FUNCTIONAL TRAITS ALONG A TRANSECT

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Different phylogenetic and environmental controls of first-order root morphological and nutrient traits: Evidence of multidimensional root traits

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Abstract

1. Although fine roots are essential for the water and nutrient uptake of plants, there is limited understanding of root trait variation and the underlying mechanism.

2. Here, six first-order root morphological and chemical traits were measured for 181 species from eight subtropical and boreal forests to test the hypothesis of different phylogenetic and environmental regulations of root morphological and nutrient traits result in the multidimensions of root traits.

3. Two independent root trait dimensions between root thickness and nutrient traits were detected at both species and community levels. At the species level, diameter-related traits were mainly restricted by phylogenetic structure and showed little plasticity to the changing environments, whereas the variation in woody root nutrient was influenced significantly by soil variables. For community-level traits, the diameter-related axis scores of principal component analysis were mainly driven by mean annual temperature through shifting species composition, whereas the root nutrient-related axis scores were strongly influenced by soil P availability.

4. From both species and community levels, our study confirms, that the root-thickness-related dimension and root nutrient dimension represent new support for the multidimensionality of root traits which are driven by different selection pressure. This study also underlines that the community-aggregated traits might serve as a promising avenue to improve our understanding of community assemblage processes, allowing us to predict changes of vegetation distributions in a changing climate.

KEYWORDS
community-level traits, environmental variables, first-order root, phylogeny, plant growth form, root nutrient, root thickness

1 | INTRODUCTION

Fine roots are the distal roots of plants, and are the primary below-ground organs in acquiring limiting nutrients and water from the soil (Bardgett, Mommer, & De Vries, 2014; McCormack et al., 2015). However, to date, knowledge of root system traits lags far behind the understanding of above-ground plant traits. In particular, there remains debate about whether fine root traits among the plant species vary along a single root economics spectrum (RES) axis, as observed in leaves (de la Riva et al., 2016; Kramer-Walter et al., 2016; Reich, 2014; Roumet et al., 2016). In contrast to RES, there is increasing evidence in support of the multidimensional functional strategies of roots (Kramer-Walter et al., 2016; Weemstra et al., 2016). For example, weak or non-significant correlations among root diameter (RD), specific root length (SRL) and root nitrogen concentration (RN) have been observed at the both species and community levels (Chen, Zeng, Eissenstat, & Guo, 2013; Kramer-Walter et al., 2016). However, an in-depth understanding of the fundamental constraints underlying these independences between root traits is lacking.

Climatic variables are often recognized as the important regulators that affect the growth of fine roots along large-scale geographical gradients (Chen et al., 2013; Freschet et al., 2017; Yuan & Chen, 2010), through directly affecting plant physiology concerned with carbon allocation among organs and indirectly via changing soil biogeographical processes and vegetation composition (Chapin, Matson, & Mooney, 2002; Yuan & Chen, 2010). Previous studies have demonstrated that tropical species generally produced thick roots with lower SRL than those from temperate and cold areas (Chen et al., 2013; Freschet et al., 2017). However, no clear difference in RN was detected between subtropical and temperate angiosperm species (Chen et al., 2013).

As the important underground organs, fine roots are exposed to complex soil habits, including variation in the availability of nutrient and water resources, as well as soil chemistry and structure. Soil nutrient supply is expected as a major determinant of nutrient concentrations in plants and thus the acquisition-conservation trade-off of roots (Bardgett et al., 2014; Eissenstat, Wells, Yanai, & Whitbeck, 2000; Hodge, 2004). Previous studies have reported a positive relationship between the quantity of root nutrients and soil nutrient availability (Holdaway, Richardson, Dickie, Peltzer, & Coomes, 2011; Kramer-Walter et al., 2016; Liu et al., 2015). For instance, declining soil fertility along a soil chronosequence favoured plant communities with low RN and high root tissue density (RTD) (Holdaway et al., 2011). Besides, some environmental variables, such as soil texture and chemistry, could present additional limits to root traits (Freschet et al., 2017; Laliberté, 2017; Weemstra et al., 2016).

In addition to heterogeneous environments, large variation in root traits among co-occurring species might be strongly controlled by the phylogenetic structure of plants (Kong et al., 2014; Valverde-Barrantes, Freschet, Roumet, & Blackwood, 2017; Valverde-Barrantes, Smemo, & Blackwood, 2015). High phylogenetic signals of root morphological traits have been detected in woody and herbaceous plant species (Kong et al., 2014; Valverde-Barrantes et al., 2017; Wang, Wang, Zhao, Yu, & He, 2017). These results indicate that variation in root traits, especially diameter-related traits, is not random, but is constrained by phylogenetic background (root trait phylogenetic conservatism hypothesis, Valverde-Barrantes et al., 2017). In addition, plant growth form and mycorrhizal type could summarize important differences in root traits (Freschet et al., 2017; Liu, He, Zeng, Lei, & Arndt, 2016; Valverde-Barrantes et al., 2017). For example, in contrast with woody species, herbaceous root systems are often characterised by faster return on investments and greater plasticity than woody species (Freschet et al., 2017; Liu et al., 2016; Valverde-Barrantes et al., 2017). Arbuscular species (AM) have been considered to bear thicker root with a large cortex in support of greater rates of fungal colonization than ectomycorrhizal (EM) plants (Comas, Callahan, & Midford, 2014; Laliberté, 2017).

