Divergences in stem and leaf traits between lianas and co-existing trees in a subtropical montane forest

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Abstract

Patterns in functional trait variation associated with the ecological strategies of lianas and trees in subtropical montane forests remain poorly understood because of lack of trait comparisons. Here, we filled this gap by investigating trait divergence between lianas and trees with different leaf habits for 13 traits of 33 species (seven deciduous and four evergreen liana species, and 10 deciduous and 12 evergreen tree species) in a subtropical montane forest in southwestern China. We found that lianas had significantly larger stem xylem vessel diameter, higher theoretical hydraulic conductivity, specific leaf area, leaf nitrogen and phosphorus concentrations, but lower leaf dry-matter content and N/P ratio than sympatric trees, indicating that lianas employ an acquisitive ecological strategy, with a more efficient stem hydraulic system and more productive leaves. In contrast to trees, lianas exhibited a larger variation in vessel diameter, with a few wide and many narrow vessels in the xylem, indicating a greater vessel dimorphism. Growth form explained 48.7% of the total trait variation, while leaf habit only explained 3.8% of trait variation, without significant interaction between growth form and leaf habit. In addition, significant stem-leaf trait relationships were only found in trees, but not in lianas, indicating decoupling of stem hydraulic function and leaf traits in subtropical lianas. These results suggest that subtropical montane lianas and trees strikingly differ in stem and leaf functional traits. Further studies are needed to strengthen our understanding of the mechanisms underlying the strong divergence in ecological strategies between lianas and trees in subtropical forest ecosystems.

Keywords functional traits, leaf habit, leaf morphology, lianas, subtropical montane forests, xylem anatomy
INTRODUCTION

Lianas (woody vines), as structural parasites, are important components of forest ecosystems worldwide (Gentry 1992; Schnitzer and Bongers 2002). For example, lianas constitute an average of 25% woody plant species in tropical forests, 9.6% in subtropical forests, and 10% in temperate forests (Gentry 1992; Hu et al. 2010). Lianas invest relatively little carbon in stem structural support, and allocate more biomass to canopy development, and stem and root elongation, resulting in a higher canopy: stem ratio than trees (Ewers and Fisher 1991; Schnitzer and Bongers 2002). Thus, lianas require higher stem hydraulic conductivity per sapwood area to supply water and support more canopy leaves than trees (Schnitzer and Bongers 2002), which may drive the differentiation in traits related to stem hydraulics and leaf performance between lianas and trees.

Plant functional traits refer to the morpho-physio-phenological characteristics that influence the growth, survival, reproduction, and overall fitness of species in various environmental conditions (Violle et al. 2007; Jiang and Jin 2021), and are the heart of functional ecology (Ackery et al. 2000). Wood and leaf traits are indicative of the allocation of biomass and the trade-offs among strategies for acquiring light, water, and nutrients, as well as the utilization of resources (Wright et al. 2004; Chave et al. 2009; Díaz et al. 2016). Therefore, a comparison of stem and leaf traits between coexisting lianas and trees is important to understand the divergence in their ecological strategies (Mello et al. 2020).

Some previous studies have found significantly greater stem xylem vessel diameter and higher hydraulic conductivity in lianas than in coexisting trees in tropical forests (Ewers and Fisher 1991; Zhu and Cao 2009; Campanello et al. 2016), evergreen temperate rainforests (e.g. Jiménez-Castillo and Lusk 2013) and a subalpine cold temperate forest (Zhang et al. 2021). It seems that lianas are able to maintain wide vessels and strong water transport capacity from warm and wet to dry and cold environments (Zhang et al. 2023). These
findings indicate that lianas possess an efficient water transport system although their stems are thin, slender, and flexible. In addition, lianas generally have higher maximum photosynthetic rate, higher specific leaf area (SLA), and lower leaf construction costs than co-occurring trees in tropical forests (Zhu and Cao 2010; Slot et al. 2013; Wyka et al. 2013; Medina-Vega et al. 2021) and a subalpine temperate forest (Zhang et al. 2021). Previous investigations have demonstrated a strong association between stem xylem traits and leaf traits in both lianas and trees (e.g. Zhu and Cao 2009; Zhang et al. 2021). For example, lianas and trees generally show similar life-history trade-offs (Gilbert et al. 2006), and coexisting lianas and trees show similar slopes for relationships between stem theoretical hydraulic conductivity and SLA in a subalpine temperate forest (Zhang et al. 2021). Whilst the linkages of stem xylem properties to leaf functional traits among lianas and trees in tropical forests have been the topic of much discussion and debate, the evidence in support of the associations among stem and leaf traits in woody species, especially in lianas in subtropical montane forests, remains rather sparse.

Plant trait variation is not only related to growth form (i.e. lianas vs. trees), but also to leaf habit (i.e. deciduous vs. evergreen; Eamus 1999; Givnish 2002; Fu et al. 2012). For example, deciduous angiosperms exhibit higher SLA, leaf nitrogen (N) and phosphorus (P) concentrations (Eamus 1999; Bai et al. 2015), as well as a higher maximum photosynthetic rate compared to evergreen angiosperms (Givnish 2002). In addition, deciduous angiosperms exhibit significantly higher stem hydraulic conductivity than evergreen angiosperms (Zhang et al. 2013) and deciduous juvenile trees show larger vessels and higher SLA than their evergreen counterparts in a subtropical montane forest in southwestern China (Qi et al. 2020). Moreover, within a subalpine temperate forest, evergreen trees demonstrate traits that align with the slower end of the plant trait spectrum, sensu Wright et al. (2004). Conversely, deciduous lianas exhibit traits that are representative of the faster end of the spectrum. This
suggests that the combination of wider vessels and higher SLA associated with the deciduous habit can effectively enhance the growth advantages of lianas (Zhang et al. 2021). Thus, trait patterns across lianas and trees may be related to growth form, leaf habit, or both. However, we still lack a comprehensive understanding of how much variation in stem and leaf traits between lianas and trees is explained by growth form, leaf habit, and their interaction.

