LETTER

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Evolutionary history resolves global organization of root functional traits

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Plant roots have greatly diversified in form and function since the emergence of the first land plants[1,2], but the global organization of functional traits in roots remains poorly understood[3,4]. Here we analyse a global dataset of 10 functionally important root traits in metabolically active first-order roots, collected from 369 species distributed across the natural plant communities of 7 biomes. Our results identify a high degree of organization of root traits across species and biomes, and reveal a pattern that differs from expectations based on previous studies[5,6] of leaf traits. Root diameter exerts the strongest influence on root trait variation across plant species, growth forms and biomes. Our analysis suggests that plants have evolved thinner roots since they first emerged in land ecosystems, which has enabled them to markedly improve their efficiency of soil exploration per unit of carbon invested and to reduce their dependence on symbiotic mycorrhizal fungi. We also found that diversity in root morphological traits is greatest in the tropics, where plant diversity is highest and many ancestral phylogenetic groups are preserved. Diversity in root morphology declines sharply across the sequence of tropical, temperate and desert biomes, presumably owing to changes in resource supply caused by seasonally inhospitable abiotic conditions. Our results suggest that root traits have evolved along a spectrum bounded by two contrasting strategies of root life: an ancestral 'conservative' strategy in which plants with thick roots depend on symbiosis with mycorrhizal fungi for soil resources and a more-derived 'opportunistic' strategy in which thin roots enable plants to more efficiently leverage photosynthetic carbon for soil exploration. These findings imply that innovations of belowground traits have had an important role in preparing plants to colonize new habitats, and in generating biodiversity within and across biomes.

Recent efforts to understand how functional traits are organized across land plants have revealed notable patterns across the leaf economic spectrum[5,6], but whether such a high degree of organization is also seen in root traits remains controversial[4,7]. A key factor that has limited progress has been the paucity of data on root traits across plant species and biomes, as roots are difficult to sample and characterize[8,9]. Yet, roots are vital for the ability of plants to acquire nutrients and water—two functions of fundamental importance to whole-plant performance and for predicting how plants respond to elevated CO_2 levels and to climate change[10–12].

Roots face ecological and physiological challenges that differ fundamentally from those encountered by leaves. Roots must compete for and acquire nutrients and water in environments that greatly vary across global biomes, with biophysical conditions ranging from relatively stable (for example, tropical rainforests) to highly seasonal (for example, deserts or boreal forests). The high diversity that exists in root form and function, and in the degree of association with symbiotic mycorrhizal fungi, raises a fundamental question: how are root traits organized across the diverse taxa that inhabit different ecological conditions worldwide?

Here we propose a model of root trait organization that is functionally decoupled from the leaf economic spectrum and that derives from the phylogenetic history of root diameter and its evolutionary consequences for plant resource acquisition.

We evaluated a species- and biome-specific dataset of 10 root traits in 3 major categories[3,13] (morphology, physiology and mycorrhizal association; Supplementary Information, note 1), collected from over 1,200 individual plants of 369 species (from 210 genera and 79 families), distributed across 7 major biomes and 3 continents (Extended Data Table 1). The observations in our dataset: (i) derive solely from native plant communities with natural soil and nutrient conditions; (ii) focus on first-order roots (the most distal and absorptive roots of the branching system) that are subject to strong selection by the local environment[8,9,14]; (iii) accurately identify species and root order (that is, measure of branching hierarchy[8]) in mixed-species ecosystems, by tracing roots to parent trees[15]; and (iv) apply consistent analytical methods to trait measures across all species and biomes. We collected 94% of the total observations used in our dataset (see Methods).

We first investigated whether first-order root traits are globally organized in a manner analogous to the leaf economic spectrum[5,6], a composite axis of trait variation that ranges from nitrogen-rich leaves with high specific leaf area and short leaf lifespan to nitrogen-poor leaves with low specific leaf area and long leaf lifespan. In roots, nitrogen supports metabolic activity, including nutrient and water transport, enzyme functioning and mycorrhizal symbiosis[16]. As a result, nitrogen has previously been proposed to serve a similarly central role in the trait organization of roots, with high levels of nitrogen in roots occurring in species with high levels of nitrogen in their leaves, rapid growth and short root lifespans[4,17].

Our results do not support the idea of an analogous organizing role for nitrogen in a global root economic spectrum, expanding on similar previous conclusions drawn from taxonomically and geographically smaller datasets[4,18,19]. First, a principal component analysis failed to identify root nitrogen, which is analogous to leaf nitrogen, as a significant contributor to the primary axis of trait variation (Extended Data Fig. 1 and Extended Data Table 2). Instead, root traits were most strongly explained by root diameter and by a group of traits associated with root construction and mycorrhizal association (principal component 1, 46%; Extended Data Fig. 1).

Second, root nitrogen was not correlated to specific root length (SRL, the length of root per unit of biomass invested) in a manner analogous to the relationship between specific leaf area and leaf nitrogen

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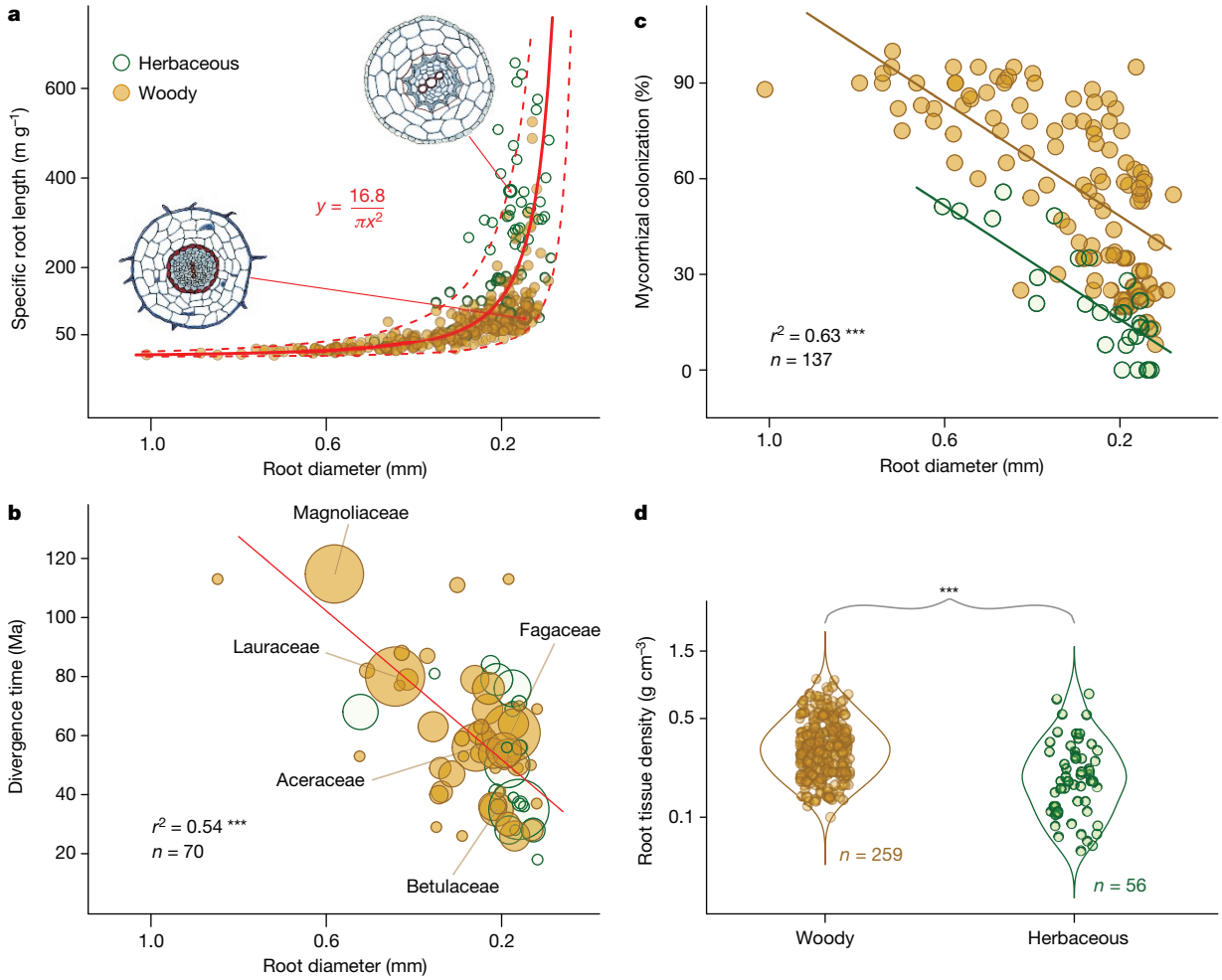