Although considerable variation in root traits among and within species and their enormous plasticity in response to changing resource supply have been observed, our understanding of the mechanism underlying variation in fine root traits remains limited. One confusing issue is that the definition of fine root and the methodology used to analyse their traits differ across studies. Analyses have been based on root diameter, order or function, which might lead to a bias when delineating functional categories (Freschet et al., 2017; McCormack et al., 2015). Due to this limitation, it has not been possible to elucidate the degree to which root traits vary in relation to environmental conditions and phylogenetic information across a variety of species, genera and biomes. Furthermore, the distribution of functional trait values within and among communities can present a better prospect of understanding how global changes will affect community processes and ecosystem function (Cornwell & Ackerly, 2009; McGill, Enquist, Weiher, & Westoby, 2006). However, the little knowledge of community-level patterns of root traits limits our ability to predict how the vegetation distribution varies in a changing environment (Simpson, Richardson, & Laughlin, 2016). Third, given the great difference in root traits between woody and herbaceous species (Freschet et al., 2017; Liu et al., 2016; Valverde-Barrantes et al., 2017), it is important to explore the variation in root traits across these two growth forms and their respective responses to changes in environmental conditions. However, few studies exploring differences in root traits by considering two plant growth forms in parallel (but see Freschet et al., 2017; Valverde-Barrantes et al., 2017). Additionally, growth forms may affect the mycorrhizal status of plants. For instance, nearly all species colonized by EM fungi are trees, while most of herbaceous plants were colonized by AM or non-mycorrhizal fungi (NM) (Brundrett, 2009; Phillips, Brzostek, & Midgley, 2013). Thus, it is imperative to consider simultaneously growth form and mycorrhizal colonization when investigating the variation in root traits.

To overcome these knowledge gaps, we collected the first-order roots of 181 species along the 3700-km latitudinal transect of eastern China, using the same protocol. Six root traits related to the resource acquisition strategies of plants were measured, including morphological traits (RD, SRL and RTD) and chemical traits (root carbon concentration, RC, RN and the ratio of root carbon to nitrogen concentration, C:N). The goal of this study was to test the hypothesis that different drivers act on root morphological and nutrient traits at both species

and community levels, which leads to the existence of multidimensional root traits rather than a single RES. Specifically, we expected that, (1) independent root trait dimensions are observed between root morphological and nutrient traits; (2) variation in diameter-related root traits is mainly determined by phylogenetic differences among species; (3) climatic factors, especially temperature, primarily drive the variation in community-level morphological root traits, whereas root nutrient traits are closely related to soil nutrient availability and (4) the way root traits are adapted to changing environmental gradients differs between woody and non-woody plants, with non-woody species displaying more environmental plasticity and less phylogenetic conservativism than woody ones.

2 | MATERIALS AND METHODS

2.1 | Root sampling and measurement

During July and August 2013, we conducted field surveys from eight forest sites along the north–south transect of Eastern China (NSTEC), including Dinghu Mountain (DH), Jiulian Mountain (JL), Shennongjia (SN), Taiyue Mountain (TY), Dongling Mountain (DL), Changbai Mountain (CB), Liangshui (LS) and Huzhong (HZ) (Table S1, Figure S1). These sites span a huge geographical and environmental range from subtropical to boreal climate zones. At each site, three or four experimental plots (30 × 40 m) were set up and floristic and environmental surveys were performed. The number, plant height, diameter at breast height (DBH) of all trees with DBH ≥2 cm (basal stem diameter for shrubs), and aboveground live-biomass of all herbs were measured. The most frequent and dominant plant species in each plot, including woody and non-woody species, were selected as target species for root sampling. Root samples from each species were collected from at least four mature and healthy plant individuals. A total of 896 species-at-site observations were completed in 29 plots across eight forest sites, representing 181 plant species from 120 genera and 68 families. These species span a broad range of phylogenetic clades, including ferns, conifers and all clades of angiosperms (Table S2, Figures S2 and S3a). The species number sampled in each site is presented in Table S1.

Root sampling were performed according to the protocol described by Guo et al. (2008). In brief, for each woody plant, we first removed the surface soil near the plant basal stem, and then traced the intact root system to the lateral root clusters. For herbaceous plants, whole root systems were obtained, using a pick or shovel. Once collected, root samples were transported to the laboratory within a few hours and frozen for later processing.

Subsequently, root clusters with intact branch orders were separated into different branch orders by hand, according to Pregitzer et al. (2002). We focused on the first-order roots, since only the most distal first-order roots with the most rapid turnover and highest metabolic activity are functionally comparable to leaves as resource acquisition organs (Guo et al., 2008; Kong et al., 2014). We randomly selected the three root samples out of four individuals per species to conduct the further measurement. In total, 672 first-order root samples were

collected. These root samples were used to measure six traits commonly used to describe root systems: RD (mm), SRL (m/g), RTD (g/cm), RC (mg/g), RN (mg/g) and C:N ratio. The root diameter, length and volume data were obtained by analysing the scanned root samples with WinRHIZO 2009 (Regent Instruments, Quebec, Canada). RTD was calculated as root dry mass divided by root volume. RC and RN were determined, using an isotope ratio mass spectrometer (MAT253, Thermo Electron Corporation, Germany).

Given the strong influence of mycorrhizal colonization on root systems (Brundrett, 2009; Laliberté, 2017; Wang & Qiu, 2006), we determined the mycorrhizal association of each species and classified them into different mycorrhizal types (Figure S3b), including AM (67.4% of the species), EM (18.2%), species dually colonized by both AM and EM fungi (AM & EM, 2.8%), NM (2.2%), species dually colonized by both AM and NM fungi (AM & NM, 3.3%), ericoid mycorrhizas (ERM, 0.6%), species without clear mycorrhizal status (No info, 5.5%), according to previous reports (Brundrett, 2009; Chen et al., 2013; Hempel et al., 2013; Koele, Dickie, Oleksyn, Richardson, & Reich, 2012; Lin, McCormack, Ma, & Guo, 2017; Liu et al., 2015; Phillips et al., 2013; Wang & Qiu, 2006). In this study, species reported as NM, ERM and No info were assigned to the 'Other' group due to the limited data, and species reported as both AM and NM were assigned to the 'AM' group.