In this study, we measured 13 traits associated with stem xylem hydraulics and leaf morphology and nutrients for 11 liana and 22 tree species with different leaf habits, co-occurring in a subtropical evergreen montane forest in southwestern China. Our investigations were undertaken in Ailao Mountains in Yunnan Province, where the forest has also been described as a subtropical cloud forest due to abundant moisture and persistent cloud cover (Zhang et al. 2023). A previous study has shown that lianas are relatively abundant in this region (Bai et al. 2022), allowing us to compare functional traits and ecological adaptation strategies between lianas and trees. We aimed to answer the following questions: (i) How do subtropical montane lianas and trees vary in stem and leaf traits? (ii) How much trait variation can be explained by growth form (lianas vs. trees), leaf habit (evergreen vs. deciduous), and their interaction? (iii) How do stem xylem traits and leaf traits associate across subtropical lianas and trees? Given that the adaptive significance of trait relationships can result in trait similarity among closely related species (Ackerly and Donoghue 1998), we evaluated stem-leaf trait relationships using phylogenetically independent contrasts.
MATERIALS AND METHODS

Study site

This study was conducted in a 20-ha forest dynamics plot (500 × 400 m), which was established according to the protocols of the Forest Global Earth Observatory (Davies et al. 2021) in 2014 in Ailaoshan National Nature Reserve, Yunnan Province, southwestern China (101°0'40" – 101°0'56" E, 24°31'54" – 24°32'11" N; 2472 – 2628 m a.s.l.; Wen et al. 2018). Mean annual precipitation is 1778 mm (2002 – 2011), with 86% of precipitation concentrated in the rainy season (from May to October). The mean annual temperature is 11.3 °C, with a mean temperature in the coldest month (January) being 5.7 °C and 15.6 °C in the warmest month (July). The mean annual lowest temperature is -3.7 °C. There are ~35 days with frost events annually. The soil type of the study site is yellow-brown soil, with organic matter content, total N, P, and potassium (K) concentrations of 170.4, 5.6, 0.97 and 9.46 g kg⁻¹, plant-available N, P, and K concentrations of 51.17, 11.10, and 185.39 mg kg⁻¹, respectively, and pH of 4.24 at a 20 cm depth.

Selection and sampling of liana and tree species

The subtropical montane forest is dominated by evergreen trees (Supplementary Table S1; Wu 1980; Wen et al. 2018). Based on the 20-ha plot census data, the abundance of evergreen trees is 88.78% of the total individuals’ stems of lianas and trees pooled. Deciduous lianas have the second-highest individual stem abundance (4.17%). Although deciduous tree species constitute 17.69% of the species diversity, they have the lowest individual stem abundance (3.44%).
In the present study, we chose plant species based on their abundance ranking in a descending order, while taking leaf habit (evergreen vs. deciduous) into consideration (Wen et al. 2018; Bai et al. 2022). We selected 11 most abundant liana species (seven deciduous and four evergreen) and most abundant 22 tree species (10 deciduous and 12 evergreen) from the 20-ha plot for the present study (Table 1). In total, these 33 species selected represent 72.55% of the total stems of all lianas and trees with diameter at breast height ≥ 1 cm in this subtropical montane forest (Supplementary Table S1). Because some lianas and trees are deciduous, all species were sampled during the rainy season (July-September during 2017-2019). Sun-exposed leaves and branches within 5 m of ground level were sampled from three to five randomly selected individuals from the open canopy using an extendable pole-pruner. For each individual, we determined stem and leaf traits.

**Trait measurements**

In total, 13 leaf and stem traits were measured for each species (Supplementary Table S2), and these traits are important indicators for ecological strategies (Wright et al. 2004; Poorter et al. 2008; Chave et al. 2009).

Three to five leaf samples were collected for each individual and measured for leaf area using an HP Scanjet G3110 scanner and the ImageJ software (https://imagej.en.softonic.com/). Fresh leaf mass was recorded and then leaf samples were oven-dried at 70 °C for 48 h for dry mass. Specific leaf area (SLA; cm² g⁻¹) was calculated as leaf area over leaf dry mass. Leaf dry-matter content (LDMC; g g⁻¹) was leaf dry-matter per unit leaf fresh mass. Five to seven leaf tissue cross-section images were taken for each species using a Binocular Biological Microscope (Leica DM2500, Wetzlar, Germany). Leaf thickness (LT; μm) was determined from these pictures using the ImageJ. Leaf density (LD;
kg m$^{-3}$) was calculated as $1/(LT \times SLA)$. Leaf vein density is an important determinant of water transport and biomechanical support (Sack et al. 2014). Three to five leaf sections from sampled leaves were immersed in a 5% NaOH solution until the veins became clear. Images of leaf veins were then taken using the Binocular Biological Microscope and leaf vein length from each image was determined using the ImageJ. Leaf vein density ($D_{\text{vein}}$; mm mm$^{-2}$) was calculated as the total vein length per unit leaf area.