Figure 1 | Root trait dimensions organized by root diameter and growth form. a–**c**, At the species level, the diameter of first-order roots is inversely correlated with SRL (**a**, $n = 323$ species), positively related to the evolutionary time of divergence of major taxonomic groups (**b**; Ma, million years ago) and positively related to the length of root (in per cent) colonized by mycorrhizal fungi (**c**). ***$P < 0.001$, linear regression. **d**, Root tissue density differs across plant growth form, with herbaceous plants (green) displaying more constrained variation than woody plants (brown) (F-test, ***$P < 0.001$; note logarithmic scale ($\log_{10}$) on the y axis). The solid red line in **a** identifies the relationship $y = 16.8/(\pi x^2)$ in which y denotes SRL and x denotes root diameter, and root tissue density is 0.25 g cm^{-3} (Supplementary Information, note 1); upper and lower dashed red lines identify tissue densities of 0.1 and 1.0 g cm^{-3}, respectively. We used a linear regression weighted by number of species in **b**, and a linear regression with woody and non-woody growth forms as categorical variables in **c**. Root cross-section images in **a** are from the low root-tissue-density grass *Agropyron cristatum* (right) and the high root-tissue-density woody shrub *Rhaphiolepis indica* (left).

(Extended Data Figs 2a, b, 3). Third, *in situ* ($n = 75$) and hydroponic-based ($n = 111$) measures showed no systematic relationship between root nitrogen uptake—which is analogous to leaf photosynthetic capacity—and root diameter, SRL or plant growth form (Extended Data Figs 2c, d, 4b, d). Taken together, these results suggest that nitrogen is less important in belowground nutrient foraging than in aboveground light and CO_2 capture (Supplementary Information, note 3). Furthermore, root lifespan, which is analogous to leaf lifespan, was correlated with root diameter and SRL but explained only 14% and 17% of the respective variance ($P < 0.01$ for both, linear model; Extended Data Fig. 4a, c).

We next analysed the organizing role of root diameter in determining trait variation across plants. We found that the length of root per biomass invested (that is, the SRL) increases nonlinearly with decreasing root diameter (D) according to the allometric relationship, $\mathrm{SRL} = 16.8/(\pi D^2)$ (Fig. 1a, solid red line; Supplementary Information, note 1). This relationship indicates that as roots get thinner, plants can explore markedly greater volumes of soil per unit of carbon they invest. We also found that woody and herbaceous plants occupy different parts of the SRL versus root diameter relationship, although there is some overlap: woody plants (Fig. 1a, brown points) tend to occupy a region in which differences in root diameter have a limited effect on SRL, whereas herbaceous plants (Fig 1a, green points) reside in a region in which even small variations in diameter cause large changes in SRL.

We further found that in thin-rooted species even modest evolutionary changes in the tissue density of first-order roots can greatly alter the soil length explored per unit of carbon invested. The dashed red lines in Fig. 1a indicate the sensitivity of the relationship between SRL and diameter to changes in root tissue density across a physiologically relevant range (0.1–1 g cm^{-3}). For example, the low root density of the grass *Agropyron cristatum* enables it to explore approximately 350 m more soil per gram of biomass than can the shrub *Rhaphiolepis indica*, despite the fact that both have root diameters of approximately 0.2 mm (Fig. 1a, red arrows and cross-section images). We infer that over evolutionary time plants have used both root diameter (Fig. 1a, x axis) and tissue density (Fig. 1a, dashed lines) to influence SRL: thin and soft first-order roots have the advantage of efficient soil exploration, but incur the cost trade-off of sacrificing water conduction, tissue permanence and the ability to penetrate the soil matrix.

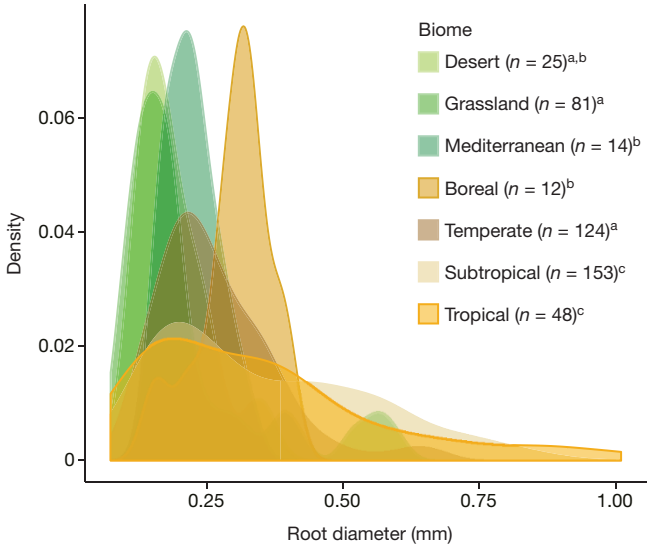

Figure 2 | Density distributions of first-order root diameter across seven biomes. The variance in root diameter declines from biomes with equable conditions (for example, tropical forests) to biomes with pronounced seasonality in soil resource supplies (for example, deserts). Numbers in brackets identify species-specific observations. Letters denote groups; pairwise differences between members of different groups are significant, Levene's variance test (for *P* values, see Extended Data Fig. 5c). Woody biomes are identified as shades of tan-to-yellow and non-woody biomes as shades of green.

We next investigate the role of evolutionary history in structuring the differences in root diameter across all major vascular plant families in our dataset (Fig. 1b). We found that, on average, thick roots are associated with evolutionarily ancient taxa (for example, Magnoliaceae) and that thin roots are increasingly common in taxa that have recently diverged from their ancestral lineage (for example, Betulaceae) (weighted linear regression: $r^2 = 0.54$; $P < 0.001$). Herbaceous plants evolved more recently (Fig. 1b, green circles) and—with the exception of Amaryllidaceae and Boraginaceae—are characterized by thin roots and SRLs that exceed those of woody plants (Fig. 1a). Together, these patterns broadly characterize an evolutionary transition from ancient tree taxa defined by thick first-order roots, to more recently radiated[20,21] woody and herbaceous plants with thin roots that can explore markedly greater lengths of soil per unit of carbon invested.

The trend towards thinner roots has had major consequences for the symbiosis between plant roots and mycorrhizal fungi. We found that mycorrhizal colonization (that is, the percentage of root length colonized) declines as roots get thinner (Fig. 1c) and that herbaceous roots have approximately 30% less colonization than woody plants at the same root diameter (linear model; $r^2 = 0.63$ with the difference between herbaceous and woody plants at $P < 0.001$). In addition, herbaceous plants have on average 33% lower root tissue density than woody plants (Fig. 1d; unequal variance *t*-test; $P < 0.001$), though considerable unexplained variation exists across taxa. These differences suggest that first-order roots have become less dependent on mycorrhizae as they have evolved thinner diameters, and that the innovation of the short-lived herbaceous growth form has fundamentally changed the relationship between root diameter and mycorrhizal colonization.

