al., 2006).

2.4. Phylogenetic Analysis of Isotopic and Root Trait Evidence of Groundwater Uptake

We evaluated the hypotheses that RD_{MAX} ($n = 502$ species) and RD_{MAX}/WT ($n = 160$ species) (Fan et al., 2017; Iversen et al., 2017) show significant phylogenetic signals (i.e., traits among closely related tree species are significantly more similar than for distantly related species). For each test, where multiple values of RD_{MAX} or RD_{MAX}/WT were available for a single species we used the median value. The significance of the phylogenetic signals of these plant traits were estimated with both Blomberg's K (Blomberg et al., 2003) and Pagel's λ_P (Pagel, 1999). Each test involves a test statistic that can be interpreted as a scaled measure of the strength of a phylogenetic signal. Blomberg's K values span $(0, \infty)$ where 0 indicates no structure and 1 indicates that the covariance of a trait is proportional to the shared history between species. Pagel's λ_P spans the range of 0–1, where larger values similarly indicate stronger phylogenetic signals. If disagreement occurred between the two tests, we accepted the results of Pagel's λ_P as prior studies have demonstrated that λ_P may be a more robust test than K and provides more stable results under the assumption of a Brownian model of evolution (i.e., trait values vary along phylogenies according to a random walk with mean of 0) (Molina-Venegas & Rodríguez, 2017; Münkemüller et al., 2012).

We evaluated the hypothesis that groundwater uptake emerged from a Brownian model of evolution with $n = 412$ species (Evaristo & McDonnell, 2017). Each species was assigned a binary variable (0—no groundwater; 1—groundwater) where the operational definition of "groundwater" followed that used by the source research. Where both presence and absence of evidence for groundwater uptake existed (i.e., variations in water sources through time or between individuals), we assigned a value of 1 given that groundwater uptake may be both a consequence of trait variations and environmental conditions. Given that cryogenic vacuum extraction (CVE) may bias stem water ^{2}H measurements (Y. Chen et al., 2020), the analysis was repeated excluding all records based on CVE (a) using only ^{2}H in source water identification and (b) analysis based on ^{2}H and ^{18}O (see Supporting Information S1). The significance of binary traits was estimated with the D statistic (Fritz & Purvis, 2010). D values span $(-\infty, \infty)$, where D of 0 indicates Brownian evolution, 1 indicates random trait dispersal, and values above 1 indicate an over dispersed trait.

3. Results

3.1. Geographic Distribution of Rooting Strategies

We observed latitudinal gradients in rooting depth that appear to follow trends in water table depth (WT; Figures 1a and 1b). Gymnosperms generally have shallower RD_{MAX} than angiosperms (Figure 1a) and occur at higher latitudes in regions with shallower WT (Figure 1b). Across all latitudes, trees exist with RD_{MAX} both shallower and deeper than the local WT (Figure 1c). The latitudinal distributions of soil water and groundwater use as determined by isotopic studies (Figure 1d) were not significantly different in either angiosperms (p-value = 0.197) or gymnosperms (p-value = 0.237) as determined by two-sample KS tests.