Leaf samples were oven-dried at 70 °C for 48 h, separately ground to a fine powder with a crusher, and then passed through a 60-mesh sieve. The N concentration (mg g$^{-1}$) was measured by a Dumas-type combustion C-N elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Hanau, Germany). Phosphorus (mg g$^{-1}$) and K (mg g$^{-1}$) were measured with an inductively coupled plasma atomic-emission spectrometer (iCAP 7400, Thermo Fisher Scientific, Bremen, Germany), after leaf samples were digested with concentrated HNO$_3$-HClO$_4$, and then dissolved in HCl.

Three to five stems ~1-m-long and 1–2 cm wide from lianas and trees were cut off in the late afternoon. Each stem segment was from a different individual. All the stem samples were immediately re-cut to ~20 cm in length and sealed in plastic bags with moist paper towels and transported to the laboratory for wood anatomy analyses. Stem sapwood density was determined from a stem segment re-cut ~5 cm in length. The volume of fresh sapwood was measured immediately using the water displacement method. The sapwood sample was then oven-dried at 70 °C for 72 h, and dry mass was determined. Sapwood density ($WD$, g cm$^{-3}$) was calculated as sapwood dry mass divided by fresh wood volume. An additional stem segment ~2-cm-long was used to measure vessel density and diameter. Ten images per individual were taken at 100× – 500× magnification using a light microscope (Smartzoom 5, Carl Zeiss, Jena, Germany), and vessel numbers, major and minor axes were determined.
using the ImageJ. Vessel density (VD; no mm\(^{-2}\)) was calculated as vessel number per area. Because most of the vessels are elliptical, each vessel diameter was calculated followed Lewis (1992) as:

\[
D_i = \left[32(ab)^3/(a^2 + b^2)^{3/2}\right]^{1/4}
\]

where \(a\) and \(b\) represent the radius of major and minor axes of each vessel. \(D_V\) (\(\mu\)m) was the hydraulically-weighted vessel diameter and was calculated as (Zhang et al. 2023):

\[
D_V = \left[\frac{1}{n} \sum_{i=1}^{n} D_i^4\right]^{1/4}
\]

The theoretical hydraulic conductivity \((K_t; \text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1})\) was determined as:

\[
K_t = \left(\pi \rho / 128 \eta A\right) \left[\sum_{i=1}^{n} D_i^4\right]
\]

where \(\pi\) equals 3.14, \(\rho\) is the density of water at 25 °C (997.05 kg m\(^{-3}\)), \(\eta\) is the viscosity of water at 25 °C (0.89 \times 10^{-9} \text{MPa s}) and \(A\) is the area of images (Tyree and Ewers 1991).

**Statistical analyses**

Data on functional traits were averaged by species and log\(_{10}\)-transformed to an approximate normal distribution. All analyses were performed in R-4.3.0 version (R Core Team 2023). An independent-samples \(t\)-test was used to compare the differences in functional traits between 11 liana species and 22 tree species, using the `stats` package (Oksanen et al. 2013). The corrected \(p\)-values were calculated using the method of Benjamini and Hochberg (1995). Pearson’s correlation analysis was used to evaluate the relationships between traits using the `Hmisc` package. We also carried out a standardized major axis (SMA) regression with
SMATR software (Warton et al. 2006) and compared the differences in slopes, intercepts and shifts along a common slope between lianas and trees to further evaluate whether the two growth forms exhibited different relationships. We evaluated the vessel dimorphism according to Carlquist (1985) and Meunier et al. (2020). Briefly, if the skewness of the vessel diameter distribution is > 0.5 or < -0.5, then the vessel diameter distribution pattern would be dimorphic, and when skewness is between -0.5 and 0.5, then the vessel diameter distribution pattern is normal.

We presented phylogenetic analyses of the chloroplast DNA marker matK sequences obtained from GenBank, representing 33 species of 19 families. The consensus sequences were automatically aligned in Mauve 2.4.0 (Darling et al. 2004) and then manually adjusted. Maximum likelihood (ML) analysis was carried out using IQ-TREE v. 2.1.1 program (Minh et al. 2020). The best-fit DNA substitution models were chosen as “TVM+F+R3”. One thousand bootstrap replicates were used to obtain node support value. To quantify the degree to which phylogenetic relatedness predicts the similarity in functional traits among tree and liana species, we calculated phylogenetic signals for all stem and leaf traits by calculating Blomberg’s $K$-values (Garland et al. 1992; Blomberg et al. 2003). This index assumes the classic Brownian motion (BM) evolutionary model, with values varying from zero to higher than one. $K$-values from zero to one indicate that the phylogenetic signal is weaker than expected from the BM model of character evolution (low levels of phylogenetic character conservation). $K$-values greater than one indicate a strong phylogenetic signal (Molina-Venegas and Rodríguez 2017). The significance of phylogenetic signals was determined by shuffling species’ character values (999 times) across the tips of the ML tree with relative branch lengths reconstructed (Supplementary Fig. S1) and comparing the resulting $K$ to those computed from the observed character data (Eichenberg et al. 2015). We also used phylogenetic independent contrasts (PICs) to examine the influence of species evolutionary
history on the correlations between stem and leaf traits (Felsenstein 1985). Pearson’s
correlation analysis was used to test for the associations among PICs between stem and leaf
traits for lianas and trees. The PICs analysis was performed using the phytools package
(Revell 2012).