A phylogenetic independence contrasts analysis[17] confirmed that variation in root diameter, SRL and mycorrhizal colonization is strongly influenced by evolutionary history (Blomberg's *K* value in Extended Data Table1). By contrast, root chemical traits did not display a clear phylogenetic signal, which indicates that for these traits ecological variation overshadows evolutionary constraints[22].

Taken together, our results identify a general evolutionary trend in vascular plants from thick roots that rely on mycorrhizal fungi for resource acquisition to thin roots that can explore the soil at high carbon-use efficiency, but with less reliance on mycorrhizae. The observed root trait combinations imply selection for two contrasting plant strategies: (i) a conservative strategy in which carbon allocation to mycorrhizae enhances the ability of plants to compete in environments with stable resources and intense plant–plant competition; and (ii) an opportunistic strategy in which thin roots benefit plants in less predictable environments (for example, seasonal drought or cold), where rapid root growth response to a fluctuating resource supply is rewarded.

It is less clear, however, why herbaceous plants have lower mycorrhizal colonization than woody plants at similar root diameters (Fig. 1c), although the softer tissues of herbaceous plants may cause their roots to be less permanent than those of woody plants (Extended Data Fig. 4c) and therefore less able to maintain stable mycorrhizal relationships.

We next evaluated whether the distribution of root diameter changed across biomes that may differ in the pattern and stability of their resource supplies. First, we found an overall trend of decreasing variance in root diameter of woody plants from the more stable conditions of tropical and sub-tropical forests to the highly seasonal conditions of boreal and desert biomes (Fig. 2, Levene's test, Extended Data Fig. 5c). Second, woody plants were limited to thin-rooted species in the most seasonal biomes, but the diameter of herbaceous plant roots did not differ systematically across biomes (Extended Data Fig. 5a, b).

These patterns are consistent with biome-specific differences in both evolutionary history and the stability of resource supply and abiotic conditions. The tropical forest biome is evolutionarily ancient[23], characterized by seasonally stable supplies of soil resources and holds species that range from ancestral thick-rooted to more-derived thin-rooted taxa. By contrast, boreal and desert biomes are evolutionarily young[24] and have been colonized mainly by thin-rooted species that, in theory, can rapidly respond[25] to fluctuating soil resources and seasonally inhospitable conditions. The coexistence in the tropical biome of thin-rooted plants and plants pursuing more-ancient thick-rooted strategies suggests that the heterogeneity of this biome is sufficient to maintain a range of niche conditions for diverse belowground strategies.

Our findings suggest that at the timescale of plant evolution innovations of belowground traits have been important for preparing plants to colonize new habitats, and for the rich generation of biodiversity within and across biomes. The dominant dimension of trait evolution for first-order roots has been a decrease in diameter, which has reduced dependence on mycorrhizal fungi, increased the efficiency of root growth and thus enhanced the ability of plants to leverage photosynthetic carbon for soil exploration. An improved functional understanding of root traits is critical for comprehending the history and distribution of plant life, and may help to predict the risk of species extinction and to conserve biodiversity in the face of environmental change.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions Z.M., D.G. and L.O.H. developed the overall conceptual approach and analysis. Z.M. compiled and analysed the data, and X.X. provided nitrogen-uptake-rate data. R.D.B., D.M.E. and M.L.M. contributed to the formulation of research questions and interpretations. Z.M., D.G., M.L. and L.O.H. wrote the paper and all authors contributed to revisions.

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METHODS

Sampling approach. We collected roots from natural plant communities across seven major biomes and three continents (Asia, Europe and North America) between 2004 and 2016. Our sampling sites range from −1.4 °C to 22.4 °C in mean annual temperature, and from 35 mm to 2,651 mm in mean annual precipitation. At each site, we selected common indigenous species that are representative of the local plant community. For each species, we sampled multiple root branches or segments from at least three individual plants to derive the mean species trait value. For species that occupied more than one sample location, we merged the local means into one species trait value. Eleven species occurred in more than a single biome; for these we calculated a mean value for each biome.

In mixed-species ecosystems we identified roots to the species level by tracing a root to its parent tree. During the growing season, we selected mature individuals and excavated the surface soil (0–20 cm) around the plant stem to expose lateral roots. We then sampled multiple intact root branches and gently cleared the attached soil. Sampled roots were bagged and immediately placed in a cooler, and then either transferred to a refrigerator for processing within the next few days or kept frozen until later laboratory analyses.

Laboratory analyses of root functional traits. We adopted a previously established (for details, see Supplementary Information, note 2, and ref. 8) approach based on root branching-order, in which absorptive fine roots are sorted on the basis of their position in the branching architecture. We dissected root branches according to standard methodology[15] and analysed four morphological traits (diameter, SRL, root tissue density and root length), three physiological–chemical traits (root nitrogen content, root carbon content and root carbon-to-nitrogen ratio) and the extent of mycorrhizal colonization (Supplementary Information, note 1).

Root diameter and length were measured using a stereomicroscope with an ocular micrometer. SRL was determined by dividing root length by the dry biomass weight. We calculated the volume of root segments from root diameter and length, assuming segments are cylinders. Root tissue density was then calculated using dry mass and volume. Sampled roots were dried in an oven at 60 °C for 48 h, and then ground to fine powder with a ball-mill for subsequent measurements of carbon and nitrogen on an elemental analyser (Vario EL Cube; Elementar).

We measured the length of root colonized by mycorrhizal fungi in 137 species from sub-tropical[19] forests, temperate forests[15] and temperate grasslands[26]. We calculated the percentage of mycorrhizal colonization by sampling first-order roots, and determining by microscope the presence of either arbuscular mycorrhizal or ectomycorrhizal fungal structures within an individual root segment. For arbuscular mycorrhizal fungi we used a standard staining technique to identify coils and arbuscules[19,26]; no stain was needed to identify ectomycorrhizal fungal sheaths[19]. For each individual plant, we selected at least ten root branches (containing multiple orders of roots). For each species, the percentage of colonization was calculated across 20–150 randomly selected first-order root segments[19,26] to ensure that each segment length was consistent across all roots sampled. The percentage of length colonization was calculated as the ratio of the sum of infected root segments over all root segments examined. We used two different techniques: one based on cross-section analysis (MC_1, denoting mycorrhizal colonization technique 1; $n = 110$ species) and one based on scanning the root surface (MC_2, denoting mycorrhizal colonization technique 2; $n = 27$ species); both enabled us to quantify fungal association within a standardized root area. We kept the effective area examined per root segment approximately the same for both methods (173 versus 169 mm^2), such that the results are equivalent ($MC_2 = 1.02 \times MC_1 - 0.02$; $r^2 = 0.988$).

Because distal fine roots (that is, first-order roots) are primarily responsible for plant nutrient acquisition[8,9], we focused our analyses on first-order root traits. We accumulated 480 species-specific observations, of which 187 are unpublished and 256 have previously been published[14,15,19,25,26]. To enhance the coverage of some biomes (for example, boreal and Mediterranean), we added 37 previously published[8,27–29] observations into our dataset (comprising ~5% of the final dataset), taking care to include only studies of first-order roots and consistent methods. In total, we gathered traits from 369 species (281 woody, and 88 herbaceous, species; Extended Data Fig. 6 and Extended Data Table 1) covering 210 genera and 79 families.

Root lifespan. We collected data on plant root lifespan for 40 species using *in situ* minirhizotrons in boreal and temperate forests of Europe[30], Asia[31,32] and North America[33,34], with individual measures spanning at least one year. We acquired additional previously published lifespan data, selecting only studies of distal roots using *in situ* minirhizotrons or root windows[35–56]. When corresponding root traits (for example, diameter or SRL) were not available, we used species-specific observations from our own dataset to match the lifespan data. In total, we obtained 70 species-specific observations and 13 community observations across 5 biomes.