3.2. Regression Analysis of Rooting and Water Table Depths

SMA regression of log-transformed RD_{MAX} against WT suggested that RD_{MAX} is strongly correlated with WT across all trees ($\beta_{SMA} = 0.919$, 95% confidence interval [0.862, 0.980]; Figure 2a). PLS regression, which accounts for the expected covariance structure of residuals stemming from phylogeny, suggested the relationship between RD_{MAX} and WT is somewhat weaker than implied by SMA ($\beta_{PLS} = 0.658$, 95% confidence interval [0.567, 0.748]; Figure 2b). These differences are likely attributable to the uneven representation of certain clades in the underlying data set where the structure of residuals exhibited a significant
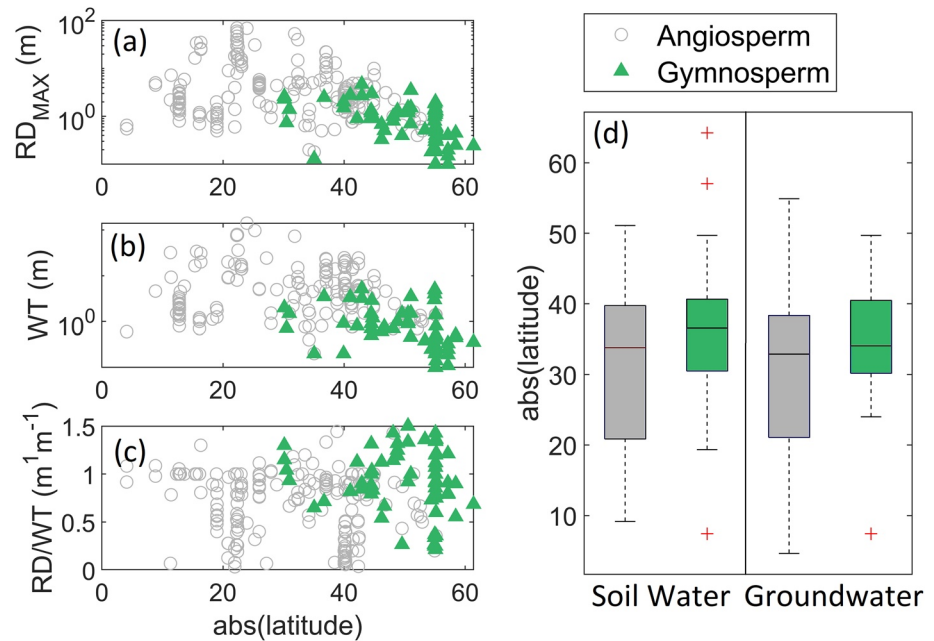
Figure 1. Relationships between latitude and RD_{MAX} (a), WT (b), RD_{MAX}/WT (c). Latitudinal distribution of isotopic studies showing soil water and groundwater use in angiosperms and gymnosperms (d).

phylogenetic signal ($\lambda_P = 0.443$, p-value = 0.000; Figure 2b). Out of 294 individual trees (where both RD_{MAX} and WT measurements were available), 105 (35.7%) exhibited $RD_{MAX}/WT \geq 0.98$. Analysis that clustered vegetation by taxonomic groupings (family) demonstrated that local groundwater depth is not a substantial predictor of RD_{MAX} for all tree families, where only 23.4% (11 of 47) exhibited a median $RD_{MAX}/WT \geq 0.98$ (Figure S3). SMA regression suggested no significant differences between gymnosperms and angiosperms (Figure 2a; p-value = 0.875). In contrast, PLS analysis identified significant differences (Figure 2b; p-value = 0.002) that suggest gymnosperm rooting depths more closely align with local WT ($\beta_{PLS} = 0.832$, 95% confidence interval [0.657, 1.003]) than the case is with angiosperms ($\beta_{PLS} = 0.639$, 95% confidence interval [0.539, 0.746]).
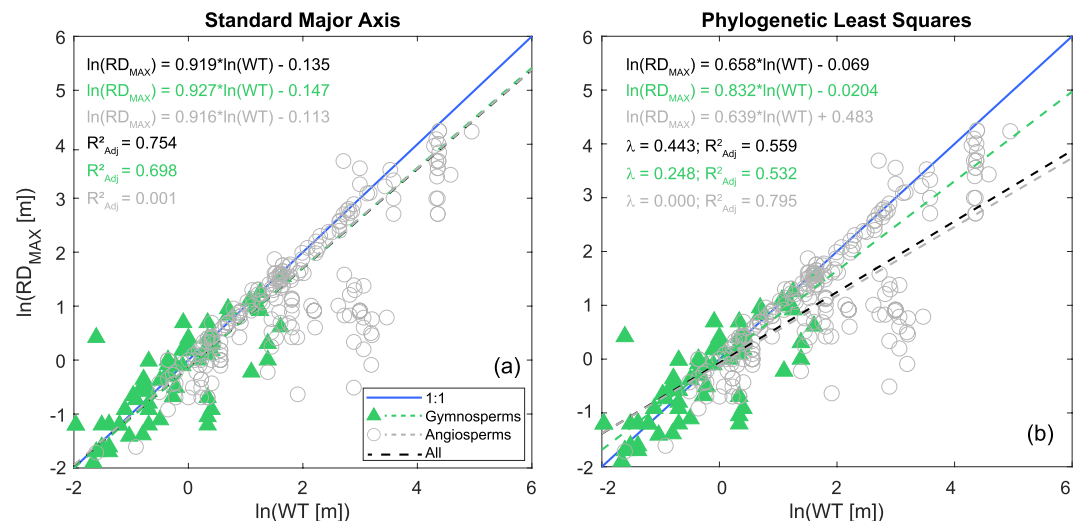

