RESEARCH ARTICLE

Lianas have a faster resource acquisition strategy than trees: Below-ground evidence from root traits, phylogeny and the root economics space

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Abstract

1. The competitive advantage of lianas over trees has been widely documented in studies of their leaf functional traits across diverse habitats; however, the relative contribution of root functional traits to the competitive superiority of lianas over trees has not yet been evaluated. The aim of this study was to explore the root functional traits, phylogenetic structure of these traits and root trait dimensions of lianas to clarify why lianas can outperform trees.

2. We sampled 69 liana species from tropical and temperate forests in China and measured nine key functional traits of first-order roots of each species, including morphological, architectural, anatomical and chemical traits, as well as the percentage of mycorrhizal colonization. Data on these traits were then compared with similar data of 127 tree species from the same biome obtained from the Global Root Traits (GRooT) database and our previous studies.

3. Liana roots had lower construction costs and could acquire resources more rapidly compared with tree roots. Significant differences were observed in most tree root traits between tropical and temperate sites. However, no significant differences were observed in any of the liana root traits between tropical and temperate sites, apart from the root branching ratio.

4. Lianas showed much weaker phylogenetic conservatism in their root traits than trees when species were pooled across sites. Phylogenetic constraint was lower for nearly all root traits of both temperate lianas and trees compared with those of tropical lianas and trees.

5. The root economics space of lianas and trees had two orthogonal dimensions with 'conservation' and 'collaboration' axes. However, lianas occupied the trait space with higher root nitrogen concentration and greater specific root length, showing 'fast' resource acquisition strategy, while trees placed opposite space and exhibited relatively 'slow' strategy.

6. *Synthesis.* The ability of lianas to outcompete trees in harsh environments might be explained by their faster resource acquisition strategy and the lower phylogenetic constraint in root traits. Generally, lianas might play an increasingly

important role in the structure and function of forest ecosystems in the future with ongoing habitat fragmentation and climate change.

1 | INTRODUCTION

The continually increasing abundance and diversity of lianas (woody climbers) in tropical and temperate forests caused by global climate change and forest fragmentation have received much research attention (reviewed by Schnitzer et al., 2015 and Schnitzer, 2018). Previous studies have shown that lianas compete intensely with trees for the same limited resources in diverse tropical habitats (Álvarez-Cansino et al., 2015; Schnitzer, 2018), and this can reduce tree growth and increase tree mortality (Schnitzer & Bongers, 2002), which can, in turn, affect forest composition (Mascaro et al., 2004) and carbon sequestration (van der Heijden et al., 2015). Resource competition between lianas and trees can occur both above-ground and below-ground, but most studies have focused on above-ground competition (Chen et al., 2015; De Guzman et al., 2017; Medina-Vega et al., 2021; Zhu & Cao, 2010). However, the strength of the competition between lianas and trees is thought to be greater below-ground (Schnitzer & Bongers, 2002; Toledo-Aceves, 2015), given that below-ground competition with lianas can reduce tree sapling biomass by as much as 83% (Schnitzer et al., 2005). Why lianas have evolved to be superior below-ground competitors and how this competitive advantage contributes to their high abundance and diversity in disturbed tropical forests remains unclear (Schnitzer, 2018; Toledo-Aceves, 2015). Given that root form and function are closely linked to resource acquisition strategies in plants (Freschet et al., 2021; McCormack et al., 2015; Reich, 2014), studies of liana roots can enhance our understanding the roles of lianas in forest ecosystems.

Root functional traits are significantly altered in response to environmental changes (Chen et al., 2013; Freschet et al., 2017; Gu et al., 2014), and characterizing changes in root functional traits can provide insights into plant life-history strategies (i.e. resource acquisition vs. resource conservation) (Ma et al., 2018; Reich, 2014; Weemstra et al., 2021). In tropical forests, many studies have shown that lianas are fast-growing species at forest edges (Campbell et al., 2018), in treefall gaps (Toledo-Aceves, 2015), and in disturbed forests (Schnitzer, 2015a; Zhu & Cao, 2010). Fast-growing species generally possess functional traits indicative of a fast resource acquisition strategy (Reich, 2014). For example, Fort et al. (2017) found that Mediterranean tree species with an acquisitive strategy had thinner roots, which allowed them to absorb large amounts of water during periods of seasonal drought, but thick-root species with a conservative strategy exhibited the opposite response. A comparative study of six confamilial pairs of lianas and trees in a tropical

forest in Panama using the root diameter (RD) approach revealed that lianas also possess characteristics indicative of fast resource acquisition, such as thin roots with a high specific root length (SRL) and low tissue density, which allow them to quickly exploit nutrients and water to support growth with less carbon investment (Collins et al., 2016). Such root traits may enable lianas to effectively outcompete trees for soil water during the dry season (Chen et al., 2015; De Decurwaerder et al., 2018). Lianas have been suspected to have well-developed root systems to compete with trees for water and nutrients (Schnitzer, 2018; Schnitzer & Bongers, 2002); however, how a fast resource acquisition strategy evolved in liana roots remains unclear. Studies of multiple liana species of different plant lineages are needed to address this outstanding question.

Characterizing the position of liana species along the root economics spectrum can provide important insights for predicting liana performance (Díaz et al., 2016; Reich, 2014; Weigelt et al., 2021). An increasing number of studies have shown that the root functional traits of trees and shrubs are multi-dimensional, and this is consistent with the high diversity in their resource acquisition strategies (Kong et al., 2014; Kramer-Walter et al., 2016; Weemstra et al., 2016). Recently, Bergmann et al. (2020) proposed the concept of the 'root economics space' with two orthogonal dimensions: one is a classical fast–slow 'conservation' gradient, which is characterized by a trade-off between root carbon investment and nutrient return, and the other is a novel 'collaboration' gradient, which ranges from resource uptake by the roots to 'outsourcing' of resource uptake to mycorrhizal fungi. This conceptual framework has been confirmed in woody and nonwoody species on a global scale (Carmona et al., 2021; Weigelt et al., 2021). The trait space occupied by species reflects their resource acquisition strategies as well as their roles in ecosystems (Bergmann et al., 2020). For example, nonwoody plants tend to be more concentrated towards the acquisitive side of the leaf and root conservation axes compared with woody species (Weigelt et al., 2021), which indicates that they are characterized by faster metabolic rates, growth and rates of species turnover. However, the position of the liana root economics space within the global root trait space remains unknown but may prove instrumental to explain their competitive abilities.