Root nitrogen uptake rates. We measured per-biomass root nitrogen uptake rates in 34 plant species using 2 standard approaches: (i) by isolating an intact living root branch and exposing it to a hydroponic solution with isotopically labelled ammonium nitrate (intrusive approach, elevated nitrogen concentration; see ref. 57); and (ii) by applying nutrient solution to soil and allowing plant roots to take up nutrients *in situ* (non-intrusive, low nitrogen concentration; see ref. 58). The first approach enables an estimation of the maximum uptake rate of absorptive roots and the second approach more accurately reflects the uptake rate of roots in natural conditions; we analysed the resulting two datasets separately. We acquired previously published data for an additional 107 species[59–101]. The resulting dataset is summarized in Extended Data Fig. 2d.

Species and phylogeny. We conducted phylogenetic analyses of our species from 210 genera and 79 families, confirming species names using The Plant List (http://www.theplantlist.org). We followed the APG III phylogenetic system[102] in all analyses and used PHYLOCOM[103] to construct phylogenetic trees (Extended Data Fig. 7). Following a previous analysis[104], we defined the divergence time of a plant family using the earliest diverging genus within that family. We calculated Blomberg's K statistic[105] using the 'Picante' package in R and evaluated the strength of the phylogenetic signal for each trait; a large Blomberg's K value is thought to indicate phylogenetic conservatism. We performed phylogenetic independent contrasts analyses to correct for shared evolutionary histories among traits and to look for the effect of environmental influences (Extended Data Table 3).

Quantitative and statistical analyses. Shapiro–Wilk tests revealed that all of our traits were significantly non-normal ($P < 0.05$), which we corrected by $\log_{10}$-transforming our data. We derived the nonlinear relationship between SRL and root diameter based on inherent biophysical constraints, as discussed in Supplementary Information, note 1. We fit the equation using the average root tissue density across all species and evaluated the sensitivity to variation in root tissue density across a tenfold range.

All statistical analyses were performed using the R software (version 2.15.0.), using the 'Factor R' package for principal component analyses and the 'lme4' package for mixed linear effect models. The linear regression between root diameter and divergence time was weighted by the number of species within each family. We used linear regression to test the effect of root diameter and growth form (woody versus herbaceous) on root mycorrhizal colonization. Across biomes, we examined equality of variance in root diameter using Levene's test and differences in mean root diameter using a linear mixed effects model.

Code availability. The R scripts used in Figs 1 and 2 are available from the corresponding author upon reasonable request.

Data availability. The data that support the findings of this study are available from the corresponding authors upon reasonable request.

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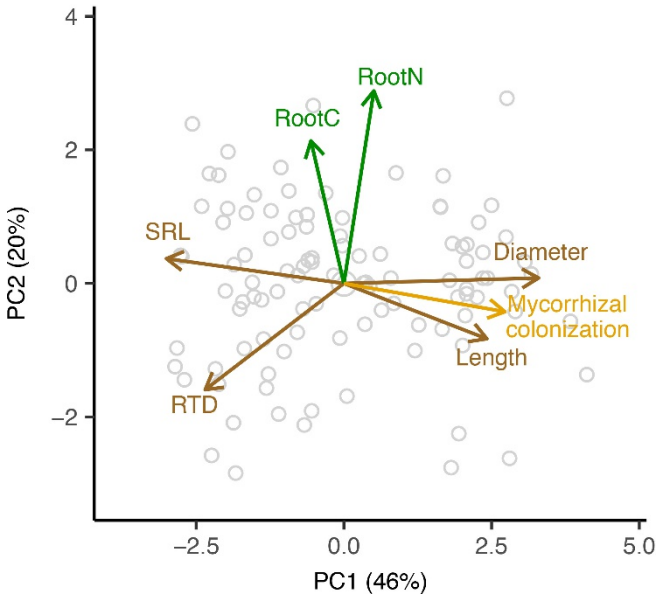
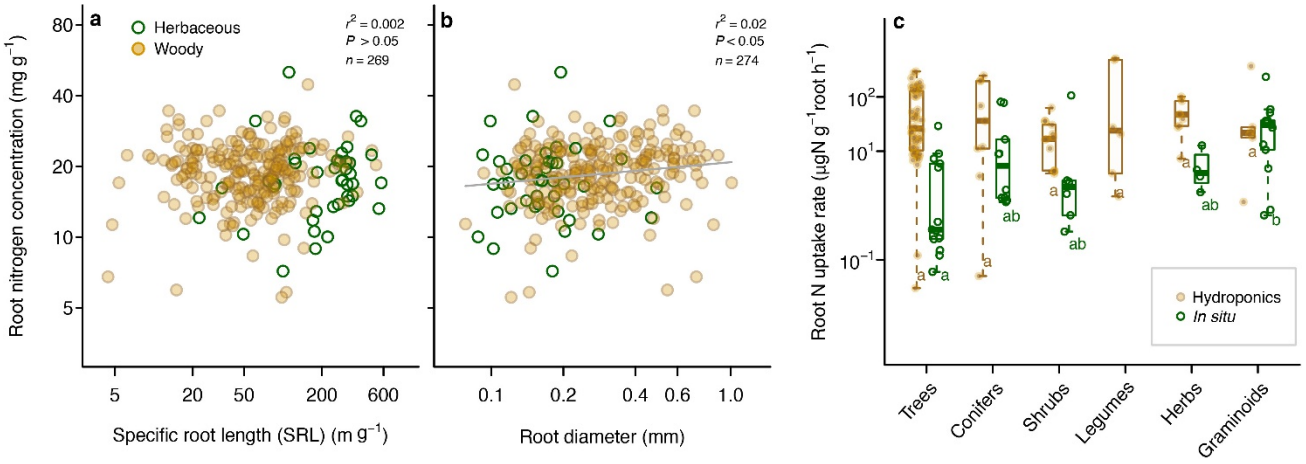