Figure 2. Standard major axis regression (a) and phylogenetic least squares regression (b) for ln(WT) and ln(RD_{MAX}) fit to all data (black), gymnosperms (green), and angiosperms (gray).

RD$_{MAX}$
n = 502 species
λ_p = 0.272 (p = 0.014)
K_b = 0.046 (p = 0.092)

RD$_{MAX}$/WT
n = 160 species
λ_p = 0.156 (p = 0.001)
K_b = 0.020 (p = 0.175)

Isotopes
n = 412 species
D = 0.804 (p = 0.000)

0° ▬▬▬ 85°
no GW ▬▬▬ GW
0 m^{1}m^{-1} ⊢─┤ 7 m^{1}m^{-1}
0 m ⊢──┤ 70 m

abs(Latitude)
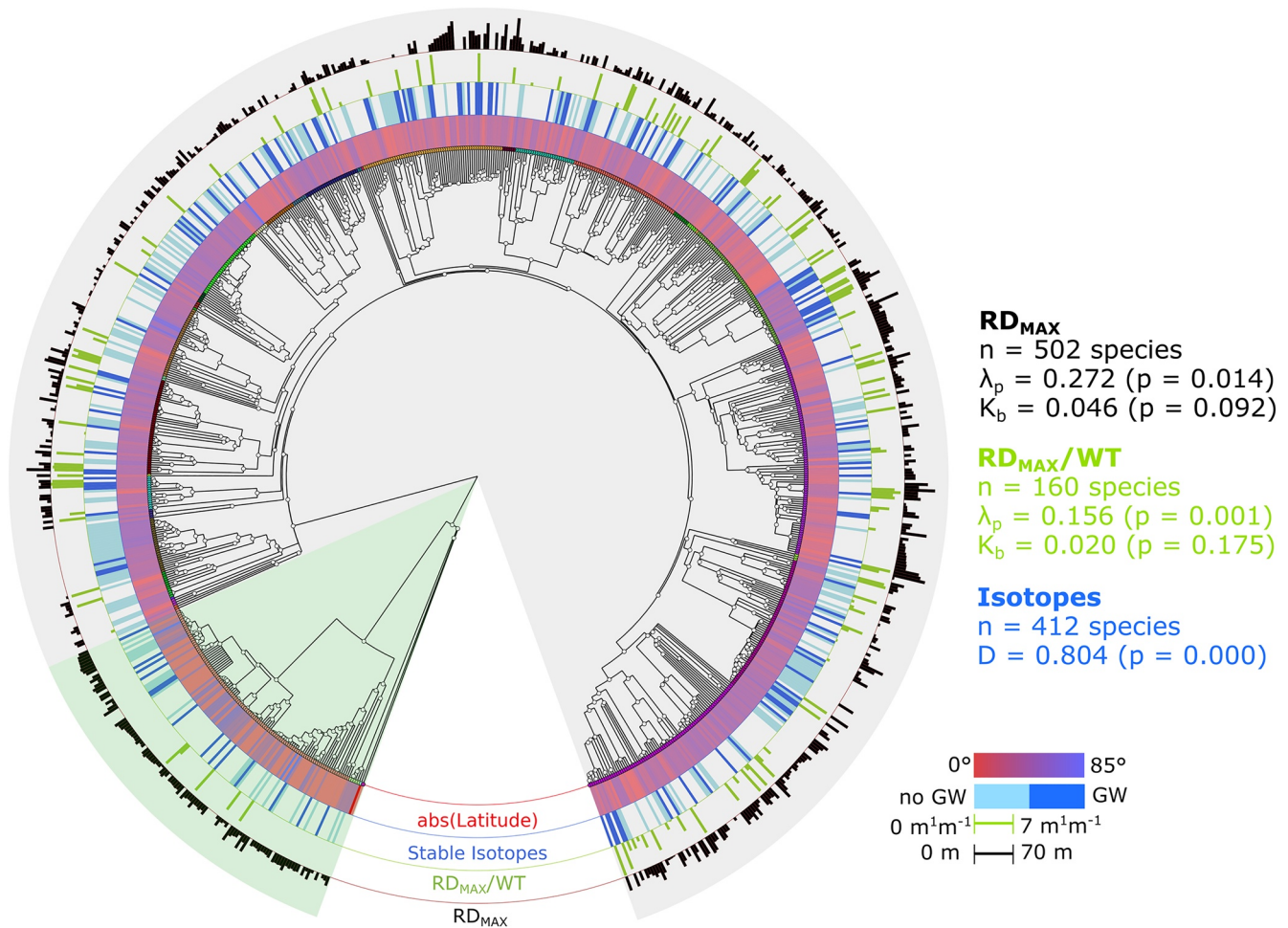Stable Isotopes
RD$_{MAX}$/WT
RD$_{MAX}$