Exploring liana resource acquisition strategies requires characterizing the effect of phylogeny on root functional traits, as phylogenetic information can provide insights into the roles of traits in evolutionary adaptation (Reich, 2014) and in shaping species distribution and diversity (Ma et al., 2018). For example, plant functional traits with less phylogenetic constraint may have a high evolutionary

rate (Ackerly, 2009) and thus be evolutionarily labile, which would, in turn, promote species diversity (Webb et al., 2002) and enhance adaptation to harsh environments (Westoby & Wright, 2006). In disturbed tropical forests, lianas generally show high abundance and diversity (Schnitzer & Bongers, 2002), and this can be attributed to the phylogenetic structure of their functional traits (Gianoli, 2015). Some studies of trees have shown that most root traits are conserved and show strong phylogenetic signal within or across forest biomes (Kong et al., 2014; Valverde-Barrantes et al., 2017), suggesting that phylogeny has a major effect on the evolution of root traits. By comparison, lianas have independently arisen numerous times throughout the evolutionary history of angiosperms (Gentry, 1991; Gianoli, 2015), which might foster greater diversity in the root traits of lianas and contribute to root trait differentiation between lianas and trees. Given that lianas and trees coexist within communities (Schnitzer & Bongers, 2002), clarification of the phylogenetic structure of the root traits of lianas and trees is necessary for understanding how lianas have become competitively superior to trees in adverse environments over evolutionary time.

In this study, we sampled 54 liana species from a tropical forest and 15 liana species from a temperate forest; the two sampling sites differ greatly in geographical, climatic and edaphic characteristics (Table S1). All 69 liana species sampled belonged to 29 families and 53 genera (Table S2). Nine key functional traits of first-order roots (i.e. the typical absorptive roots; Guo et al., 2008) were measured for each species, including root morphological, architectural, anatomical and chemical traits, as well as the percentage of mycorrhizal colonization (Table 1). We also collected data on 127 tree species from the same forest biome in China from previous studies (Table S3). Specifically, data on 92 species from the South Chinese tropical forests were collected from the Global Root Traits (GRooT) database (Guerrero-Ramírez et al., 2021), and data on 35 species from a temperate forest (the same site of the current study) were collected from previous studies conducted by our team (Dong, 2015; Shi, 2008). Our overall aim was to explore why lianas are superior below-ground competitors to trees in diverse habitats. Herein, we proposed the three following hypotheses: (1) liana roots should have a fast resource acquisition strategy (Collins et al., 2016; Reich, 2014), given that they are fast-growing species and superior below-ground competitors than trees (Schnitzer et al., 2005; Toledo-Aceves, 2015); (2) liana root traits should be less constrained by phylogeny given that they have been found to outperform trees in stressful environments (Schnitzer, 2018), which is thought to be related to the phylogenetic structure of their functional traits (Gianoli, 2015); and (3) the root economics space of lianas should comprise two orthogonal trait dimensions as has been observed in trees (Bergmann et al., 2020; Weigelt et al., 2021), but lianas should tend to be concentrated towards the acquisitive side of the root economics space, given that their roots showed higher SRL and root nitrogen (RN) concentration relative to trees (Collins et al., 2016). We also compared the root functional traits, the phylogenetic structure of these traits and the root trait dimensions of lianas from the two study sites, as well as of evergreen and deciduous lianas.

TABLE 1 List and descriptive statistics of nine functional traits of first-order roots in lianas (n = 69) and trees (n = 127), and the results of MANOVA

Traits	Unit	[1]Abbr	Lianas				Trees				
			Mean	[2]Max	[3]Min	[4]CV	Mean	Max	Min	CV	p-value
Root diameter	mm	RD	0.32	1.11	0.17	0.41	0.33	1.01	0.07	0.53	0.652
Specific root length	$m\,g^{-1}$	SRL	163.72	802.58	9.77	0.73	62.26	203.82	4.42	0.65	**0.000**
Root tissue density	$g\,cm^{-3}$	RTD	0.11	0.25	0.01	0.47	0.32	0.72	0.06	0.40	**0.000**
Root nitrogen concentration	$mg\,g^{-1}$	RN	23.95	41.84	14.96	0.22	20.82	44.62	5.55	0.31	**0.001**
Ratio of root carbon to nitrogen	—	RCN	19.55	32.40	10.87	0.21	25.16	87.82	10.86	0.48	**0.018**
Root branching ratio	—	BR	3.39	9.44	2.28	0.34	2.99	10.09	1.21	0.42	**0.018**
Cortex thickness	μm	CT	88.96	310.22	32.94	0.44	100.94	337.41	14.35	0.68	0.722
Stele diameter	μm	SteleD	69.73	210.74	31.04	0.41	77.11	257.78	24.07	0.50	0.738
Mycorrhizal colonization	%	Myc	57.55	100.00	5.00	0.54	63.40	100.00	8.00	0.37	0.138
MANOVA between lianas and trees									F		p-value
Wilks' Lambda									20.050		**0.000**

Note: Bold values indicate significant difference in root trait between lianas and trees. [1]Abbr, abbreviation; [2]Max, maximum; [3]Min, minimum; [4]CV, the coefficient of variation; MANOVA, multivariate analysis of variance.

2 | MATERIALS AND METHODS

2.1 | Study sites

Our two study sites were located in tropical and temperate regions of China. Site I was located in tropical forest at Limushan National Reserve (19°07′–19°14′N, 109°39′–109°48′E) in Hainan, southern China. This site has a tropical climate with mean January, July and annual temperatures of 17.4, 27.1 and 23.1°C, respectively. The mean annual precipitation is 2343 mm. The soils are Humic Acrisol and rich in nutrients (Gong et al., 1999). Tropical seasonal rainforest dominates the mountainous areas. We sampled lianas in stands that have not experienced any anthropogenic disturbance in recent decades. Site II was located in a temperate forest at Maoershan Research Station (45°21′–45°25′N, 127°30′–127°34′E) in Heilongjiang, northeastern China. This site has a continental temperate monsoon climate with mean January, July and annual temperatures of −19.6, 20.9 and 2.8°C, respectively. The mean annual precipitation is 730 mm. The soils are Hap-Boric Luvisols and rich in organic matter (Gong et al., 1999). The site is dominated by secondary forests that regenerated following the harvest of old-growth forest over 70 years ago. All information on the two study sites is summarized in Table S1.