A principal component analysis (PCA) was performed to evaluate how these traits were
associated with one another, using the vegan package (Oksanen 2013). The factor loadings
and the scores of the first two principal components (PC1 and PC2) in the PCA were
calculated to show the multivariate spatial associations of traits and species. A permutational
analysis of variance (PERMANOVA) was carried out using the adonis function (Anderson
2001) to test how growth form and leaf habit affect trait variation (Euclidean distances,
number of permuted data sets = 1,000,000). Since no significant interaction between growth
form and leaf habit was found, the additive model was retained and Type II sums of squares
were used in the PERMANOVA analysis.

RESULTS

Differences in stem and leaf traits between lianas and trees

Subtropical montane lianas had significantly higher values for vessel diameter ($D_V$),
theoretical hydraulic conductivity ($K_t$), specific leaf area (SLA), and concentrations of N and
P, but lower leaf dry-matter content (LDMC) and N/P ratio than co-occurring trees (adjusted
$P < 0.05$; Fig. 1; Supplementary Table S3). Meanwhile, we found no significant differences
in vessel density (VD), sapwood density (WD), leaf density (LD), leaf thickness (LT), leaf
vein density ($D_{vein}$) and leaf K concentration between lianas and trees (adjusted $P > 0.05$; Fig.
1; Supplementary Table S3). Among species studied, all lianas exhibited a bimodal vessel
distribution pattern, while most trees (except four species) showed a normal vessel
distribution pattern (Fig. 2; Supplementary Figs S2-S5).

**Associations between stem and leaf traits across lianas and trees**

For stem xylem traits, $K_t$ was positively related to $D_v$ for lianas and trees ($r = 0.81$, $P < 0.01$
and $r = 0.69$, $P <0.01$, respectively), with a common slope but different intercepts, and
negatively to VD ($r = -0.66$, $P < 0.01$ and $r = -0.54$, $P < 0.05$), with a more significantly
negative slope for lianas than for trees (Table 2; Fig. 3).

Among leaf traits, lianas and trees generally showed similar relationships (Table 2; Fig. 4). For example, lianas and trees showed similar negative relationships between SLA and
LDMC ($r = -0.67$, $P <0.05$ and $r = -0.43$, $P <0.05$), between SLA and LD ($r = -0.77$, $P$
<0.01 and $r = -0.61$, $P <0.01$), between LT and LD ($r = -0.66$, $P <0.05$ and $r = -0.46$, $P$
<0.05), with a common slope, and similar positive relationships between LDMC and LD ($r =
0.87$, $P <0.01$ and $r = 0.70$, $P <0.01$; Fig. 4).

For patterns between stem and leaf traits, however, contrasting relationships were found
between lianas and trees. Many significant stem-leaf trait relationships (i.e. $D_v$, $D_{v\text{ein}}$, $D_v$-LT,
VD-LT, WD-LD, VD-N, WD-N, VD-K, and WD-P) were found only for trees (Table 2; Figs 5 and 6). By contrast, most relationships between stem and leaf traits across lianas were
decoupled, with few stem-leaf traits being significantly correlated (e.g. $K-D_v$ and LDMC-$K_t$).

Generally, the PIC analysis showed similar patterns to the Pearson’s correlation analysis
for both lianas and trees (Supplementary Tables S4 and S5). There were no significant
phylogenetic signals for 11 stem and leaf traits of lianas and trees, except for $D_v$ and $K_t$ of
lianas (Blomberg’s $K$ values $> 1$ and $P$ values $< 0.05$) (Supplementary Table S6).
Results of the PCA based on 13 traits for 33 species showed that PC 1 and PC 2 explained 44.0% and 17.7% of the total variation, respectively (Fig. 7). Functional traits related to high hydraulic efficiency or fast growth (e.g. $K_t$, $D_v$, $D_{vein}$, SLA, N, and P) were loaded onto the positive side, while traits related to high hydraulic safety (e.g. VD and WD) were loaded onto the negative side of PC 1. Traits associated with leaf construction cost (LD, LDMC, and LT) were loaded onto the axis of PC 2. Overall, lianas and trees were separated with partial overlap, while evergreen and deciduous species showed a considerable overlap. Furthermore, deciduous lianas tended to be more related to $K_t$, $D_v$, SLA, N, and P, and were clearly separated from evergreen trees in the multivariate trait space. The PERMANOVA analysis was conducted to assess the impact of growth form (lianas vs. trees) on trait variation (Table 3). The results indicated that growth form accounted for approximately 48.7% of the observed trait variation. Additionally, leaf habit was found to explain only about 3.8% of the total trait variation. Furthermore, no significant interaction was observed between growth form and leaf habit in relation to trait variation.

**DISCUSSION**

**Divergences in traits between subtropical montane lianas and trees**

Our findings indicate that subtropical montane lianas exhibit an ecological strategy characterized by wider xylem vessels and higher potential hydraulic conductivity compared to co-existing trees. This ecological strategy is consistent with patterns observed in previous studies conducted in tropical forests (e.g. Zhu and Cao 2009; Wyka et al. 2013; Campanello...
et al. 2016). For instance, average stem hydraulic efficiency in subtropical montane lianas was much higher than that of co-existing trees due to wider vessels of the lianas, with a ~14-fold difference in potential hydraulic conductivity calculated by vessel diameter and density. Similar to our results, previous studies showed ~11 to 24-fold difference in stem potential hydraulic conductivity between lianas and trees in tropical and temperate rainforests (Gartner et al. 1990; Jiménez-Castillo and Lusk 2013). These findings indicate that lianas consistently possess a potential stem xylem hydraulic advantage over coexisting trees in diverse ecosystems, where droughts or frost may occur, but rapid growth is possible when water is abundant.