2.2 | Community-level root traits

To measure root traits at the community level, we calculated the community weighed means (CWM) of root traits as community-level integrative parameters (Garnier et al., 2004), as follows:

$$CWM = \sum P_i \times trait_i$$

where P_i is the relative dominance of species i within a community. Here, we used the aboveground biomass ratio as a surrogate for root biomass due to large uncertainty in estimating the root biomass for each species. Further, previous studies had showed that it was feasible to use the aboveground dominance in calculation community-aggregated root trait values (Holdaway et al., 2011; Kramer-Walter et al., 2016). Aboveground biomass for woody plants was calculated, using allometric regressions with DBH and height (detailed methods in Wang et al., 2015). The species on which traits were measured accounted for an average of 93% of the total aboveground biomass across all the plots.

2.3 | Climate and soil variables

The climatic variables, including mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm), were extracted from the meteorological database produced by the Chinese Ecosystem Research Network (http://cerndis1.cern.ac.cn/).

Soil samples (0–10 cm depth below the surface) were collected randomly from 30 to 50 points, using a 5-cm-diameter auger in each plot. In the laboratory, soil samples were air-dried and then sieved to remove roots and visible organic debris by hand. Soil pH was measured at a soil-to-water ratio of 1:5. Soil texture was determined by a particle

size analyser (Malvern Masterizer 2000, Malvern, Worcestershire, UK). The percentage of soil clay particle (<2 μm) was used to represent textural characteristics in the statistical analyses. Soil total C and N concentrations (mg/g) were determined from the dry combustion of the ground samples (100-mesh), using a C/N analyser (Elementar, Vario Max CN, Germany). Soil total P concentration (mg/kg) was measured by the ammonium molybdate method, using a continuous-flow analyser (AutoAnalyzer 3 Continuous-Flow Analyzer, Bran Luebbe, Germany) after H_2SO_4–H_2O_2-HF digestion. To avoid the issues of collinearity (Table S3), only MAT, soil P, pH and clay percentage were kept in subsequent analyses. These environmental variables were chosen because they are widely used to assess relationships among fine root traits and soil properties (Freschet et al., 2017; Holdaway et al., 2011; Kramer-Walter et al., 2016).

2.4 | Species phylogeny

Species names were checked and standardized according to The Plant List (http://www.theplantlist.org/). Angiosperm order and family assignments were based on the Angiosperm Phylogeny Group III classification. We constructed a phylogenetic tree, using the comprehensive angiosperm species-level phylogeny from Zanne et al. (2014), as updated by Qian and Jin (2016). We used the tool of S.PhyloMaker to generate a phylogeny containing all 181 species from this mega-phylogeny of plants (Figure S2).

2.5 | Data analysis

Root traits were analysed at two levels: the species level (data averaged within species, grouped into woody and non-woody species) and the community level (CWM values). Data were $\log_{10}$-transformed when it was necessary to obtain approximate normality and homogeneity of residuals.

To examine the root trait coordination, we conducted a principal component analysis (PCA) to investigate the extent of covariation between the six root traits at the species and community levels, respectively. Given the strong phylogenetic conversation in root trait (Kong et al., 2014; Valverde-Barrantes et al., 2017), we calculated phylogenetic signals in all traits by performing the Pagel's λ test in R software (Pagel, 1999). Also, species-level trait relationships were conducted, using phylogenetic PCA (pPCA) and phylogenetic-independent contrasts (PICs), to account for shared evolutionary histories among species.

To determine how phylogenetic and environmental parameters affected the root traits, a general linear models and phylogenetically nested ANOVA were first performed to partition the variation components for each trait. The variance component of the total variance for each trait was partitioned into phylogenetic (or taxonomic), environmental (site) and residual components,using residual maximum likelihood (REML) procedures. The phylogenetic effect was defined as a hierarchically nested structure '(clade/family/species)', which is described in detail by Watanabe et al. (2007) and Valverde-Barrantes et al. (2017). The overall random term within the variance components

model was (site + [clade/family/species]) and no fixed factors were defined. Thus, variation in root traits caused by environmental variables was assigned to the 'site' component of the model, while variation resulting from sampling error was assigned to the 'residual' term (Watanabe et al., 2007).

Then, we quantified each effect of four environmental variables (MAT, soil P, pH and soil clay) on root traits, using linear mixed-effect model with REML method in the R package 'lme4'. In these analyses, we treated site as a random effect and each environmental variable and their interactions as fixed effects. To avoid problems of collinearity among these variables, we calculated the variance inflation factors (VIFs) for each term in the model. Terms with VIF > 10 were excluded from the final models. The interactions among the four environmental variables were not presented in this study because of their high VIF values and insignificant effects on all six root traits. The environmental variables that had significant effects ($p < .05$) on root traits were included in the final model (Table S7). Due to the unbalanced data, we calculated the variance explained by the model, using type III sums of squares and conservatively partitioned it among fixed factors by calculating the variance explained by adding the focal factor after other factors had been included in the model. The sums of squares explained by random effect and its significance were estimated, using the 'r.squaredGLMM' function and 'exactRLRT' function in R software, respectively (Johnson, 2014).

Last, we extracted the first two community-level PCA axis scores (CWM_PC1 and CWM_PC2), as a measure of trait coordination, for each plant community and investigated the effect of environmental variables on community-level PCA axis scores.

All analyses were conducted with R 3.1.1 statistical platform (R Core Development Team, http://www.r-project.org/).

3 | RESULTS

3.1 | Trait variation

Six first-order root traits of the 181 plant species varied greatly across species, with the morphological traits showing overall more variation than chemical traits (Table 1). Specifically, there was approximately a 6-fold variation in RD across all species, ranging from a minimum of 0.12 mm in *Rubus rosifolius* to a maximum of 0.68 mm in *Machilus breviflora*. A similar range of variation was obtained for RTD, with 7-fold variation. SRL showed the greatest variation out of all observations (54-fold variation). However, three chemical traits only exhibited 2–5-fold across all species.