2.2 | Species selection and root sampling

Site I is a typical tropical forest ecosystem, and lianas are highly abundant and diverse at this site; the abundance and diversity of lianas are low at the temperate forest site (Site II) (Hu et al., 2010; Hu & Li, 2015). Given that the natural distribution of lianas along latitudinal and climatic gradients is disproportionate (Hu et al., 2010; Schnitzer, 2005), we sampled 54 liana species from Site I (hereafter 'tropical lianas') and 15 liana species from Site II (hereafter 'temperate lianas') during the summer of 2019, which accounted for 18% and 69% of the total number of tropical and temperate liana species recorded in China, respectively (Hu et al., 2010). The taxonomic binomials of all liana species were verified using The Plant List (TPL, http://theplantlist.org/), and our sampled taxa were classified into 29 families and 53 genera (Table S2), including various angiosperms (magnoliids, rosids, asterids and monocotyledons) and one gymnosperm (*Gnetum montanum*). With regard to the five largest families in southeastern (i.e. tropical) and eastern (i.e. temperate) Asia (Hu & Li, 2015) accounted for 44% and 52% of all climbing plants, respectively, our samples comprised four families of tropical lianas (i.e. Apocynaceae, Vitaceae, Convolvulaceae and Rubiaceae) and three families of temperate lianas (i.e. Ranunculaceae, Apocynaceae and Vitaceae) (Table S2).

The roots of temperate and tropical lianas were sampled in July and August in 2019, respectively. At each site, measurements were taken from at least three individuals of each species, and we obtained at least three root branches per individual from the top 20-cm mineral soil layer following the procedure in Guo et al. (2008).

Root branches were traced to the stem and cut from the main lateral woody roots. Once collected, the soil particles attached to each root sample were carefully removed, and samples were divided into two subsamples: one was washed gently with deionized water and immediately fixed in formalin-aceto-alcohol (FAA) solution (90 ml of 50% ethanol, 5 ml of 100% glacial acetic acid and 5 ml of 37% methanol) for subsequent anatomical analysis; the other was immediately placed into a Ziploc bag for subsequent morphological and chemical analyses. All samples were kept in a cooler with ice and transported to the laboratory within 4 h. Root subsamples for morphological and chemical measurements were kept refrigerated until analysis.

2.3 | Root trait measurements

In the laboratory, root subsamples for morphological analysis were carefully dissected and separated by root branching order with forceps following the procedure described in Pregitzer et al. (2002) and Gu et al. (2014); distal nonwoody roots were defined as first-order roots. The number of first-order roots born by second-order roots was recorded manually for at least one intact root branch (including five order roots) for each root subsample for each species. Next, 150–300 root tips were randomly selected and scanned with an Epson Expression 10000XL colour scanner (800 dpi, Seiko Epson Cor.). Mean RD (mm), total length and the volume of each root subsample were determined using root system analyser software (WinRhizo 2004b, Regent Instruments Inc.). These roots were then oven-dried at 65°C to determine the constant weight (nearest 0.0001 g), and the SRL (mg^{-1}) and root tissue density (RTD, g cm^{-3}) were calculated. All dried root subsamples were ground to a fine powder for determination of the RN concentration (mg g^{-1}) and carbon concentration (C, mg g^{-1}) using an elemental analyser (Vario Macro, Elementar Co.), and then the ratio of root carbon to nitrogen (RCN) was calculated. The root branching ratio (BR) was calculated as the number of first-order roots divided by the number of second-order roots (Chen et al., 2013).

For root anatomy measurements, roots in each FAA subsample were dissected carefully and separated by root branching order. In all, 30 randomly selected root tips of each species were stained with safranine-fast green; dehydrated in 70%, 85%, 95% and 100% alcohol; and embedded in paraffin. Slides of 8-µm-thick root sections were prepared using a microtome for measurements of anatomical characteristics (Gu et al., 2014). These slides were photographed under a compound microscope (BX-51, Olympus Corporation). Cortex thickness (CT, µm) and stele diameter (SteleD, µm) were measured from three cross-sections of each root segment using Motic Images Advanced 3.2 software (Motic Corporation).

For mycorrhizal colonization assessment, we first identified the mycorrhizal type of the root tips, arbuscular mycorrhiza (AM) or ectomycorrhiza (EM), using a compound microscope (BX-51, Olympus Corporation). For EM species, the percentage of mycorrhizal colonization (Myc) was determined as the number of root tips with the fungal sheath or mantle divided by the number of total root tips

(approximately 100 root tips) present in the counting dish under a microscope. For AM species, 50 root tips stored in FAA solution for each species were randomly selected, washed with deionized water and then soaked in 10% (w/v) KOH solution at 90°C for 50 min. These root tips were rinsed three times with deionized water, placed in 5% HCl solution at room temperature for 5 min and then stained with Trypan blue solution (2.5% glacial acetic acid, 50% glycerol, 47.5% deionized water and 0.05% (w/v) trypan blue) overnight at room temperature (Sharda & Koide, 2008). All root tips were randomly selected for measurements of AM colonization at 200× magnification (BX-51, Olympus Corporation) using the line-intersect method as described by McGonigle et al. (1990), and then Myc was calculated for each AM species. If an AM species had Hartig net around epidermal cells, it was considered to have AM and EM colonization (Brundrett, 2004; Yu et al., 2001).

2.4 | Tree root data collection

We collected tree root data for 127 species belonging to 38 families and 86 genera in tropical and temperate forests in China (Table S3). Data on 35 temperate tree species (hereafter 'temperate trees') were obtained from our previous studies (Dong, 2015; Shi, 2008), which were conducted at the same site where the temperate lianas were sampled. Tree root data, including root morphological, architectural, anatomical and chemical traits, as well as the percentage of mycorrhizal colonization, from these studies were collected using the same procedures that were used to collect liana root data.