Interestingly, we found that subtropical montane lianas had a dimorphic vessel pattern, with a few wide and many narrow vessels in the xylem (Fig. 2; Supplementary Figs S2-S5), consistent with previous studies (Hacke et al. 2017; Olson, 2020; Zhang et al. 2023). On the one hand, few wide vessels contribute to much more efficient hydraulic transport for lianas during the frost-free season (Jiménez-Castillo and Lusk 2013; Zhang et al. 2023). On the other hand, it is likely that lianas will suffer higher percentage of loss of hydraulic conductivity during frost season because vessel diameter strongly determines the xylem vulnerability to freeze-thaw-induced embolism (Feild and Brodribb 2001; Jiménez-Castillo and Lusk 2013). For instance, lianas on average suffered higher levels of freeze–thaw embolism than trees (29.9 vs. 12.8% loss of hydraulic conductivity); however, partially embolized lianas still possess greater water transport capacity than trees in an evergreen temperate rainforest located on the south-eastern slopes of the Cordillera de Nahuelbuta (750 m a.s.l.) in south-central Chile (Jiménez-Castillo and Lusk 2013). These results indicate that dimorphic vessel structure in lianas might contribute to their distribution in the present subtropical montane forest with frost events. We call for more evidence in support of linking
liana vessel dimorphism to freeze thaw-induced embolism during frost events in the future (Jiménez-Castillo and Lusk 2013; Zhang et al. 2023).

Subtropical montane lianas also showed a syndrome of leaf traits associated with rapid resource acquisition, including higher SLA, leaf N and P concentrations than trees. Higher SLA and N can increase light interception and absorption and hence higher maximum photosynthetic rate and growth rate (Wright et al. 2004). Similar to our results, previous studies found similar patterns for SLA, leaf N and P between tropical lianas and trees (Reich et al. 1992; Zhu and Cao 2010; Werden et al. 2018). The LDMC of subtropical montane lianas was found to be significantly lower compared to that of trees. This finding aligns with a similar observation made in an Australian lowland rainforest (Buckton et al. 2019). The findings indicate that lianas exhibit an ecological strategy that is characterized by rapid resource acquisition and minimal investment in construction costs (Zhu and Cao 2010; Collins et al. 2016). In addition, leaf N/P ratio can be used as an indicator of nutrient limitation (Aerts and Chapin 1999), which was divided into: N/P < 14 (N limitation), N/P > 16 (P limitation), 14 ≤ N/P ≤ 16 (common limitation of N and P or both not) (Koerselman and Meuleman 1996; Zhang et al. 2022). In the present study, N/P ratio was 11.08 and 15.28 for lianas and trees in this subtropical montane forest (Supplementary Table S3), probably indicating N limitation of growth for lianas, but not for trees. Soils in subtropics or at higher elevation are generally N limited (Yin et al. 2022), and low N/P ratio in lianas may indicate a luxury uptake of P by lianas or proportionally greater allocation to N-rich leaves in lianas, as indicated by higher N and P concentrations in lianas, than to low-N leaves of trees (Fig. 1). Nevertheless, Zhu and Cao (2009) reported that both lianas and trees are limited by N and P, as indicated by high N to P ratio (N/P being 18.22 and 19.84 for lianas and trees, respectively) in tropical rainforest in the same region of the present study, where soils are mainly limited by P rather than N.
Differences in associations of stem-leaf traits for lianas and trees

In this study, we found that the potential stem hydraulic conductivity was significantly related to vessel diameter and density for lianas and trees. This finding indicates that xylem vessel characteristics are closely associated with the potential hydraulic conductivity across woody species (Gartner et al. 1990; Zhu and Cao 2009; Fan et al. 2012). However, the relationships between $K_{t}$-VD and $D_{v}$-VD had significantly more negative slopes for lianas than for trees (Fig. 3), suggesting that a similar decrease in vessel density can lead to a higher increase in water-transport efficiency in lianas. In addition, there were significant correlations between stem xylem traits associated with hydraulic safety (e.g. VD and WD) and some leaf traits for trees, suggesting strong linkages between stem and leaf traits (Santiago et al. 2004; Zhu and Cao 2009; Nolf et al. 2015; Mello et al. 2020). However, we found that VD and WD were not related to any leaf traits for lianas (Supplementary Table S4). Consistently, hydraulic safety (the xylem water potential at 50% loss of conductivity) shows no correlation with leaf morphological and photosynthetic traits (van der Sande et al. 2019). The lack of correlations for lianas is in part caused by the small range in relatively low hydraulic safety values (van der Sande et al. 2019).

The trait-trait relationships with and without incorporation of phylogeny were mostly consistent, suggesting an evolutionarily independent trait-based correlation (Supplementary Tables S4 and S5). In addition, we found that there were relatively weak phylogenetic signals of most traits in either lianas or trees as indicated by Blomberg’s $K$-values < 1 (Supplementary Table S6), which may be because these liana or tree species are from diverse families, with minimal common ancestral effect (Ackerly et al. 2000). However, vessel diameter and theoretical hydraulic conductivity for lianas showed strong phylogenetic signals.
(Supplementary Table S6), indicating phylogenetic conservatism of vessel traits (Chave et al. 2006; Fortunel et al. 2014).