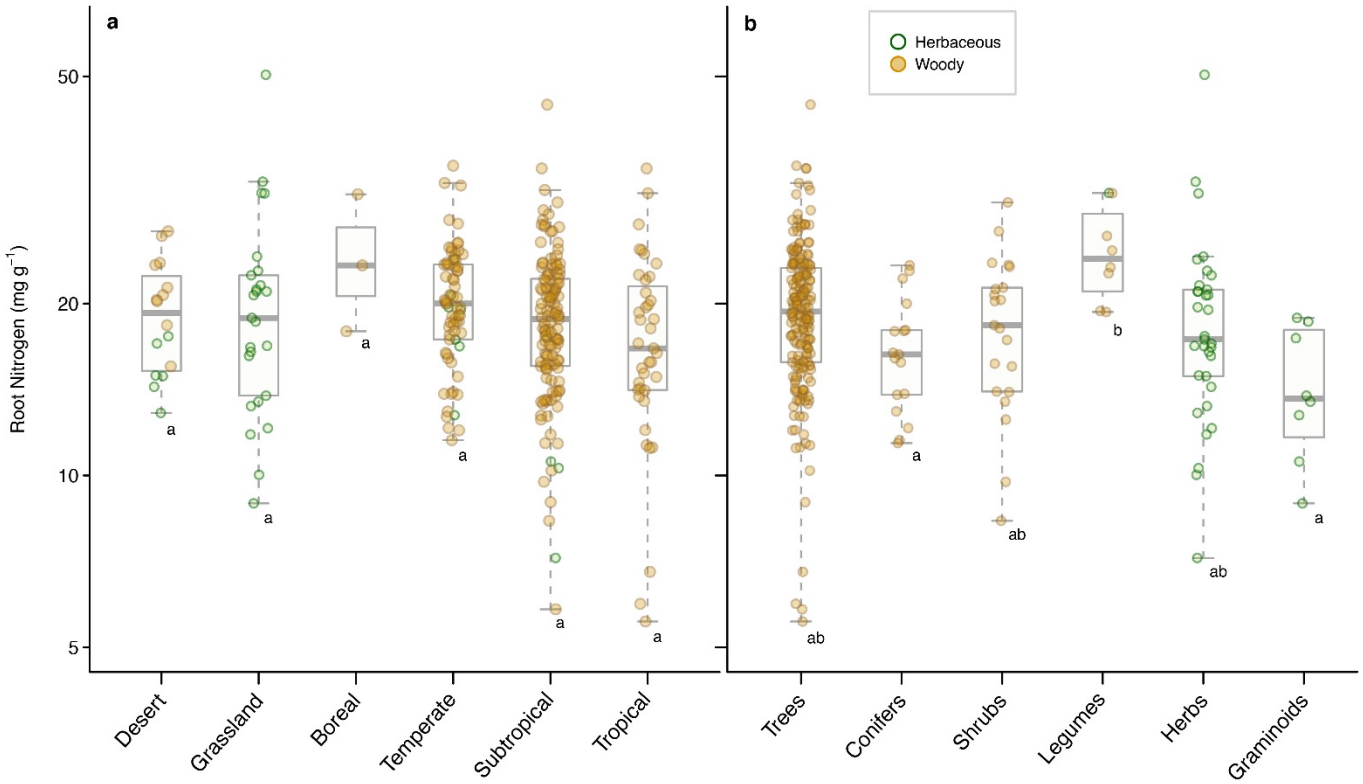
Extended Data Figure 1 | Principal component analysis of 7 root functional traits across 104 species. Trait loading on the plane defined by principal components 1 and 2 (PC1 and PC2). Brown arrows indicate four morphological traits; diameter, length, SRL and root tissue density (RTD). Green arrows indicate two physiological–chemical traits; root carbon (RootC) and root nitrogen (RootN). The yellow arrow shows mycorrhizal colonization. Three different analyses confirm the results shown here (detailed in Extended Data Table 2): (i) all data excluding the mycorrhizal colonization trait ($n = 217$ species); (ii) gaps in mycorrhizal colonization data interpolated using the regression from Fig. 1c (n = 217 species); and (iii) gaps in any trait value interpolated ($n = 369$) using the regressions in Fig. 1a, c or the multiple imputation method in the MICE R package).



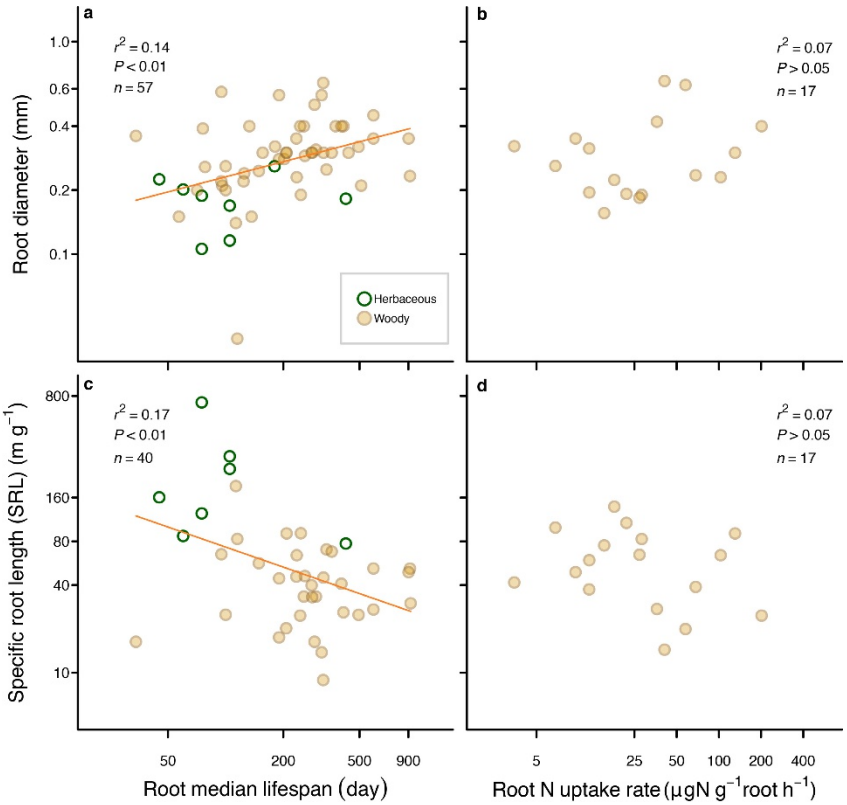
d

	Hydroponics* (μg N g^{-1} Root h^{-1})					*In situ*† (μg N g^{-1} Root h^{-1})				
Biome	*n*	Mean	SE	Minimum	Maximum	*n*	Mean	SE	Minimum	Maximum
Grassland	3	139.8	114.3	23.3	368.5	4	20.16	6.88	9.24	40.22
Boreal	5	199.24	42.57	74.44	336.67	17	24.72	11.30	0.33	164.08
Temperate	41	96.46	15.30	0.03	315.93	38	17.70	7.74	0.72	222.13
Subtropical	38	59.68	17.88	1.16	511.00	7	59.89	29.60	8.87	234.67
Tropical	24	29.47	8.03	5.61	193.85	9	1.64	1.39	0.06	12.73

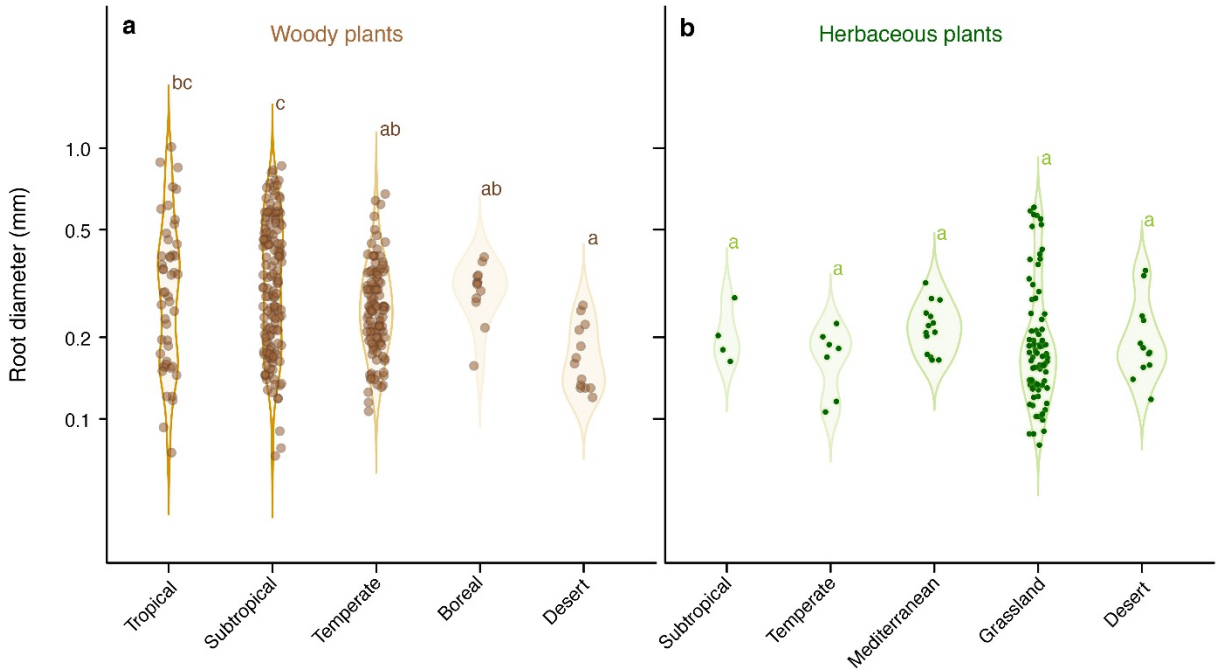
Extended Data Figure 2 | Root nitrogen concentration and root nitrogen uptake rate. a, There is no correlation between root nitrogen and SRL ($r^2 = 0.002$, $P = 0.81$, $n = 269$). **b**, There is no correlation between root nitrogen and diameter ($r^2 = 0.02$, $P = 0.01$, $n = 274$). Each point represents one species: brown, woody plants; green, herbaceous plants (**a**, **b**). **c**, Across plant growth forms, nitrogen uptake rates per root biomass did not vary significantly ($P > 0.05$) based on hydroponic measurements (brown). For *in situ* experiments (green) we observed a growth-form effect ($P < 0.01$), which was caused solely by higher root uptake in graminoid species compared to trees. All other growth forms were statistically indistinguishable. The letters 'a' and 'b' indicate significant difference based on an ANOVA across growth forms. **d**, Summary table of nitrogen uptake rates across different biomes by two approaches. This dataset included previously unpublished data from 22 species. A detailed description of these two approaches can be found in the Methods. Additional data were collected from refs 59–101.