Figure 3. Global database of angiosperm (gray) and gymnosperm (green) trees showing the absolute value of latitude of the original study (red and blue ring), stable isotopic evidence for groundwater uptake (dark blue), and soil water uptake (light blue), the ratio of rooting depth to water table depth (RD$_{MAX}$/WT), and RD$_{MAX}$. Colored dots on the inner ring indicate tree family.

3.3. Phylogenetic Signal of Rooting Depth and Groundwater Uptake

The data sets describing RD$_{MAX}$, RD$_{MAX}$/WT (Fan et al., 2017; Iversen et al., 2017), isotopic evidence of groundwater uptake (Evaristo & McDonnell, 2017), and the absolute value of latitude (i.e., distance from the equator) are arranged on a phylogenetic dendrogram (Figure 3). Not all tree species are represented in these data sets, though we demonstrate that these data sets capture broad variations in rooting depth and that isotopic evidence for groundwater uptake occurs across a range of evolutionary history and latitudes (Figure 3).

RD$_{MAX}$ exhibited a significant phylogenetic signal at the $\alpha \leq 0.05$ threshold across 502 tree species as estimated by Pagel's λ_P (λ_P = 0.272, p-value = 0.014), and at the $\alpha \leq 0.1$ threshold Blomberg's K (K_B = 0.046, p-value = 0.092; Figure 3). Maximum root depth relative to the local mean water table, RD$_{MAX}$/WT, within 160 tree species was significantly related to phylogenetic structure at the $\alpha \leq 0.01$ threshold with Pagel's λ_P (λ_P = 0.156, p-value = 0.001), but not with Blomberg's K (K_B = 0.020, p-value = 0.175; (Figure 3). As previously discussed, we accept the interpretation provided by λ_P based on the result of critical reviews of both statistics for the identification of phylogenetic signals (Molina-Venegas & Rodríguez, 2017; Münkemüller et al., 2012). The λ_P values for RD$_{MAX}$ (0.272) and RD$_{MAX}$/WT (0.156) indicated that both phylogenetic signals are weaker than would be expected under a model of perfect Brownian evolution (λ_P = 1), but significantly greater than 0 (no signal).

Isotopic groundwater and soil water signatures within the xylem water of 412 tree species (Evaristo & McDonnell, 2017) yielded similar results. The D statistic of 0.804 indicates that isotopic evidence of groundwater use was significantly different from both 0 (p-value = 0.000) and 1 (i.e., random occurrence, p-value = 0.000). Similar to the interpretation of λ_p for RD_{MAX} and RD_{MAX}/WT, the D statistic indicates a significant phylogenetic signal, but not as strong as would be expected under a purely Brownian model.