Remarkable trait variation also occurred among plant functional groups (Table 1, Figure 1 and Table S2). When compared with non-woody species, woody species had an average thicker root with lower SRL and higher RTD (all $p < .05$), but did not differ significantly in root chemical traits (all $p > .05$, Table 1). With regard to investigated phylogenetic clades (Figure 1, Table S2), conifers had on average thick roots with low SRL but high RTD, and their roots were usually colonized by EM fungi. Magnoliids tended to exhibit thick root with

TABLE 1 Summary statistics of first-order root traits for woody and non-woody species

	Woody species (*n* = 135)				Non-woody species (*n* = 46)				All (*n* = 181)	
	M	Min	Max	*SD*	*M*	Min	Max	*SD*	*M*	*SD*
RD	0.28a	0.12	0.68	0.12	0.25b	0.14	0.46	0.09	0.28	0.11
SRL	109.37a	10.73	580.27	77.53	178.36b	23.52	479.16	97.53	125.39	87.39
RTD	228.86a	62.50	455.00	70.674	167.28b	83.33	370.00	58.83	214.56	72.85
RC	518.89a	359.864	751.16	70.26	507.36a	413.23	730.88	80.74	516.22	72.80
RN	19.365a	10.03	39.93	5.55	18.73a	9.35	33.81	5.93	19.43	5.46
C:N	28.46a	13.38	60.33	8.45	29.25a	16.43	62.20	9.07	28.64	8.58

RD, root diameter; SLA, specific root length; RTD, root tissue density; RC, root carbon concentration; RN, root nitrogen concentration; C:N, ratio of root carbon to nitrogen concentration; *n*, species number; M, mean; Min, minimum; Max, maximum; *SD*, standard deviation. Statistical differences between woody and non-woody species are denoted by different letters (*p* < .05).

low SRL and RTD, in favour of providing the enough volume for AM fungi colonization. Most of monocots were non-woody plants with the characteristic of high SRL (thin roots) and association with AM fungi. Eudicots (including rosids, asterids and unranked eudicots) accounted for the largest number of species sampled here (134 species, 74% of this dataset, Figure S3), and generally produced thin roots with relatively high SRL.

3.2 | Root trait covariation

Based on the results of PCA analysis, the six root trait measured at the species level could be summarized by two principal components, which together accounted for 84.9%–87.5% of the total variance (Figure 1, Table 2). The first PCA axis explained approximately 67% of the variance and was heavily loaded on SRL and RD, representing variation along the root thickness. The second PCA axis described an additional 17.4%–19.9% of the variance and was heavily loaded on root nutrient traits (i.e. RN and C:N) and RTD. These three traits were weakly correlated with all traits that were loaded on the first principal component (Table S4). Similar result was observed for woody and non-woody species (Figure 1, Table 2).

Given that most of traits exhibited a significantly phylogenetic signal (Table 2), we conducted a pPCA analysis on species-level traits. After controlling for phylogenetic relatedness among species, two main axes of trait variation (root thickness vs. nutrient traits and RTD) remained strong (Table 2). But the loadings of two main components differed between growth forms. In the case of non-woody species, consistent result was observed between ordinary and phylogenetic PCA. However, for woody species, the first pPCA axis was mainly related with RTD and root nutrient traits, the second pPCA axis loaded most heavily on root diameter-related traits, which was contrary with the result of ordinary PCA (Table 2). This discrepancy may result from the reduced interspecies variation in woody root morphology after phylogenetic correction.

When PCA were conducted at the community level, we found that, similar to the species-level result, the first PCA axis could account for 72.8% of the variance and was defined by both CWM_SRL and CWM_RD; the second PCA axis was mainly driven by root nutrient traits (i.e. CWM_RN and CWM_C:N) (Figure 2, Table S5). Moreover, community-level root traits differed among climatic areas. Generally, subtropical forests tended to produce relatively thin and long roots, whereas species from boreal forest had the opposite characters (Figure 2). Some temperate forests (e.g. CB) had species with high CWM_RN and low CWM_C:N (Figure 2).

3.3 | Factors influencing variation in species-level root traits

Using phylogenetically nested random model, we found that phylogenetic (or taxonomic) effect was a considerable source of variation in root traits for both woody and non-woody species. The variation explained by taxonomy (incorporating effects of clade, family and species) accounted for an average of 51.4% and 49.4% of the total variation of root traits for woody and non-woody specie, respectively (Figure 3, Table S6). Moreover, the phylogenetic influence on most root traits was mainly observed at the clade level (Table S6), reflecting that substantial divergence between basal phylogenetic clades (i.e. gymnosperms, basal angiosperms and magnoliids) and the recently diverged clades. Different form root morphological and nutrient traits, variation in RC was little influenced by the phylogenetic structure (0%–9.8%, Table S6), possibly due to the large RC variation caused by environmental factors ('site' effect, 13.6%–20.3%) and microhabitat or sampling error ('residual' effect, 69.9%–86.4%). In addition, the influences of environmental variables differed among root traits, with more 'site' effect detected in root chemistry than morphology (7.4%–32.3% vs. 0%–11.9%), especially for woody species (Table S6).