Data on 92 tropical tree species (hereafter 'tropical trees') were obtained from the GRooT database (Guerrero-Ramírez et al., 2021), and all these species grow in tropical forests of China. Tree species included in analyses were required to meet the following criteria: (i) data on first-order root traits were reported; (ii) data were collected from the field (data from studies conducted in croplands and greenhouses and common garden experiments were excluded); (iii) root samples were collected from mature trees and live roots; and (iv) at least nine root traits (the same traits measured from the lianas) were measured. All tree species names were verified using TPL (http://theplantlist.org/).

2.5 | Data analysis

For each liana species, the mean and standard error of root traits were calculated using measurements from three individual lianas. For each root trait, the mean, maximum, minimum, and interspecific coefficient of variation (CV) for first-order roots were calculated across all 69 lianas. These statistical indices were also calculated separately for the 54 tropical and 15 temperate lianas. Additionally, the intraspecific coefficient of variation (ITV) for lianas was calculated separately for the two study sites, and differences in each trait were compared using ANOVA. The same indices (except for ITV) were calculated in the same way for all tree species. MANOVA was used to test for differences in the nine root traits between lianas and trees, tropical and temperate lianas, tropical and temperate trees, as well as evergreen and deciduous lianas. All tests were performed using SPSS software (2010, V.19.0, SPSS Inc.). Data were log-transformed prior to ANOVAs, to improve normality.

To evaluate the effect of phylogeny on root trait variation, we used the backbone phylogeny from Zanne et al. (2014) to construct a phylogenetic tree for the 196 species (69 lianas and 127 trees) (Figure S1) using the 'phylo.maker' function in the R package V.PHYLO-MAKER (Jin & Qian, 2019). To identify the effect of phylogeny on root trait variation in lianas and trees, the phylogenetic signal of each root trait for the 69 lianas and 127 trees was tested using Blomberg's K statistic with the 'phyloSignal' function in the R package PHYLOSIGNAL (Keck et al., 2016). Blomberg's K statistic of each root trait was also calculated separately for lianas and trees at the two study sites, as well as for evergreen and deciduous lianas, to determine whether the effect of phylogeny varies among study sites and leaf habit. A value of K close to 0 indicates that trait evolution is independent of phylogeny; a value of K close to 1 indicates greater phylogenetic conservatism for a given trait; and $K > 1$ indicates a stronger similarity between close relatives than expected under a random model (Blomberg et al., 2003).

We used phylogenetically informed methods in all subsequent analyses. To investigate multivariate trait space, we performed phylogenetically informed principal component analysis (pPCA) for the nine root traits in all species (lianas and trees) and in all lianas. We also conducted separate pPCAs for tropical and temperate lianas. The pPCAs were performed using the 'phyl.pca' function in the R package PHYTOOLS (Revell, 2012). Next, we used MANOVA to test the differences in the mean pPCA scores of species in the first and second principal component (PC) axes using SPSS software (2010, V.19.0, SPSS Inc.) to evaluate differences in the distribution of lianas and trees, tropical and temperate lianas, as well as evergreen and deciduous lianas in trait space. Finally, we used phylogenetically independent contrasts (PICs) in which the effect of phylogeny was removed to conduct Pearson's correlation analyses of the nine key root traits for all lianas and trees. These correlation analyses were also conducted for tropical and temperate lianas. The PICs for each root trait were generated using the 'pic' function in the R package APE (Paradis et al., 2004). All phylogenetic relevant analyses were carried out in R software 4.0.3 (R Development Core Team, 2020).

3 | RESULTS

3.1 | Variation in the root traits of lianas and trees

There were significant differences in the nine root traits between lianas and trees (Table 1). Mean SRL, RN and BR were significantly higher and RTD and RCN were significantly lower in lianas than in trees, and no differences were observed in the other four root traits (RD, CT, SteleD and Myc) (Table S4). SRL, RN, CT and SteleD were higher and RTD, RCN and BR were lower in temperate trees than in

tropical trees (Figure 1, Table S5b). There were no significant differences in all root traits between tropical and temperate lianas; the only exception was BR, which was significantly higher in temperate lianas than in tropical lianas ($p = 0.014$, Figure 1, Table S5a). There were also no significant differences in most root traits between evergreen and deciduous lianas (Table S6).

The CVs of SRL, RTD and Myc were higher and the CVs of the other six traits were lower in lianas than in trees (Table 1). All the CVs of root traits, with the exception of RTD, were higher in tropical trees than in temperate trees (Table S5b). The CVs of most traits were higher in tropical lianas than in temperate lianas; however, the opposite pattern was observed for BR, RN and RCN (Table S5a). ITV

in most root traits (seven of the nine) was higher in temperate lianas than in tropical lianas (Figure S2). ITV in two anatomical traits (CT and SteleD) was lower in temperate lianas than in tropical lianas (Figure S2). Significant differences in ITV were observed in only three root traits (RD, RN and RCN) (Figure S2).