We repeated this phylogenetic analysis excluding all records where water extractions were performed with CVE and analysis using only ^{2}H. This subset produced similar results (n = 266 species, D = 0.624, p-value = 0.000). No significant signal was identified when both ^{2}H and dual isotope analysis records were discarded (n = 117 species, D = 0.904, p-value = 0.203) (see Supporting Information S1).

4. Discussion and Conclusions

4.1. Locality, Niche, and Phylogenetic Hypotheses for RWU

Prior analyses of observations from diverse climates have provided evidence for a correlation between plant rooting depths and environmental conditions (Barbeta & Peñuelas, 2017; Canadell et al., 1996; Evaristo & McDonnell, 2017; Fan et al., 2017; McCormack et al., 2020, 2020; Schenk & Jackson, 2005). Our SMA regression analysis of the RD_{MAX} database suggested that RWU strategies were explained well by the locality hypothesis where RD_{MAX} was significantly linearly correlated with WT (Figure 2a). We argue that the SMA regression result (paralleling the methodologies of prior studies) is flawed and occurs only because the underlying statistical test incorrectly assumes independence among database records. A substantial fraction of this database is comprised of several vegetation families that cluster near RD_{MAX}/WT = 1 (*Myrtaceae* [n = 16], *Tamaricaceae* [n = 8], and *Pinaceae* [n = 72]; Figure S4). PLS regression analysis indicated that the residuals of the linear regression exhibited a significant phylogenetic signal (λ_p = 0.443; Figure 2b), and therefore violate the assumptions of SMA regression. In contrast, the PLS regression suggested that rooting depths were only approximately equal to water table depths in gymnosperms (Figure 2b).

Prior studies provide corroborating evidence for variations in RWU between gymnosperms and angiosperms. Meta-analysis of long-term research catchments across five northern/cold regions demonstrated that angiosperms exhibited greater evidence of isotopic overlap with enriched shallow soil moisture whereas gymnosperm xylem water deviated from measured end members (Tetzlaff et al., 2021). Global data indicates that angiosperms invest more in fine roots than gymnosperms (C. Wang et al., 2019), possibly driving variations in RWU. The rooting depth (Fan et al., 2017; Iversen et al., 2017) and isotopic (Evaristo & McDonnell, 2017) data sets exhibited some disagreement on the relative groundwater use by angiosperms and gymnosperms. Gymnosperms, specifically *Pinaceae*, exhibited more consistent evidence of root growth into the saturated zone than angiosperms (Figures 2b and S3) potentially indicating more groundwater use. The global isotopic data set demonstrated less difference between these clades where 36.3% of gymnosperm species exhibited evidence of groundwater uptake versus 36.1% of angiosperms. Notwithstanding, a meta-analysis has shown that the proportion of groundwater contribution to xylem water mixture is greater in angiosperms than in gymnosperms (Evaristo & McDonnell, 2017). These results suggest that more complex models based on phylogenetic dendrograms (Figure 3) are needed to explain variations in tree water use that occur within the broad clades of angiosperms and gymnosperms (Figure 2).

Isotopic data and RD_{MAX}/WT showed high variance among angiosperms (Figures 2 and 3), indicating the evolution of diverse water use strategies, including some species that grow deep roots but do not extend to groundwater (Figure 2). Root access to soil water is necessary to avoid xylem embolism and death. Deep roots not reaching groundwater may reflect the depth at which water uptake requires the least energy for the majority of the year (Brantley et al., 2017). Alternately, trees may grow different rooting systems because they vary in the need for energetically available water volumes related to variations in above-ground height (Trugman et al., 2021), stomatal regulation strategies (Klein, 2014), stem resistance to cavitation (Urli et al., 2013), or soil water potential thresholds for root uptake of moisture (Brantley et al., 2017). High variance in RD_{MAX}/WT may also reflect ecosystem pressures. Investment in dense shallow rooting systems may allow trees to outcompete neighbors for recent precipitation, whereas deeper roots can potentially sustain growth during periods of drought (Silvertown et al., 2015). Trees with shallow rooting systems may have

evolved to rely on the redistribution of deeper water sources by neighboring species (Hafner et al., 2017; Sun et al., 2018).