The effect of leaf habit on variation in traits between lianas and trees

Our results showed that trait variation between lianas and trees was minimally explained by leaf habit, in contrast to some studies in which trait variation of trees is related to differences in leaf habit (Eamus 1999; Qi et al. 2020). When taking leaf habit into account, deciduous tree species generally employ leaf traits related to fast resource acquisition (Eamus 1999; Bai et al. 2015; Qi et al. 2020), so the deciduous tree species overlap with lianas to a large extent in the trait space (Fig. 7). In the present study, ~42% liana species (10 of 24) exhibit deciduous habit based on an investigation in a 20-ha subtropical montane forest dynamics plot (Bai et al. 2022). It indicates that deciduous leaf habit may be an important adaptive strategy for lianas in subtropical montane forests (Jiménez-Castillo and Lusk 2013). Deciduous lianas were more related to high stem xylem hydraulic efficiency and rapid leaf resource acquisition (higher $K_t$, $D_v$, SLA, N, P, and K). These results suggest that more efficient stem xylem and more productive leaves might be related to both deciduous habit and liana growth form (Zhang et al. 2021).

CONCLUSIONS

We found a strong divergence in stem hydraulic traits and leaf morphological and nutrient traits between lianas and trees in a subtropical montane forest. The differentiation between the growth forms drives this pattern, with lianas employing high potential hydraulic efficiency, SLA, leaf N and P concentrations, and trees showing high vessel density and
sapwood density. We also found a larger variation of vessel diameters in lianas than in trees. The dimorphic vessels (very wide and very narrow vessels together) of lianas theoretically should allow them to transport water efficiently but meanwhile maintain high resistance to embolism, which might contribute to their occurrence in the present site, and explain the decoupled relationship between hydraulic efficiency and safety for lianas observed by van der Sande et al. (2019). In addition, contrasting relationships of stem hydraulic traits and leaf traits were also found between subtropical lianas and trees. Given the striking differences in stem and leaf traits, and in stem-leaf trait relationships between lianas and trees, further studies are needed to investigate the mechanisms underlying the strong divergences in functional traits between these two growth forms.
**Funding**

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**Acknowledgements**

Thanks to the Institutional Center for Shared Technologies and Facilities of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for analyzing the foliar nutrient concentrations and permit to use microscope. We thank the National Forest Ecosystem Research Station at Ailaoshan for providing climate data and logistic support. We also thank Yu Song and Shang-Wen Xia for assistance with phylogenetic comparative analysis. We are grateful to two anonymous reviewers for their comments and suggestions which substantially improve the quality of our manuscript.

**Conflict of interest statement.** The authors declare that they have no conflict of interest.
REFERENCES


Figure legends

**Figure 1:** Differences in (a) vessel diameter ($D_V$), (b) theoretical hydraulic conductivity ($K_t$), (c) vessel density (VD), (d) sapwood density (WD), (e) specific leaf area (SLA), (f) leaf dry-mass content (LDMC), (g) leaf density (LD), (h) leaf thickness (LT), (i) vein density ($D_{vein}$), (j) leaf nitrogen concentration (N), (k) leaf phosphorus concentration (P), (l) leaf potassium concentration (K), (m) N/P ratio between lianas and trees in a subtropical montane forest. The adjusted $P$ values were given based on the $t$-test and the method of Benjamini and Hochberg (1995).

**Figure 2:** Frequency distribution of xylem vessel diameter in (a) a liana species (*Rosa longicuspis* Bertol.) and (b) a tree species (*Camellia forrestii* (Diels) Coh. St.), as an example.

**Figure 3:** Log-log bivariate relationships between (a) theoretical hydraulic conductivity ($K_t$) and vessel diameter ($D_V$), (b) $K_t$ and vessel density (VD), and (c) $D_V$ and VD across 11 liana species (solid line) and 22 tree species (long-dashed line). Open circles, filled circles, open diamonds and filled diamonds indicate deciduous lianas, evergreen lianas, deciduous trees, and evergreen trees, respectively. Trend lines were given when relationships were significant.
See Table 2 for the standardized major axis regression slope, intercept and shift along the common slope for lianas and trees. * $P < 0.05$; ** $P < 0.01$.

**Figure 4:** Log-log bivariate relationships between (a) specific leaf area (SLA) and leaf dry-mass content (LDMC), (b) SLA and leaf density (LD), (c) LDMC and LD, and (d) leaf thickness (LT) and LD across 11 liana species (solid line) and 22 tree species (long-dashed line). Open circles, filled circles, open diamonds and filled diamonds indicate deciduous lianas, evergreen lianas, deciduous trees, and evergreen trees, respectively. Trend lines were given when relationships were significant. See Table 2 for the standardized major axis regression slope, intercept and shift along the common slope for lianas and trees. * $P < 0.05$; ** $P < 0.01$.

**Figure 5:** Log-log bivariate relationships between (a) vein density ($D_{\text{vein}}$) and vessel diameter ($D_v$), (b) leaf thickness (LT) and $D_v$, (c) $K$ and $D_v$, and (d) leaf dry-mass content (LDMC) and theoretical hydraulic conductivity ($K_t$) across 11 liana species (solid line) and 22 tree species (long-dashed line). Open circles, filled circles, open diamonds and filled diamonds indicate deciduous lianas, evergreen lianas, deciduous trees, and evergreen trees, respectively. Trend lines were given when relationships were significant. See Table 2 for the
standardized major axis regression slope, intercept and shift along the common slope for lianas and trees. *\( P < 0.05 \).