To quantify the effects of climate and soil factors on root trait variation, we further performed the linear (nested) model and ANOVA analysis. Results showed that the chemical traits of woody species were mainly influenced by environmental differences among site, whereas no significant environmental effects were found in their morphological traits and non-woody root traits (Table S7). Specifically, RC was significantly associated with changes in the soil clay, but with a weak variance explained (0.1%, Table 3). Both RN and C:N were influenced by soil P, pH and soil clay, with 12.5%–23.1% of variance being explained. First-order roots with high nutrient were found under the soil conditions of higher soil P, low pH and soil clay content (Table 3).
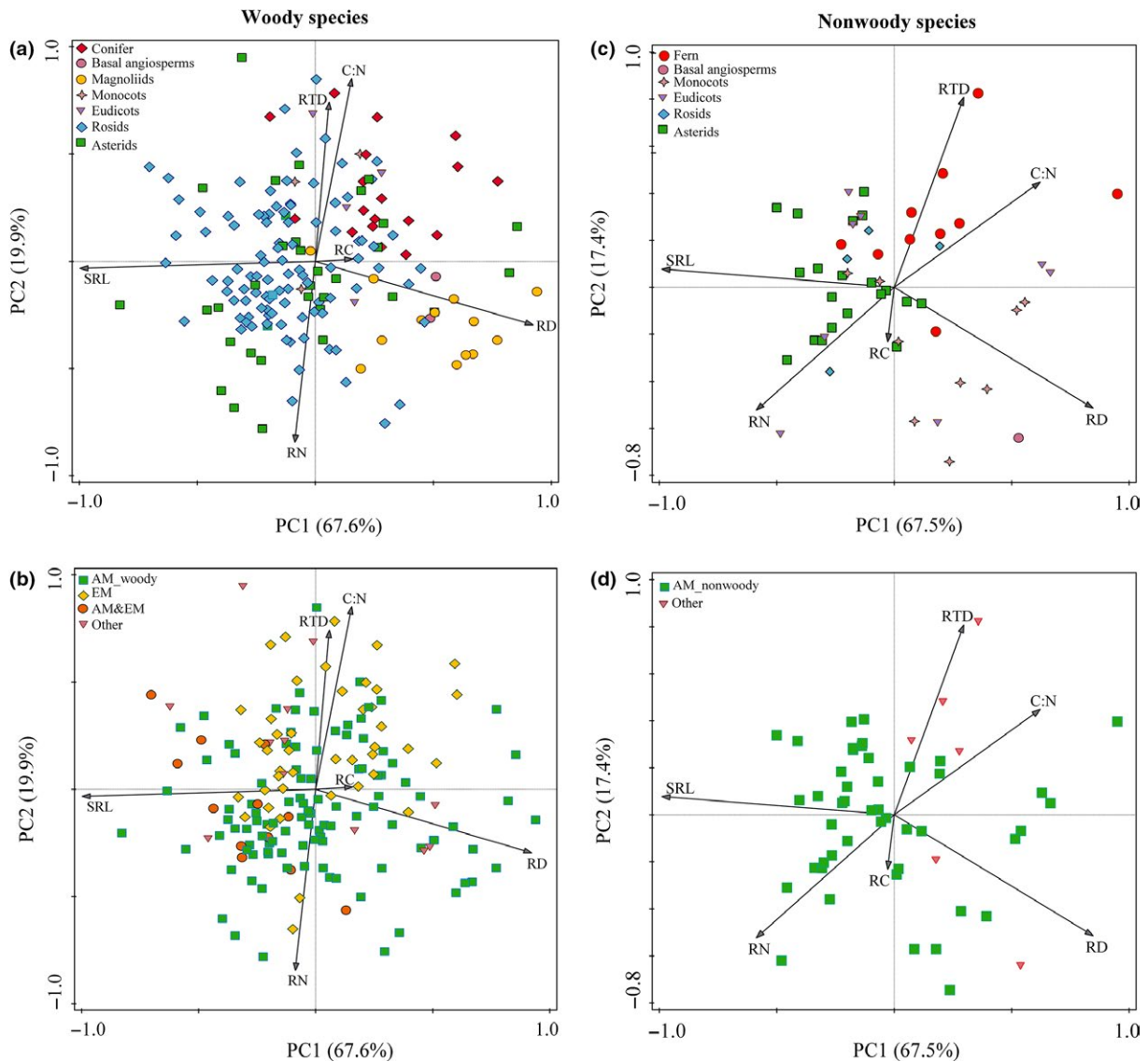
FIGURE 1 Results of principal components analysis (PCA) coded by phylogenetic group and mycorrhizal type for woody (a–b) and non-woody (c–d) root traits, respectively. Loading scores of root traits on each component of PCAs are given in Table 2. In phylogenetic group, eudicots only included those unranked eudicots species, i.e. species which are not included in the clades of rosids and asterids. Mycorrhizal type: EM, ectomycorrhizas (EM), woody and non-woody species with arbuscular mycorrhizas (AM_woody and AM_non-woody), species dually colonized by both AM and EM fungi (AM & EM) and other types (Other). All of root traits are $\log_{10}$-transformed and their abbreviations are provided in Table 1

3.4 | Factors influencing variation in community-level trait coordination

CWM_PC1 and CWM_PC2 were significantly influenced by environmental variables, especially MAT and soil P (Figure 4, Table S8). As MAT increased, CWM_PC1 first decreased and then slightly increased (Figure 4a, $R^2 = 0.61$, $p < .001$), while the inverse relationship was observed between CWM_PC2 and soil P (Figure 4b, $R^2 = 0.28$, $p = .013$).

4 | DISCUSSION

Base on a large dataset, three key findings were obtained here. First, we identified two independent root trait dimensions that were represented by diameter-related traits (i.e. RD and SRL) and root nutrient (including RN and C:N) at both species and community levels. Second, phylogenetic and environmental regulations differed among root traits and growth forms. Compared with root chemistry, root morphology exhibited stronger taxonomic conservatism and less environmental control, especially in woody species. Third, for community-level trait coordination, MAT was the main environmental variable influencing the first PCA axis scores associated with root thickness. In comparison, soil P availability strongly affected the second PCA axis scores represented by root nutrient. Overall, our results confirm that, from both species and community levels, the independence between root thickness and nutrient traits are caused by different selective pressures, providing new support for the multidimensions of root traits (Laughlin, 2014; Weemstra et al., 2016).