The phylogenetic signals of RD_{MAX}/WT and isotopic evidence for groundwater uptake were significant, but likely shaped by both species identity and environmental conditions (Figure 3). Xylem isotopic measurements collected across mixed-species temperate forests suggest that the seasonal origin of water stored in trees was consistent within each tree species sampled, but differed across species (Allen et al., 2019), possibly indicating the role of species identity in shaping water uptake. Similarly, ecohydrological model calibration to continuous streamflow records demonstrated consistency in derived rooting parameters among monoculture catchments of the same species (Knighton, Singh, & Evaristo, 2020). This result is supported by prior evidence for phylogenetic signals in root traits that may carry implications for RWU (Comas & Eissenstat, 2009; McCormack et al., 2020; Valverde-Barrantes et al., 2017). Some ecosystems show evidence of seasonal oscillations between niche segregation and direct competition driven by seasonal soil water limitation (Andrews et al., 2012; De Deurwaerder et al., 2018; Kulmatiski et al., 2020; McCormack et al., 2020; Rodríguez-Robles et al., 2020), suggesting higher-order interactions between the phylogenetic, niche, and locality hypotheses. In a mixed species forests, co-occurring trees may rely on similar water sources during dry days, but exhibit divergent RWU depths in response to recent precipitation (Grossiord et al., 2017; Liu et al., 2019; Volkmann et al., 2016). In a temperate beech-hemlock catchment, beech trees consistently used older soil water (and therefore more likely tightly bound shallow soil water) than hemlock trees (Knighton, Souter-Kline, et al., 2019). The age of water used by both species varied by season and topographic position within the forest, though the relative differences in xylem water age remained, demonstrating effects of both environmental conditions and species identity on RWU.

4.2. Implications for Improving RWU Representation in Terrestrial Biosphere Models

Climate change is expected to alter the composition of forest ecosystems. Thus, without an adequate representation of the nuanced patterns that exist in RWU across phylogenetic clades, current generation models will fail to capture the dynamics of climate-driven perturbations to ecosystem composition and downstream hydrological impacts. Terrestrial Biosphere Models (TBMs) and hydrological models frequently characterize vegetation with presumed functional groups (e.g., coniferous vs. deciduous or broadleaf vs. needleleaf forest). Our research demonstrates that strategies for water uptake vary considerably within angiosperms (Figures 2 and 3) and therefore heterogeneity in functional groups often described in models. Phylogenetic dendrograms could potentially support a refinement of functional group definitions that would more accurately represent variations in soil water and plant interactions.

Parameterization of RWU for individual species has largely depended on resource intensive measurements of internal tree hydraulics (Yang et al., 2013), xylem water isotopic measurements (Knighton, Kuppel, et al., 2020), soil moisture profiles (Hupet et al., 2003), or spatially integrated measures of latent heat fluxes (Sulis et al., 2019; P. Wang et al., 2018) and stream discharge (Knighton, Singh, & Evaristo, 2020). Recent calls for ecosystem model progress suggest that future research explores parameterizing RWU by assuming a locality hypothesis where critical zone moisture content drives subsurface root growth and subsequent uptake (Fan et al., 2019). However, our re-analysis of global plant rooting depths yielded a contrasting interpretation (Figure 2b).

Our hypothesis of a phylogenetic framing of community RWU patterns could add nuance to conceptual and numerical models of RWU and possibly improve the representation of plant hydraulic strategies in TBMs. Traits of unstudied species can be estimated with rich trait databases and phylogenetic dendrograms, provided the traits are significant phylogenetic signals (Debastiani et al., 2021; Guénard et al., 2013; Penone et al., 2014). The phylogenetic dendrograms established in this research may support accurate estimation of RD_{MAX}, RD_{MAX}/WT, and groundwater uptake for unstudied species and therefore aid model parameterization of vegetation where empirical studies are lacking. Further research is needed to test the viability of phylogenetic parameter estimation for TBMs and hydrological models.

Data Availability Statement

All data used in this study are previously published (Evaristo & McDonnell, 2017; Fan et al., 2017; Iversen et al., 2017).

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