3.2 | Effect of phylogeny on the root traits of lianas and trees

Phylogenetic signal, as indicated by Blomberg's K statistic, was detected for all root traits examined, but the strength of the signal
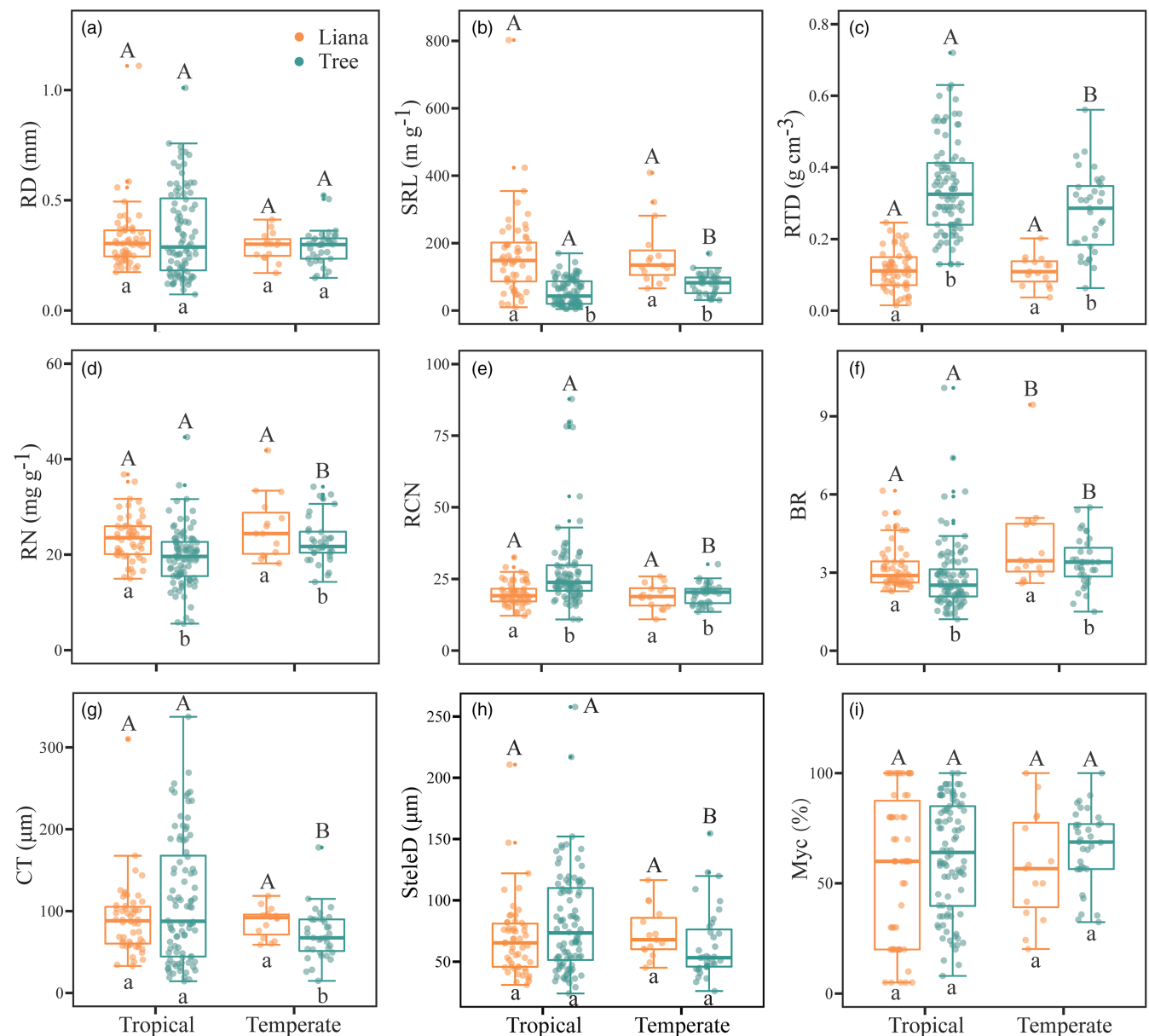

FIGURE 1 Distribution of the nine functional traits of first-order roots in tropical and temperate lianas and trees. Boxplots include the median (horizontal line within boxes), the first and third quartiles (bottom and top parts of the box, respectively), and the two whiskers (10th and 90th percentiles). Different lowercase letters indicate significant differences between the two plant growth forms ($p < 0.05$); different uppercase letters indicate significant differences between tropical and temperate sites within the same plant growth form ($p < 0.05$). Trait abbreviations are provided in Table 1.

differed between lianas and trees (Table 2). In all tree species, significant phylogenetic signal was observed for five of the nine root traits (RD, RTD, RCN, CT and Myc) (Table 2), indicating that over half of the tree root traits were phylogenetically conserved. However, significant phylogenetic signal was detected for only three of the nine root traits (RD, CT and SteleD) across all lianas (Table 2), indicating that most liana root traits were evolutionarily labile. The proportion of root traits with significant phylogenetic signal was higher in tropical trees (six of nine traits, 66%) than in tropical lianas (three of nine traits, 33%) (Table 2). However, none of the root traits exhibited significant phylogenetic signal in temperate trees and temperate lianas, with the exception of RN in temperate trees (Table 2), suggesting that there was a weaker effect of phylogeny on the root traits of temperate trees and temperate lianas. The effect of phylogeny was also weaker on the root traits of deciduous lianas than on those of evergreen lianas (Table 2).

3.3 | Root trait dimensions

The results of pPCA revealed that the root traits of all liana and tree species had two orthogonal dimensions, which formed a root economics space (Figure 2a). The first and second PC axes accounted for 34.90% and 28.54% of the total variation, respectively (Figure 2a, Table 3). SRL, RD, CT and SteleD loaded heavily on the first axis (Table 3), and RD was negatively correlated with SRL and positively correlated with CT (Table 4); thus, the two ends of this axis represent the dimension of resource absorption by the roots themselves and by mycorrhizal fungal partners (Figure 2a). RTD, C/N and RN loaded heavily on the second axis (Table 3), and both RTD and RCN were negatively correlated with RN (Table 4); thus, the two ends of this axis represent the dimension of fast and slow resource return on investment such as nutrients and carbon (Figure 2a).

We found that the root trait dimensions of lianas and trees were similar (Figure 2b, Table 3), but both plant groups were

clearly separated in the root economics space (Figure 2a). Lianas were concentrated on the high physiological performance and fast resource acquisition side of the space (Figure 2a), which reflects their higher SRL and RN (Figure 1b,d). By contrast, tree species occupied a wider area of trait space than lianas, but they were mainly concentrated on the resource conservation side of the space (Figure 2a), which reflects their higher RTD, shorter SRL and lower RN (Figure 1b–d). The analysis of root traits of tropical and temperate lianas also revealed similar root economics spaces (Figure S3, Table S7), and pairwise correlations among root traits (e.g. RD vs. SRL, RTD vs. RN) were similar (Table S8). However, minor differences were observed. BR was not correlated with other traits in tropical lianas (Table S8a), but it was correlated with RD, SRL, CT and SteleD in temperate ones (Table S8b). Myc was not correlated with CT, but it was correlated with RD in all tropical and temperate lianas (Table S8).