**Figure 6:** Log-log bivariate relationships between (a) leaf thickness (LT) and vessel density (VD), (b) N and VD, (c) K and VD, (d) leaf density (LD) and sapwood density (WD), (e) N and WD, and (f) P and WD across 11 liana species and 22 tree species. Open circles, filled circles, open diamonds and filled diamonds indicate deciduous lianas, evergreen lianas, deciduous trees, and evergreen trees, respectively. Relationships between traits were only significant across trees, as indicated by long-dashed lines. See Table 2 for the standardized major axis regression slope, intercept and shift along the common slope for lianas and trees. *\( P < 0.05 \); **\( P < 0.01 \).

**Figure 7:** Results of the first and second factor loadings from a principal component analysis for the 13 stem and leaf traits and the loadings of 33 species (seven deciduous liana, four evergreen liana, 10 deciduous tree, and 12 evergreen tree species). Data were log_{10}-transformed before analysis. See the legend of Fig. 1 and text for trait abbreviations.
Table 1: Information on 11 liana and 22 tree species co-existing in a 20-ha subtropical montane forest dynamics plot, southwestern China.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Growth form</th>
<th>Leaf habit</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rosa longicuspis</em> Bertol.</td>
<td>Rosaceae</td>
<td>Liana</td>
<td>Evergreen</td>
<td>1081</td>
</tr>
<tr>
<td><em>Holboellia latifolia</em> Wall.</td>
<td>Lardizabalaceae</td>
<td>Liana</td>
<td>Evergreen</td>
<td>305</td>
</tr>
<tr>
<td><em>Kadsura heteroclita</em> (Roxb.) Craib</td>
<td>Schisandraceae</td>
<td>Liana</td>
<td>Evergreen</td>
<td>114</td>
</tr>
<tr>
<td><em>Callerya dielsiana</em> (Harms) P. K. Loc ex Z. Wei &amp; Pedley</td>
<td>Leguminosae</td>
<td>Liana</td>
<td>Evergreen</td>
<td>103</td>
</tr>
<tr>
<td><em>Rubus paniculatus</em> Smith</td>
<td>Rosaceae</td>
<td>Liana</td>
<td>Deciduous</td>
<td>423</td>
</tr>
<tr>
<td><em>Celastrus hookeri</em> Prain</td>
<td>Celastraceae</td>
<td>Liana</td>
<td>Deciduous</td>
<td>364</td>
</tr>
<tr>
<td><em>Actinidia callosal</em> Lindl.</td>
<td>Actinidiaceae</td>
<td>Liana</td>
<td>Deciduous</td>
<td>358</td>
</tr>
<tr>
<td><em>Parthenocissus semicordata</em> (Wall.) Planch.</td>
<td>Vitaceae</td>
<td>Liana</td>
<td>Deciduous</td>
<td>296</td>
</tr>
<tr>
<td><em>Celastrus hirsutus</em> Comber</td>
<td>Celastraceae</td>
<td>Liana</td>
<td>Deciduous</td>
<td>265</td>
</tr>
<tr>
<td>Species</td>
<td>Family</td>
<td>Type</td>
<td>Habit</td>
<td>Common Name</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>--------------</td>
<td>------------</td>
<td>---------</td>
<td>-------------</td>
</tr>
<tr>
<td>Sabia yunnanensis Franch.</td>
<td>Sabiaceae</td>
<td>Liana</td>
<td>Deciduo</td>
<td></td>
</tr>
<tr>
<td>Actinidia glaucocallosa C. Y. Wu</td>
<td>Actinidiaceae</td>
<td>Liana</td>
<td>Deciduo</td>
<td></td>
</tr>
<tr>
<td>Camellia forrestii (Diels) Coh. St.</td>
<td>Theaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Vaccinium duclouxii (Levl.) Hand.-Mazz.</td>
<td>Ericaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Symplocos ramosissima Wall. ex G. Don</td>
<td>Symplocaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Lithocarpus hancei (Bentham) Rehd.</td>
<td>Fagaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Eriobotrya bengalensis (Roxb.) Hook. f.</td>
<td>Rosaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Castanopsis wattii (King ex J. D. Hooker) A. Camus</td>
<td>Fagaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Symplocos sumuntia Buch.-Ham. ex D. Don</td>
<td>Symplocaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Symplocos poilanei Guill.</td>
<td>Symplocaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Lithocarpus xylocarpus (Kurz) Markgraf</td>
<td>Fagaceae</td>
<td>Tree</td>
<td>Evergre</td>
<td></td>
</tr>
<tr>
<td>Plant Name</td>
<td>Family</td>
<td>Life Form</td>
<td>Life Form</td>
<td>Number</td>
</tr>
<tr>
<td>------------------------------------------------</td>
<td>-----------------</td>
<td>-----------</td>
<td>-----------</td>
<td>--------</td>
</tr>
<tr>
<td><em>Eurya obliquifolia</em> Hemsl.</td>
<td>Pentaphylaciae</td>
<td>Tree</td>
<td>Evergreen</td>
<td>1446</td>
</tr>
<tr>
<td><em>Cinnamomum chago</em> B. S. Sun &amp; H. L. Zhao</td>
<td>Lauraceae</td>
<td>Tree</td>
<td>Evergreen</td>
<td>1236</td>
</tr>
<tr>
<td><em>Stewartia pteropetiolata</em> W. C. Cheng</td>
<td>Theaceae</td>
<td>Tree</td>
<td>Evergreen</td>
<td>1118</td>
</tr>
<tr>
<td><em>Styrax perkinsiae</em> Rehd.</td>
<td>Styracaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>322</td>
</tr>
<tr>
<td><em>Clethra delavayi</em> Franch.</td>
<td>Clethraceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>233</td>
</tr>
<tr>
<td><em>Populus rotundifolia</em> Griff.</td>
<td>Salicaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>197</td>
</tr>
<tr>
<td><em>Acer campbellii</em> Hook. f. et Thoms. ex Hiern</td>
<td>Sapindaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>170</td>
</tr>
<tr>
<td><em>Meliosma kirkii</em> Hemsl. et Wils.</td>
<td>Sabiaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>102</td>
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<tr>
<td><em>Gamblea ciliata</em> C. B. Clarke</td>
<td>Araliaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>73</td>
</tr>
<tr>
<td><em>Sorbus rhamnoides</em> (Dcne.) Rehd.</td>
<td>Rosaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>13</td>
</tr>
<tr>
<td><em>Prunus cerasoides</em> Buch.-Ham. ex D. Don</td>
<td>Rosaceae</td>
<td>Tree</td>
<td>Deciduous</td>
<td>12</td>
</tr>
</tbody>
</table>
Species were listed by descending abundance within the same leaf habit of the same growth form. Species names are standardized by the Flora of China (http://www.iplant.cn/foc/).
Table 2: Tests of the SMA regression slopes, intercepts, and shifts along the common slopes for log-log bivariate relationships across 11 liana and 22 tree species. See the legends of Fig. 1 and text for trait abbreviations. Significant differences (P < 0.05) are indicated in bold.