Extended Data Figure 3 | First-order-root nitrogen concentration across biomes and plant functional groups. a, We did not detect a distinct pattern in first-order-root nitrogen concentration across biomes (**a**) (ANOVA; $P > 0.14$, $n = 284$ species). **b**, We detected a slight difference in first-order-root nitrogen concentration among plant functional groups (**b**) (ANOVA; $P < 0.01$, $n = 284$ species), which was mostly driven by the higher root nitrogen concentrations found in legumes. Each point represents one species; brown, woody plants; green, herbaceous plants. The letters 'a', 'b' and 'ab' indicate significant differences between categories.



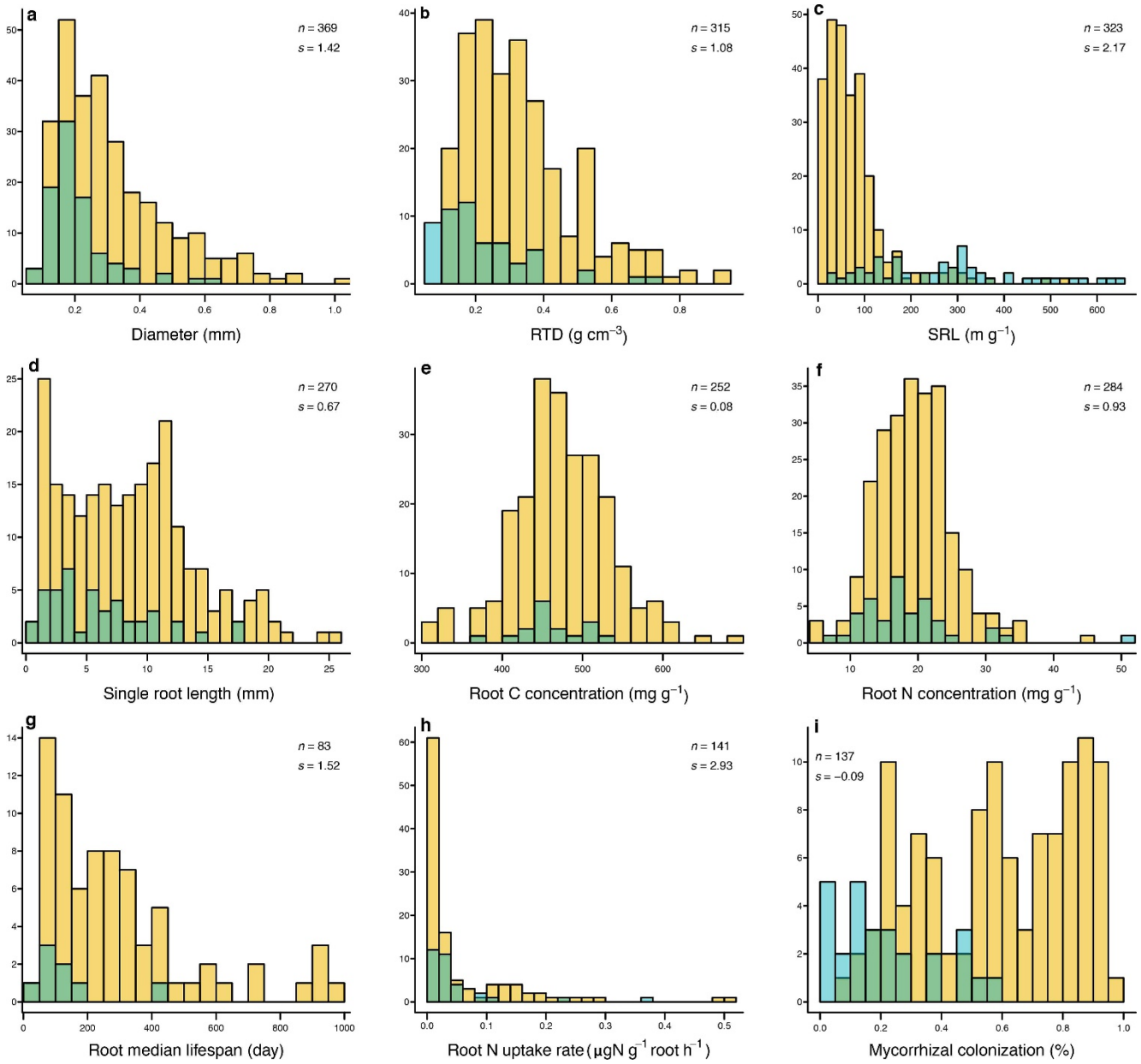
Extended Data Figure 4 | Relationship between root functional and morphological traits. a, **c**, Root median lifespan is significantly correlated with root diameter (**a**, $r^2 = 0.14$, $P < 0.01$, linear regression) and SRL (**c**, $r^2 = 0.17$, $P < 0.01$, linear regression). **b**, **d**, Root nitrogen uptake rate is not correlated with root diameter (**b**, $r^2 = 0.07$, $P > 0.05$, linear regression) or with SRL (**d**, $r^2 = 0.07$, $P = 0.29$, linear regression) in woody plants. Data are presented on a logarithmic scale ($\log_{10}$), with each point representing one species.