4 | DISCUSSION

4.1 | Variation in the root traits of lianas and trees

The findings of the current study support our first hypothesis that liana roots have a fast resource acquisition strategy, which is consistent with their higher SRL and RN and lower RTD (Figure 1), and this might contribute to their competitive advantage over trees in the acquisition of below-ground resources. Lianas deploy relatively large numbers of leaves over a broad area at the top of the forest canopy (Schnitzer & Bongers, 2002); given that the activities of the roots and shoots are coordinated to achieve a functional equilibrium (Bloom, 2005), ensuring an adequate supply of water and nutrients to support the leaves requires specific root traits. Liana roots have a high RN (Figure 1), which might indicate greater metabolic activity (e.g. root respiration) (Burton et al., 2002; Reich et al., 2008), as well as a high SRL and BR, which could increase the efficiency of soil resource exploration and acquisition (Freschet et al., 2021;

TABLE 2 Values of Blomberg's *K* statistic for nine functional traits in lianas and trees. Trait abbreviations are provided in Table 1

	Lianas					Trees		
	All	**Tropical**	**Temperate**	**Evergreen**	**Deciduous**	**All**	**Tropical**	**Temperate**
Traits	*K*	*K*	*K*	*K*	*K*	*K*	*K*	*K*
RD	**0.224**	**0.262**	0.418	**0.350**	0.295	**0.147**	**0.150**	0.179
SRL	0.110	0.120	0.436	0.177	0.337	0.045	0.037	0.258
RTD	0.086	0.123	0.082	0.153	0.198	**0.126**	**0.142**	0.109
RN	0.087	0.130	0.114	0.140	0.132	0.084	**0.072**	**0.356**
RCN	0.077	0.104	0.113	0.080	0.216	**0.135**	**0.133**	0.158
BR	0.150	0.118	0.442	0.116	0.466	0.051	**0.172**	0.231
CT	**0.234**	**0.370**	0.141	**0.394**	0.190	**0.174**	0.032	0.228
SteleD	**0.203**	**0.233**	0.348	0.315	0.251	**0.040**	**0.044**	0.130
Myc	0.122	0.124	0.177	0.118	0.191	**0.088**	**0.082**	0.126

Note: Bold values indicate traits that showed stronger phylogenetic signal than expected at random ($p < 0.05$).
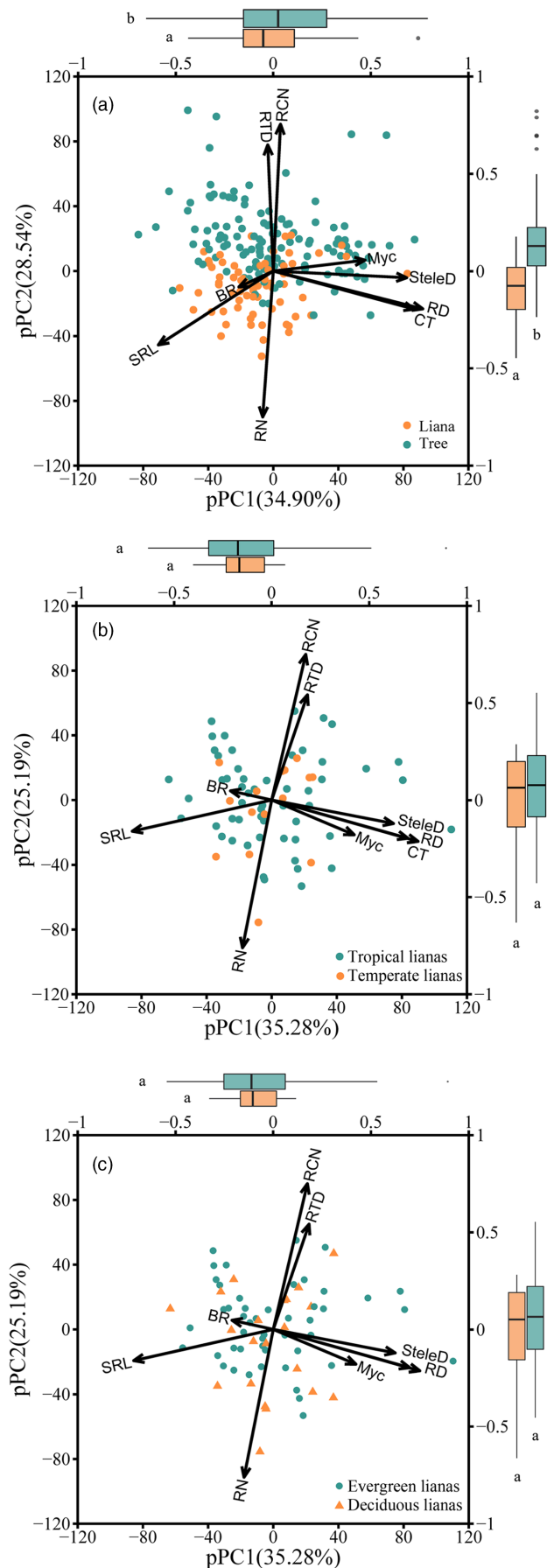
FIGURE 2 Phylogenetically informed principal component analyses (pPCA) of nine root functional traits in all liana and tree species (a), all tropical and temperate lianas (b), and evergreen and deciduous lianas (c). Loading scores are shown in Table 3. Points indicate the position of species along the first two axes. Box-and-whisker plots on the top and right of each panel show the median (thick bar), upper and lower quartiles (edge of rectangle), and maximum and minimum (outer bars) of principal component axes 1 and 2. Groups with different letters are significantly different ($p < 0.05$). Trait abbreviations are provided in Table 1.

TABLE 3 Loading scores of nine functional traits in the pPCA for all liana and tree species (Figure 2a) and all liana species (Figure 2b,c). Trait abbreviations are provided in Table 1

Traits	Lianas and trees		Lianas	
	pPC1	pPC2	pPC1	pPC2
Variation explained	34.90%	28.54%	35.28%	25.19%
RD	0.919	−0.233	0.899	−0.256
SRL	−0.707	−0.455	−0.857	−0.193
RTD	−0.034	0.778	0.220	0.650
RN	−0.065	−0.900	−0.179	−0.913
RCN	0.044	0.906	0.209	0.900
BR	−0.212	−0.098	−0.253	0.057
CT	0.868	−0.235	0.838	−0.237
SteleD	0.820	−0.041	0.749	−0.145
Myc	0.565	0.067	0.507	−0.215

McCormack et al., 2015). Although many previous studies have shown that lianas are superior competitors for above-ground resources (Mello et al., 2020; Visser et al., 2018; Zhu & Cao, 2010), our findings clearly demonstrate that lianas are also superior competitors for below-ground resources in temperate and tropical regions according to their root functional traits. In addition, the low RTD and RCN in lianas (Figure 1) indicate that liana roots have lower construction costs and shorter life spans and can more rapidly decompose, which promotes below-ground carbon and nutrient cycling at the ecosystem level (Collins et al., 2016; Schnitzer, 2015b).