TABLE 2 Results of the ordinary and phylogenetic principal components analysis (PCA and pPCA) and Pagel's λ test for phylogenetic signal in each trait

		PCA		pPCA		
		PC1	PC2	pPC1	pPC2	λ
Woody	Eigenvalues	0.34	0.19	0.13	0.07	
	Variation explained (%)	67.6	19.9	73.6	19.1	0.81**
	RD	0.43	0.26	0.24	0.85	0.69**
	SRL	−0.90		0.35	−0.93	0.41**
	RTD		−0.56	−0.82	−0.04	<0.01
	RC			−0.14	0.60	0.45**
	RN		0.55	0.97	0.16	0.39**
	C:N		−0.56	−0.99	0.02	0.81
Non-woody	Eigenvalues	0.33	0.17	0.08	0.04	
	Variation explained (%)	67.5	17.4	70.6	13.6	
	RD	0.36	0.43	0.95	−0.03	0.83**
	SRL	−8.61	−0.13	−0.99	0.08	0.35*
	RTD	0.13	−0.71	−0.08	−0.09	0.73**
	RC			−0.11	−0.95	<0.01
	RN	−0.24	0.42	−0.47	−0.83	0.41*
	C:N	0.23	−0.33	0.55	−0.01	0.82**

All the trait data are $\log_{10}$-transformed prior to analysis. The abbreviations for root traits are in Table 1. *$p < .05$; **$p < .01$.
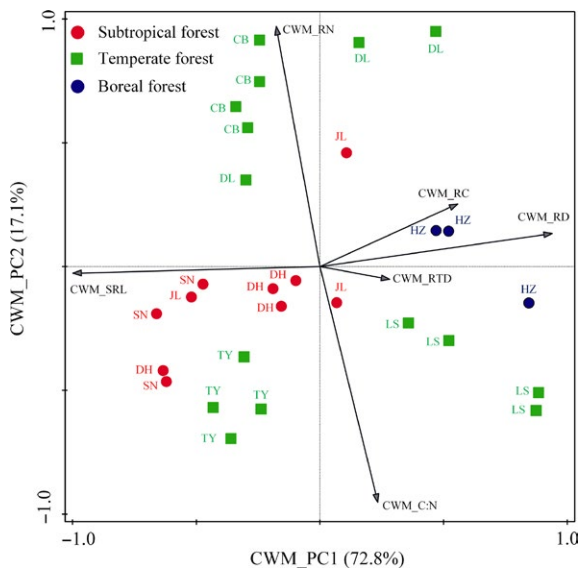
FIGURE 2 Results of principal components analysis (PCA) coded by different forest sites for community-level traits. Loading scores of root traits on each component of PCAs are given in Table S5. All the original data were $\log_{10}$-transformed prior to analysis. CWM, community-weighted mean. The abbreviations for root traits are in Table 1. DH, Dinghu Mountain; JL, Jiulian Mountain; SN, Shennongjia; TY, Taiyue Mountain; DL, Dongling Mountain; CB, Changbai Mountain; LS, Liangshui; HZ, Huzhong

4.1 | Independence between root thickness and nutrient

In support of the first hypothesis, we identified two independent dimensions of root trait variation: one dimension was related to root thickness, while the second orthogonal dimension was associated with root nutrients. More importantly, these trait dimensions were observed both for different growth forms and at the community level (Figures 1 and 2).

The first dimension describes the coordinated variation between RD and SRL. Similarly, both of Kong et al. (2014) and Liese, Alings, and Meier (2017) identified the diameter-related root dimension in tree species, and proposed that it was strong phylogenetic conservation that made diameter-related traits independent form the other trait dimension. Our study supports this idea, based on the high phylogenetic signal of root thickness and the majority of variation caused by phylogenetic structures (Table 2, Figure 3).

The second dimension, represented by RN and C:N, might be important for the constructive strategy and nutrient uptake of roots from the soil. Our study showed that root nutrient traits exhibited lower phylogenetic conservation and more plastic to soil variables when compared with root morphology (Figure 3, Tables S6 and S7). Similar result can be found in a recent study which reported that root morphological traits were of the least plastic to changes in soil nutrient availability, whereas root nitrogen and phosphorus concentrations showed the largest plasticity (Kramer-Walter & Laughlin, 2017). Thus, environment and ecological filtering appear to have a strong regulation on the root nutrient concentrations. Indeed, previous studies have demonstrated that a significant relationship between RN and soil fertility occurred at both the species and community levels (Holdaway et al., 2011; Kramer-Walter et al., 2016). In our previous study, N concentrations of leaves and first-order roots were positively correlated independent of phylogeny and plant growth forms, whereas morphological traits of above- and below-ground organs varied independently (Wang, Wang, Zhao, Yu et al., 2017). Taken together, root nutrient
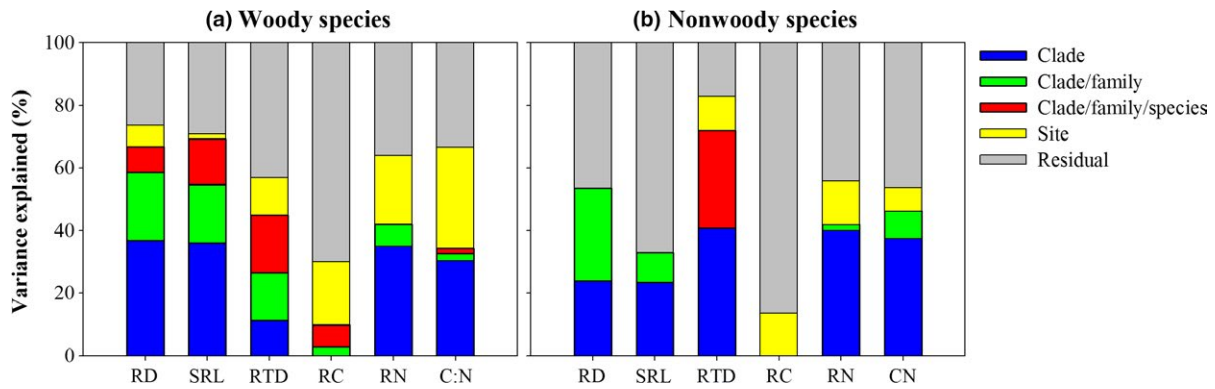
FIGURE 3 Variance component analysis of woody (a) and non-woody (b) root traits, using phylogenetic nested ANOVA. All root traits are $\log_{10}$-transformed before analysis and their abbreviations are provided in Table 1