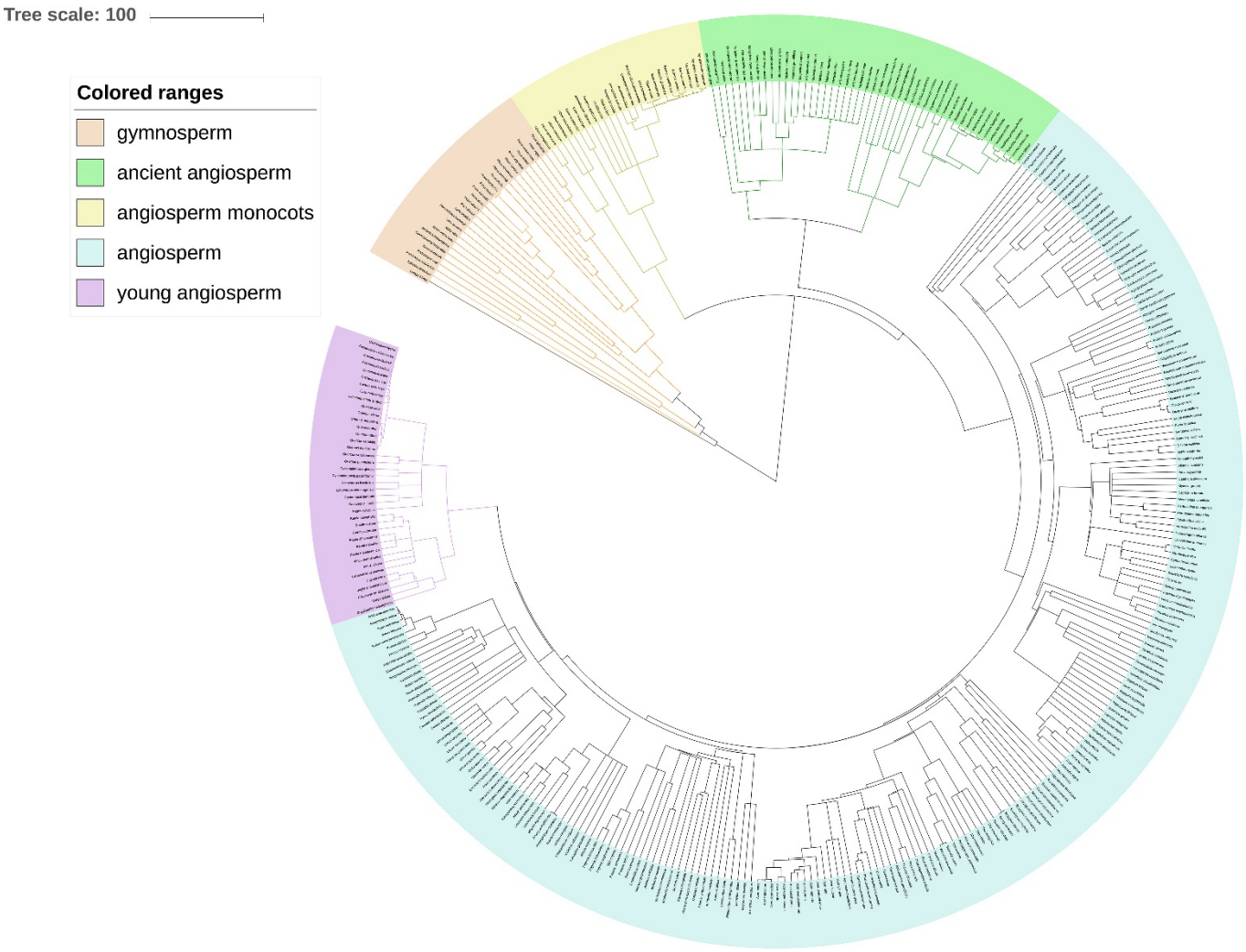
c

Desert	Desert	Grassland	Mediterranean	Boreal	Temperate	Subtropical
Grassland	0.07					
Mediterranean	0.16	<0.05*				
Boreal	0.25	<0.05*	1.00			
Temperate	0.20	0.10	<0.05*	<0.05*		
Subtropical	<0.001***	<0.05*	<0.001**	<0.001**	<0.001**	
Tropical	<0.001**	<0.05*	<0.001**	<0.01**	<0.001**	0.45

Extended Data Figure 5 | Distribution of first-order-root diameter for woody and herbaceous plants across biomes. a, Woody plant root diameter deceases from tropical to desert biomes, with the most frequent occurrence of coarse-root ancestral woody species in tropical and subtropical biomes. **b**, Herbaceous plant root diameters do not display a clear trend across biomes. In both panels, the letters 'a', 'b' and 'c' denote significant differences ($P < 0.05$) between biomes based on a linear mixed effects model (generated using the lmer function in R) with species included as a random effect. Diameter was first $\log_{10}$-transformed to correct for non-normality. Each point represents a species-specific observation at one site. The background violin plot characterizes the distribution of points in each biome. **c**, Pairwise comparisons for equal variance in first-order-root diameter using Levene's test. Levene's test is used for testing the homogeneity of variance, and is used here to explain biome differences in variance of root diameter.



Extended Data Figure 6 | Frequency distributions of nine root functional traits. a–c, Cyan bars identify the distribution of herbaceous plants, yellow bars identify woody plants, and green colour is where two distributions overlap. *n*, total number of species; *s*, skewness of all data.



Extended Data Figure 7 | Phylogenetic tree of 365 taxa in the study. The oldest taxonomic groups are highlighted in orange (gymnosperms), yellow (monocotyledons) and green (for example, Magnoliales, Lauraceae). The youngest taxonomic groups are highlighted in purple (for example, Betulaceae, Fagaceae).

Extended Data Table 1 | Summary of ten functional traits of first order roots

Functional traits	Abbreviation	*n*	Mean	SE	Median	Min	Max	CV%*	Blomberg's K†
Root diameter (mm)	Diam	369	0.29	0.01	0.24	0.08	1.01	57%	0.11***
Specific root length (m g^{-1})	SRL	323	110.9	6.6	72.2	4.4	657.1	107%	0.10***
Root length (mm)	Length	270	8.10	0.31	7.63	0.70	25.7	64%	0.08**
Root tissue density (g cm^{-3})	RTD	315	0.32	0.01	0.29	0.06	0.95	52%	0.03
Root N concentration (mg g^{-1})	RootN	284	19.3	0.3	19.0	5.6	50.3	30%	0.03
Root C concentration (mg g^{-1})	RootC	252	473.0	3.7	467.0	307.7	684.4	12%	0.01
Root C:N ratios	RootCN	272	25.0	0.7	23.7	2.1	77.8	48%	0.03
Mycorrhizal colonization (%)	MC	137	52	2	55	0	100	54%	0.32**
Root median lifespan (days)‡	RL	75	272	24	234	34	924	77%	0.04
Root N uptake rates (μg N g^{-1} Root h^{-1})§	RNU	141	52.5	7.3	18	0	511	164%	0.02

n, number of species analysed.
*CV%, the coefficient of variance.
†Blomberg's *K* value; the strength of phylogenetic signal with significance level (**$P < 0.01$; ***$P < 0.001$).
‡Root median lifespans were derived from direct field observations using minirhizotrons and root windows (see Methods).
§Root nitrogen uptake rates were compiled from 43 publications[59–101] and unpublished data.

Extended Data Table 2 | Principal component analyses of global root functional trait data

	Main analysis		Excl.MC		Gapped.MC.data		Gap-filled	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Eigenvalue	3.21	1.37	2.25	1.32	2.71	1.33	2.35	1.57
Proportion of Variance	46%	19%	38%	22%	39%	19%	34%	22%
Root diameter (Diam)	0.94	0.09	0.78	-0.48	0.84	-0.37	0.88	-0.25
Root length (Length)	0.71	-0.19	0.82	-0.12	0.72	-0.03	0.13	-0.24
Specific root length (SRL)	-0.87	0.05	-0.81	-0.09	-0.81	-0.21	-0.76	-0.29
Root tissue density (RTD)	-0.64	-0.5	-0.09	0.84	-0.15	0.85	-0.09	0.88
Root C concentration (RootC)	-0.2	0.60	0.39	0.12	0.07	0.01	0.07	0.07
Root N concentration (RootN)	0.09	0.83	-0.11	-0.72	-0.02	-0.71	-0.13	-0.65
Mycorrhizal colonization (MC)	0.79	-0.07			0.79	-0.14	0.87	0.06

Eigenvalues and loading scores of principal components 1 and 2 (PC1 and PC2) in four different principal component analyses. For all four analyses, the loading scores show that the PC1 axis is composed of root diameter, SRL and length, and the PC2 axis is mainly influenced by root nitrogen concentration. The 'main analysis' is reported in Extended Data Fig. 1, and was conducted on 104 species for which all 7 traits were available. The 'Excl.MC' analysis excluded mycorrhizal colonization, which enabled us to increase the number of species to 217. In the 'Gapped.MC.data' analysis, we filled gaps in the mycorrhizal colonization data based on the relationships in Fig. 1c, resulting in 217 species being analysed. Finally, in the 'Gap-filled' analysis, we filled all gaps in trait values based either on the relationships in Fig. 1a, c or on interpolations using the MICE multiple imputation method. The results of all four principal component analyses show the same overall result, which indicates that the pattern shown in Extended Data Fig. 1 is robust.