Consistent with previous studies conducted at regional and global scales (Freschet et al., 2017; Gu et al., 2014; Ma et al., 2018), temperate tree roots tended to have thinner RD and higher SRL and RN than tropical tree roots, which indicates a shift in acquisition strategy between temperate and tropical environments (Chen et al., 2013). However, such a pattern was not observed for any root traits in lianas (Table S5a), with the exception of BR ($p = 0.014$, Figure 1f). The exact mechanism underlying these patterns remains unclear, but environmental differences might select for different acquisition strategies among taxa, for example, through alterations in their root morphology (e.g. RD, Chen et al., 2013), architecture (e.g. BR, Kong et al., 2014), or both (Fitter, 1987). In our study, the root branching pattern of temperate lianas appears to be modified more readily compared with other traits to mediate adaptation to drier

TABLE 4 Pearson's correlation coefficients for pairwise comparisons of root traits with phylogenetically independent contrasts (PICs) for all tree species (lower diagonal, $n = 127$) and all liana species (upper diagonal, $n = 69$). Trait abbreviations are provided in Table 1

	RD	SRL	RTD	RN	RCN	BR	CT	SteleD	Myc
RD		−0.522	−0.086	−0.033	0.105	−0.232	**0.618**	**0.573**	**0.239**
SRL	**−0.181**		**−0.728**	**0.434**	−0.305	0.224	−0.331	−0.329	−0.314
RTD	**−0.342**	−0.203		**−0.621**	**0.483**	−0.116	−0.096	0.039	0.205
RN	0.165	**0.799**	**−0.440**		**−0.955**	0.050	−0.121	−0.228	0.020
RCN	**−0.615**	−0.106	**0.577**	**−0.570**		−0.022	0.142	**0.290**	−0.020
BR	**0.257**	**0.649**	0.020	**0.552**	−0.089		−0.209	−0.058	−0.070
CT	**0.804**	0.001	**−0.211**	0.058	**−0.312**	**0.420**		**0.498**	0.092
SteleD	**0.807**	**−0.440**	**−0.225**	−0.095	**−0.580**	−0.103	**0.454**		−0.058
Myc	0.108	**−0.794**	−0.086	**−0.652**	−0.010	**−0.733**	−0.044	**0.409**	

Note: Bold values represent significant correlations ($p < 0.05$).

and cooler conditions in temperate areas. In addition, temperate lianas with highly branched roots tended to have high SRLs and low RDs (Table S8b), which might enhance their ability to rapidly colonize patches of water and nutrients (Collins et al., 2016; Kong et al., 2014) and efficiently absorb soil resources during short growth periods (Hodge, 2004; Liese et al., 2017).

The degree of interspecific variation in the root traits of lianas substantially differed between the two study sites. Specifically, all CVs of root traits, with the exception of the chemical traits (i.e. RN and RCN) and BR, were lower in temperate lianas than in tropical lianas (Table S5a), and this might be caused in part by differences in levels of taxonomic diversity. Tropical habitats facilitate the coexistence of species with diverse evolutionary histories, and the roots of such species often differ, which can increase interspecific variation (Chen et al., 2013). By contrast, ITV in most root functional traits was higher in temperate lianas than in tropical lianas (Figure S2). ITV has important implications on the performance of plants, interactions among plants and their responses to environmental gradients (Albert et al., 2011). Higher ITV in temperate lianas might reflect the greater plasticity of their roots, their enhanced ability to adapt to diverse micro-habitats (e.g. local topography) and the strong seasonality in temperate areas. Additional studies are needed to clarify whether lianas generally show higher interspecific variation in root traits in tropical areas but greater intraspecific variation in root traits in temperate areas.

4.2 | Effect of phylogeny on the root traits of lianas and trees

The degree of variation in root traits has been shown to be affected by plant phylogeny at the global scale (Ma et al., 2018), but the magnitude of the phylogenetic effect varies among root traits and growth forms (Valverde-Barrantes et al., 2017). The results of our study demonstrated that there was an effect of phylogeny on the root traits of lianas. According to Blomberg's *K* statistic, however, most liana root traits displayed weak phylogenetic signal compared with the root traits of trees in our study (Table 2) and in other studies (Bergmann et al., 2020; Kong et al., 2014; Valverde-Barrantes

et al., 2017), which might confer lianas with the ability to faster develop diverse types of roots in various habitats. This finding supports our second hypothesis.

Lianas occur in most major clades of extant land angiosperms (Isnard & Field, 2015; Figure S1) and coexist with host trees in the same forest (Schnitzer et al., 2015). However, the mechanism of weak phylogenetic effect on liana root traits remains unclear, but it might be related to the evolution of the climbing habit in lianas, which is considered a key innovation in their evolutionary history (Gentry, 1991; Gianoli, 2015) that has promoted species diversification (Isnard & Field, 2015). Generally, the evolution of the climbing habit might have permitted the splitting of various angiosperm lineages. For example, Rios et al. (2014) reported that the mean phylogenetic distance among liana species was 1.2 times greater than that among tree species; Gianoli (2015) found that the mean genetic distance was two-fold higher in climbers than in non-climbers. Greater phylogenetic or genetic distances may increase the diversification potential of lianas (Gianoli, 2015; Rios et al., 2014), thereby decreasing the effect of phylogeny on variation in root functional traits.