TABLE 3 Results of linear mixed-effects models for woody root traits

		RC			RN				C:N			
		n	R^2	p		n	R^2	p		n	R^2	p
Full Model		167	0.23	<.001		167	0.20	<.001		167	0.35	<.001
Model variables	df	Estimate	SS%	p	df	Estimate	SS%	p	df	Estimate	SS%	p
Fixed factor												
Intercept		2.60		<.001		2.37		<.001		<0.001		.999
Soil P					1	0.26	3.1	<.001		−0.24	1.3	.014
pH					1	−1.90	3.2	<.001		0.21	5.9	.008
Clay	1	0.13	0.1	.09	1	−0.30	6.2	.008		−0.44	15.9	.013
Random factor												
Site	7		12.9	<.001	7		0.2	.37			6.4	.016

Soil P, soil phosphorus concentration; Clay, soil clay percentage; n, number of species-by-site observations; R^2, variance explained of full model; df, degrees of freedom; SS%, percentage of sum of squares explained. All the trait data and soil P are $\log_{10}$-transformed prior to analysis. The abbreviations for root traits are in Table 1.
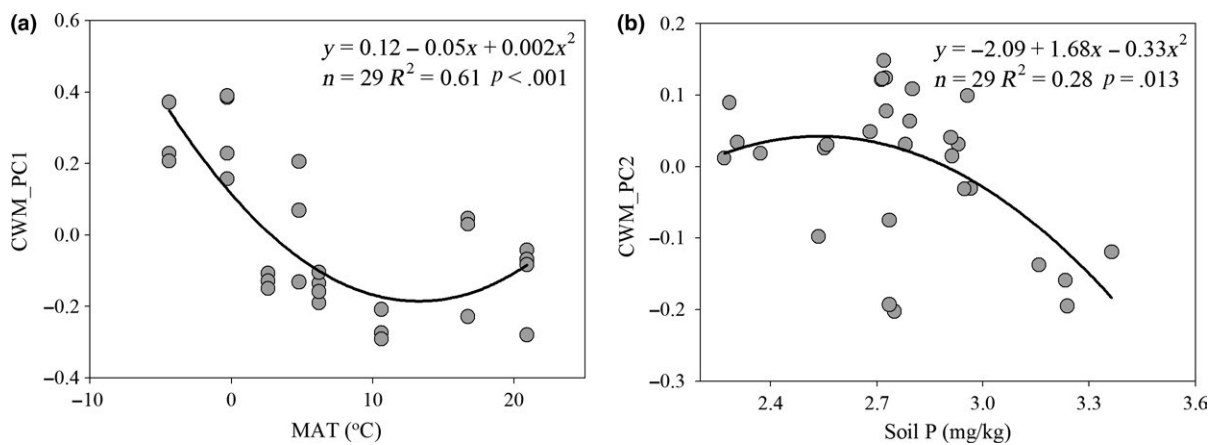
FIGURE 4 Relationships between two main community-level PCA axes (CWM_PC1 and CWM_PC2) and environmental variables. CWM_PC1 was defined by CWM_SRL and CWM_RD, CWM_PC2 was mainly associated with CWM_RN and CWM_C:N (see details in Figure 2 and Table S5). CWM: community-weighted mean; MAT, mean annual temperate; Soil P, soil phosphorus concentration. The abbreviations for root traits are in Table 1. All the trait data and soil P are $\log_{10}$-transformed prior to analysis

might reflect inherent physiological and life-history trade-offs across the entire plant. Such information could provide a valuable avenue to link different plant organs and their environments from the ecological to biogeographic scales.

The independence between root thickness and nutrients observed in our study is in line with some previous studies which focus on separately woody or herbaceous plant species (Chen et al., 2013; Tjoelker, Craine, Wedin, Reich, & Tilman, 2005; Valverde-Barrantes et al., 2015). However, this result also challenges the classic view that 'fast'-rooted species should produce thin, short-lived fine roots with high SRL and RN, while 'slow' species possess the opposite set of traits (Reich, 2014). The decoupling pattern in root traits allows for a variety of ecological strategies through adjusting independently root morphology and nutrient to adapt to multiple environmental filters (Laughlin, 2014). More combinations of trait dimensions may enable species to better adapt to multifarious niche dimensions, thus enhancing species coexistence and ecosystem stability (Laughlin, 2014; Weemstra et al., 2016).

4.2 | Phylogenetic effect on species-level root traits

As expected, diameter-related root traits, such as RD and SRL, displaying higher phylogenetic conservatism and less environmental regulation than other traits. This result provides support for the root trait phylogenetic hypothesis (Valverde-Barrantes et al., 2017), which proposes that differences in root morphology are attributed to intrinsic evolutionary adaptations among major phylogenetic clades, with plants evolving thinner and longer roots as an adaptation to decline in atmospheric CO_2 concentrations during the Cretaceous, or due to the decreased soil nutrient availability and a cooling climate (Ehleringer, Cerling, & Dearing, 2005; Zanne et al., 2014).