Extended Data Table 3 | Spearman's correlation coefficients and phylogenetically independent contrasts among eight root functional traits

	Diam	SRL	RTD	Length	RootN	RootC	RootCN	MC
Root diameter (Diam)		-0.87***	-0.26***	0.34***	0.21***	0.04	-0.05	0.67***
Specific root length (SRL)	-0.59***		-0.09	-0.25***	-0.22***	0.15**	-0.07	-0.69***
Root tissue density (RTD)	-0.27***	-0.15**		-0.33***	-0.05	-0.30***	0.13*	0.06
Root length (Length)	0.32***	-0.15**	-0.29***		0.37***	0.04	0.05	0.06
Root C concentration (RootC)	0.19***	-0.12*	-0.09	0.32***		0.14**	0.23***	0.14**
Root N concentration (RootN)	0.09	0.11*	-0.24***	0.03	0.21***		-0.65***	-0.08
Root C:N ratios (RootCN)	0.05	-0.08	0.05	0.08	0.16**	-0.51***		-0.02
Mycorrhizal colonization (MC)	0.32***	-0.25***	0.01	-0.03	-0.06	-0.18***	0.06	

Spearman's correlation coefficients (upper diagonal) and phylogenetically independent contrasts (lower diagonal) among eight root functional traits for 365 species. Significant correlations are indicated; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

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Experimental design

1. Sample size

   Describe how sample size was determined.

   We analyzed root functional traits across 369 species (210 genera, and 79 families). The dataset was based on the 480 species-specific observations, of which 187 are unpublished and 256 published by our groups. To enhance the coverage of certain biomes (e.g., boreal and Mediterranean), we added 37 observations from the literature into our dataset, taking care to only include studies of first-order roots and consistent methods.

2. Data exclusions

   Describe any data exclusions.

   Once we compiled the dataset according to our criteria, we did not deliberately delete any data.

3. Replication

   Describe the measures taken to verify the reproducibility of the experimental findings.

   We collected roots from natural plant communities across seven major biomes and three continents. At each sampling site, we selected common indigenous species that are representative of the local plant community. For each species, we sampled at least three individual plants to derive mean trait values for each species. All procedures are standard.

4. Randomization

   Describe how samples/organisms/participants were allocated into experimental groups.

   This research is based on observations, thus only involves random sampling, but did not involve random assignment (which applies only to controlled experiments). All sampling procedure is according to standard established approach.

5. Blinding

   Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

   N/A

Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐ A statement indicating how many times each experiment was replicated
☐	☒ The statistical test(s) used and whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒ Test values indicating whether an effect is present *Provide confidence intervals or give results of significance tests (e.g. P values) as exact values whenever appropriate and with effect sizes noted.*
☐	☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒ Clearly defined error bars in all relevant figure captions (with explicit mention of central tendency and variation)

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.

We constructed the plant phylogenetic relationship using PHYLOCOM 23 (http://phylodiversity.net/phylomatic).

All statistical analyses were performed using the R software, version 2.15.0.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party.

N/A

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

N/A

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

N/A

b. Describe the method of cell line authentication used.

N/A

c. Report whether the cell lines were tested for mycoplasma contamination.

N/A

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

N/A

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.

N/A

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	N/A

CORRECTIONS & AMENDMENTS

ERRATUM
doi:10.1038/nature26163

Erratum: Evolutionary history resolves global organization of root functional traits

Zeqing Ma, Dali Guo, Xingliang Xu, Mingzhen Lu, Richard D. Bardgett, David M. Eissenstat, M. Luke McCormack & Lars O. Hedin

Nature **555,** 94–97 (2018); doi:10.1038/nature25783

In this Letter, owing to an error during the production process, only author L.O.H. was listed as a corresponding author, instead of both D.G. (guodl@igsnrr.ac.cn) and L.O.H. (lhedin@princeton.edu). This has been corrected online.

CORRECTION

https://doi.org/10.1038/s41586-019-1214-3

Author Correction: Evolutionary history resolves global organization of root functional traits

Zeqing Ma, Dali Guo, Xingliang Xu, Mingzhen Lu, Richard D. Bardgett, David M. Eissenstat, M. Luke McCormack & Lars O. Hedin

Correction to: *Nature* https://doi.org/10.1038/nature25783, published online 21 February 2018.

We thank reader Joseph Craine for pointing out three inadvertent errors in this Letter. First, 4 of the 71 divergence dates extracted from ref. [1] of this Amendment and used in Fig. 1b of the original Letter were overestimated. The correct values are 45 million years ago (Ma) for Apocynaceae, 51 Ma for Anacardiaceae, 40 Ma for Primulaceae, and 53 Ma for Amaryllidaceae. These errors had little influence on the overall trend of Fig. 1b (r^2 is now 0.48 rather than 0.54, with no change to $P < 0.001$) and do not change our conclusion and inferences. Second, we neglected to note that since refs. [2] and [1] of this Amendment considered only angiosperms, our Fig. 1b necessarily did not include gymnosperm taxa. The in-text reference to Fig. 1b should therefore read "all major angiosperm plant families in our dataset" rather than "all major vascular plant families in our dataset". Third, in Fig. 1c the trait value of mycorrhizal colonization for *Machilus kwangtungensis* was erroneously given the value 0.25 instead of 1.0. This error had little influence on the overall Fig. 1c trend, reducing r^2 from 0.64 to 0.63 (with no change to $P < 0.001$).

In the Methods, we neglected to note that the divergence time for Magnoliaceae was taken from the recent analysis of ref. [2]. In addition, the Methods description should have noted that we excluded one specific root length (SRL) value (for *Vaccinium mandarinorum*) because its inferred tissue density (1.96 g cm^{-3}) implausibly exceeded a value that was twice as dense as water and close to the density of rock.

In addition, there were five typographical errors in the Extended Data display items. (1) In Extended Data Fig. 2c, a tick and its corresponding tick label (10^0) was missing from the *y* axis. (2) In Extended Data Fig. 4b, r^2 should be 0.06 instead of 0.07. (3) In Extended Data Fig. 5a, the letters indicating significance should be 'b' instead of 'ab' for the temperate biome, and 'abc' instead of 'ab' for the boreal biome. (4) In Extended Data Fig. 6h, the *x*-axis unit should be milligrams (mg) rather than micrograms (μg) of nitrogen per gram of root per hour (mg N g^{-1} root h^{-1}). (5) In Extended Data Table 3, the column variable names 'RootN' and 'RootC' should be swapped.

Although the principal component analysis was not central to our main findings, we also now provide the abundances of species of different growth forms (woody versus herbaceous) and species from different biomes in Extended Data Table 2. In 'Main analysis', there were 104 woody and 0 herbaceous species; and 31 Tropical, 64 Subtropical and 9 Temperate biome species. In 'Excl.MC', there were 201 woody and 16 herbaceous species; and 39 Tropical, 118 Subtropical, 44 Temperate, 15 Desert and 1 Boreal biome species. In 'Gapped.MC.data', there were 201 woody and 16 herbaceous species; and 39 Tropical, 118 Subtropical, 44 Temperate, 15 Desert and 1 Boreal biome species. In 'Gap-filled', there were 281 woody and 88 herbaceous species; and 46 Tropical, 137 Subtropical, 104 Temperate, 14 Mediterranean, 53 Grassland, 24 Desert and 3 Boreal biome species. In the 'Gap-filled' analysis, the biome species count ($n = 381$) exceeds the total species number ($n = 369$) because several species occurred in more than one biome. None of these errors has been corrected online.

Dali Guo is deceased.

1. Wikstrom, N., Savolainen, V. & Chase, M. W. Evolution of the angiosperms: calibrating the family tree. *Proc. R. Soc. Lond. B.* **268**, 2211–2220 (2001).
2. Massoni, J., Couvreur, T. L. & Sauquet, H. Five major shifts of diversification through the long evolutionary history of Magnoliidae (angiosperms). *BMC Evol. Biol.* **15**, 49 (2015).