We also found that the effect of phylogeny on the root functional traits of both lianas and trees was reduced in temperate forest (Table 2), indicating that the root traits of temperate species experience less phylogenetic constraint. This finding has two potential explanations. First, the reduced phylogenetic constraint on the root traits in temperate area might facilitate the evolution of flexible below-ground ecological strategies that allow them to cope with changing environments. Previous studies have suggested that plant functional traits with lower phylogenetic signal generally show higher evolutionary rates (Ackerly, 2009) and are more evolutionarily labile (Blomberg et al., 2003). Thus, the root traits of temperate species might be more evolutionarily labile, which would improve their survival under harsh environmental conditions such as low rainfall and cold temperature (Chen et al., 2013). Second, the weak effect of phylogeny on the temperate species in this study might also be caused by their smaller sample size (15 liana species, Table S2) which could reduce the statistical power of a phylogenetic test (Blomberg et al., 2003; Münkemüller et al., 2012). This smaller sample size partly results from the overall lower taxonomic diversity

(Hu et al., 2010; Schnitzer & Bongers, 2002), and as our dataset still covered three of the five largest families of climbing plants in eastern Asia (Ranunculaceae, Apocynaceae and Vitaceae), and accounted for 69% of the total number of liana species recorded in temperate forests of China (Hu et al., 2010), we expect our findings to be robust.

4.3 | Differences in the root economics space between lianas and trees

The results of our study demonstrated the existence of a 'root economics space' in lianas, similar to that observed in other plant growth forms (Bergmann et al., 2020; Sun et al., 2021; Sweeney et al., 2021). Two orthogonal dimensions were identified across all 69 liana species: one dimension formed by SRL, RD and CT represented the 'collaboration' axis of resource uptake by the roots themselves and mycorrhizal fungi partners, and the other dimension formed by RN, RTD and RCN represented the classical fast–slow 'conservation' gradient, which reflects a trade-off between resource return and carbon investment (Figure 2b). When lianas and trees were pooled, we found that both groups were significantly separated along the fast–slow 'conservation' gradient; specifically, lianas occupied the side corresponding to a higher metabolic rate (i.e. greater RN) and faster resource return on investment, and trees occupied the opposite side (i.e. higher RTD, Figure 2a). In addition, lianas were more concentrated on the 'do-it-yourself' side of the 'collaboration' gradient than trees. This provided support for our third hypothesis.

The separation of lianas from tree species in the root economics space reflects differences in life-history strategies and has important ecological implications. First, the root functional traits (Figure 1) of lianas along the 'conservation' gradient provide them with a 'fast' resource acquisition strategy, which is characterized by roots with low tissue construction cost, short life span and possibly high resource acquisition ability (Freschet et al., 2021; Grassein et al., 2015). Lianas with such root traits may have higher root growth rates (Eissenstat et al., 2000; Ryser, 1996), which enable them to quickly colonize resource-rich soil patches and take up available resources before trees (Comas & Eissenstat, 2004; Reich, 2014). The 'fast' resource acquisition strategy of liana roots might promote rapid above-ground growth and canopy occupation when coexisting with host trees. Second, the higher SRL of lianas reflects the 'do-it-yourself' strategy along the 'collaboration' gradient. Collins et al. (2016) also reported that lianas had high SRL and highly branched roots and seldomly relied on mycorrhizal symbionts for resource absorption. However, tree species were distributed more evenly along the gradient and adopted both 'do-it-yourself' and 'outsourcing' strategies. Lastly, the distribution of lianas in the root economics space may be explained based on their evolutionary pathway (Gianoli, 2015). Some studies of trees have reported that marked changes in root morphology and anatomy had occurred approximately from 120 to 60 million years ago, and tended to be steady afterwards (Chen et al., 2013; Gu et al., 2014). In the period before 60 million years

ago, RD evolved to be thinner while SRL to be higher, which may be caused by the drier paleoclimate since the mid-Cretaceous (Chen et al., 2013; Gu et al., 2014; Kong et al., 2014). According to the divergence time at the family level estimated by APG III (Wikström et al., 2001), we compared how the root traits between lianas and trees concurrently diverged before or after 60 million years ago, and found that liana root traits displayed consistently more acquisitive strategies over the two periods, such as high SRL and RN, and low RTD (Table S9). Therefore, we inferred that liana roots might be always more acquisitive than tree roots during evolutionary history.

Despite the existence of a 'root economics space' in lianas, their resource acquisition strategies differed somewhat between tropical and temperate forests (Figure S3, Table S7). BR was not correlated with any of the other root traits in tropical lianas (Table S8a), but it was significantly negatively correlated with RD and positively correlated with SRL in temperate lianas (Table S8b). Thus, the evolution of the 'do-it-yourself' strategy along the 'collaboration' gradient in temperate lianas may be achieved through changes in root morphology (e.g. SRL) or root architecture (e.g. BR) (Figure S3b). This finding suggests that improvements in resource acquisition in temperate lianas can be achieved in more diverse ways compared with tropical lianas. RD appears to be jointly regulated by the cortex and stele in tropical lianas (Table S8a) but solely by the cortex in temperate lianas (Table S8b). This decoupling of RD from regulation by the stele might allow temperate liana roots to regulate the balance between resource absorption and transportation more flexibly (Kong et al., 2017), which can enhance resource acquisition efficiency. There was no difference in the trait space between evergreen and deciduous lianas (Figure 2c), indicating that the effect of leaf habit on root traits in lianas is weak (Table S6). Our findings regarding differences in the root traits between the two study sites should be interpreted with caution because of the lack of replication of forest type. Additional studies of more forest types are needed to clarify whether the evolution of below-ground acquisition strategies of lianas observed here globally characterize tropical versus temperate biomes.

5 | CONCLUSIONS

Our study of the root functional traits of 69 liana species and 127 tree species provided novel insights into variation in root traits, the effect of phylogeny on root trait evolution and the root economics space of lianas. We found that lianas had a fast resource acquisition strategy, which might provide them with a below-ground competitive advantage over trees. Our results also demonstrated that lianas occupied the acquisitive side of the root economics space, whereas trees displayed a more conservative strategy. This faster acquisitive strategy in lianas might allow them to adapt rapidly to fluctuating environmental conditions than cooccurring trees, giving them a unique role in forest assembly. Moreover, liana root acquisitive strategy was related to their phylogenetic structure. Less phylogenetic constraint might facilitate the evolution of flexible below-ground ecological strategies in lianas, which would enhance their ability to colonize

new habitats. Our findings may represent a valuable step for better understanding of the mechanisms by which lianas engage in resource competition and adapt to diverse habitats, as well as their negative effects on forest functioning.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.4tmpg4fdx (Wang et al., 2022).

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