In addition, the influences of phylogenetic structures on root traits also differed between woody and non-woody species. Previous studies showed that herbaceous species were characterised by faster return on investments, greater plasticity and lower phylogenetic structuring than woody species (Freschet et al., 2017; Roumet et al., 2016; Valverde-Barrantes et al., 2017). In contrast with existing assumptions, our study found that overall phylogenetic structure at the clade level explained more variation in herbaceous root traits, whereas soil variables only significantly influenced woody root chemistry (Figure 3, Tables S6 and S7). The high phylogenetic conservation in non-woody root traits might be related to the sampled species. In our study, asterids account for the largest species number of non-woody plants (41.3% of the non-woody dataset, Figure S3a), followed by fern (20.0%) and monocots (17.4%). Differences among these phylogenetic groups accounted for the majority of variation in non-woody root traits. For example, ferns were characterized by high RTD and C:N, whereas monocots tended to produce thick root with low RTD. For non-woody asterids, their root generally had low RD and high SRL (Figure 1). Moreover, neither N-fixing plants, such as Fabaceae, Betulaceae and Rhamnaceae, nor graminoids were included in our non-woody dataset. Additionally, non-woody species were sampled form only six forest sites with the smaller range of variation in soil fertility when compared with the distribution of woody species (soil P range: 203.68 to 832.50 mg/kg vs. 203.68 to

1797.88 mg/kg, Table S1). Taken together, these limited data possibly resulted in the weak relationships between root traits of non-woody species and soil fertility.

4.3 | Environmental control of community-level root traits

In our study, MAT was the main driver of community-level variation in root thickness, while soil P strongly influenced root nutrient traits. As MAT increased, the first principal component, which was positively associated CWM_RD and negatively with CWM_SRL, initially decreased and then slightly increased (Figure 4). This result contrasts with the traditional concept that warm sites have thick rooted plants (Chen et al., 2013; Freschet et al., 2017). Through investigating the biogeographic patterns of species-level root traits, we found that woody species from low latitude (warm habitat) generally owned the thicker root with lower SRL than those from high latitude (Figure S4), in line with classic view. However, it should be stressed that, in contrast to interspecific variation, trait composition at the community level results from both a hierarchy of abiotic (climate, resource availability and disturbances) and biotic filters (competition and predation) that constrain which species and traits are dominant in a given habitat (Cornwell & Ackerly, 2009). Therefore, we propose that a potential explanation for the observed changes in community-aggregated values is an indirect effect of changes in species composition.

First of all, woody angiosperms colonized by EM or AM fungi (e.g. Fagaceae and Theaceae) dominated in subtropical and temperate forests, while conifers with EM fungi (e.g. *Larix* and *Pinus*) dominated in boreal forest where had lower temperatures and slower metabolic processes (Chapin et al., 2002; Zadworny et al., 2016b). In comparison with woody angiosperms, coniferous species from boreal forest had relatively higher RD and lower SRL (Figure S5). Thick roots allow conifers to enhance root elongation performance and root protection from environmental stresses (resource-conservation strategy) (Yuan & Chen, 2010; Zadworny et al., 2016b), which thus resulted in high CWM_RD and low CWM_SRL in boreal forest. Furthermore, the observed increases in coniferous root diameter may be due to the increased percentage of mycorrhizal mantle area on the surface and epidermal cell enlargement in the Hartig net (Brundrett, 2009; Zadworny, McCormack, Mucha, Reich, & Oleksyn, 2016a), which can be associated with enhanced root absorptive capacity. Last, the incomplete decomposition of recalcitrant coniferous leaf litter at higher latitudes leads to an increase of Al^{3+} availability and soil acidification, which can impede meristem differentiation and reduce or stunt root growth (Hirano & Hijii, 1998; Zadworny et al., 2016b). Additionally, Al^{3+} accumulation and low soil pH are also common in the subtropical area due to strong leaching, which may partly lead to the high species-level average trait values (Figure S4a) and the slight increase in commnuty-level root thickness in warm sites (Figure 4a).

Soil fertility has been widely documented to cause shifts in the community-level distribution of below-ground morphological, chemical and architectural traits of roots (Holdaway et al., 2011; Kramer-Walter et al., 2016; Liu et al., 2015). In our study, soil P had

a significant influence on PCA axis associated with CWM_RN and CWM_C:N (Figure 4b, Table S8). The positive relationship between community-level root nutrient and soil fertility is consistent with the published literatures which report the acquisition strategy of root mineral nutrients in fertile sites and the inverse strategy in less fertile soils (Eissenstat & Yanai, 1997; Eissenstat et al., 2000; Holdaway et al., 2011). From a cost-benefit perspective, optimal root deployment should maximise the efficiency of nutrient uptake per unit C expended (Eissenstat & Yanai, 1997). First-order roots with high N were reported in some studies to have higher metabolic activity and respiration rates (Liu et al., 2016; Roumet et al., 2016), but lower longevity (Liu et al., 2016; McCormack, Adams, Smithwick, & Eissenstat, 2012; Tjoelker et al., 2005). These traits are competitive for plants grown in fertile sites as the higher resource availability offsets the expense of root maintenance (Eissenstat et al., 2000; Hodge, 2004). In contrast, under nutrient-limited conditions, root foraging strategies should avoid unnecessary nutrient loss. Thus, the lower cost of maintaining existing roots (related to lower RN) and long tissue lifespan facilitate the nutrient conservation in infertile environments (Eissenstat & Yanai, 1997; Eissenstat et al., 2000; Hodge, 2004).

Previous studies identified RTD as a key trait of the RES, because of its close association with the acquisition-conservation tradeoff (Kramer-Walter et al., 2016; Roumet et al., 2016). However, this interpretation is not supported by our study. We failed to detect any significant effect of climate or soil parameters on variation in species-level RTD and CWM_RTD along the forest transect in China. These inconsistent results suggest that the resource-conservation strategy with high RTD in infertile soil is not universal, with large differences depending on the specific constraints of each ecosystem.

ACKNOWLEDGEMENTS

AUTHORS' CONTRIBUTIONS

G.Y., N.H. and Q.W. conceived the ideas and designed the methodology; R.W., N.Z., Z.X., X.Z. and C.J. collected the data; R.W. analysed the data; R.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data associated with this article can be found in the Dryad Digital Repository https://doi.org/10.5061/dryad.3rj81 (Wang, Wang, Zhao, Xu et al., 2017).

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