<table>
<thead>
<tr>
<th></th>
<th>$r^2$</th>
<th>P</th>
<th>Slope/common slope</th>
<th>Intercept</th>
<th>Shifts along the common slope</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Liana</td>
<td>Tree</td>
<td>Liana</td>
<td>Tree</td>
<td>Liana</td>
</tr>
<tr>
<td>Log $K_t$ ~ Log $D_v$</td>
<td>0.65</td>
<td>0.48</td>
<td>0.003</td>
<td>0.000</td>
<td>1.44</td>
</tr>
<tr>
<td>Log $K_t$ ~ Log VD</td>
<td>0.44</td>
<td>0.29</td>
<td>0.027</td>
<td>0.009</td>
<td>-0.89</td>
</tr>
<tr>
<td>Log $D_v$ ~ Log VD</td>
<td>0.80</td>
<td>0.86</td>
<td>0.000</td>
<td>0.000</td>
<td>-0.59</td>
</tr>
<tr>
<td>Log SLA ~ Log LDMC</td>
<td>0.44</td>
<td>0.19</td>
<td>0.025</td>
<td>0.045</td>
<td>-1.53</td>
</tr>
<tr>
<td>Log SLA ~ Log LD</td>
<td>0.59</td>
<td>0.37</td>
<td>0.006</td>
<td>0.002</td>
<td>-0.88</td>
</tr>
<tr>
<td>Log LDMC ~ Log LD</td>
<td>0.76</td>
<td>0.49</td>
<td>0.001</td>
<td>0.000</td>
<td>0.59</td>
</tr>
<tr>
<td>Log LT ~ Log LD</td>
<td>0.43</td>
<td>0.21</td>
<td>0.028</td>
<td>0.031</td>
<td>-0.78</td>
</tr>
<tr>
<td>Log P ~ Log N</td>
<td>0.45</td>
<td>0.29</td>
<td>0.023</td>
<td>0.009</td>
<td>1.24</td>
</tr>
<tr>
<td>Log $D_{vein}$ ~ Log $D_v$</td>
<td>0.24</td>
<td>0.20</td>
<td>0.127</td>
<td>0.036</td>
<td>-0.75</td>
</tr>
<tr>
<td></td>
<td>0.00</td>
<td>0.24</td>
<td>0.913</td>
<td><strong>0.021</strong></td>
<td>-0.94</td>
</tr>
<tr>
<td>------------------</td>
<td>------</td>
<td>------</td>
<td>-------</td>
<td>-----------</td>
<td>-------</td>
</tr>
<tr>
<td>Log LT ~ Log Dv</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log K ~ Log Dv</td>
<td>0.39</td>
<td>0.09</td>
<td><strong>0.039</strong></td>
<td>0.164</td>
<td>0.59</td>
</tr>
<tr>
<td>Log LDMC ~ Log Kt</td>
<td>0.37</td>
<td>0.05</td>
<td><strong>0.049</strong></td>
<td>0.334</td>
<td>-0.44</td>
</tr>
<tr>
<td>Log LT ~ Log VD</td>
<td>0.01</td>
<td>0.26</td>
<td>0.818</td>
<td><strong>0.016</strong></td>
<td>0.34</td>
</tr>
<tr>
<td>Log N ~ Log VD</td>
<td>0.12</td>
<td>0.35</td>
<td>0.292</td>
<td><strong>0.004</strong></td>
<td>-0.28</td>
</tr>
<tr>
<td>Log K ~ Log VD</td>
<td>0.21</td>
<td>0.20</td>
<td>0.162</td>
<td><strong>0.039</strong></td>
<td>-0.42</td>
</tr>
<tr>
<td>Log LD ~ Log WD</td>
<td>0.15</td>
<td>0.25</td>
<td>0.246</td>
<td><strong>0.018</strong></td>
<td>2.78</td>
</tr>
<tr>
<td>Log N ~ Log WD</td>
<td>0.07</td>
<td>0.20</td>
<td>0.419</td>
<td><strong>0.036</strong></td>
<td>-1.86</td>
</tr>
<tr>
<td>Log P ~ Log WD</td>
<td>0.30</td>
<td>0.30</td>
<td>0.080</td>
<td><strong>0.008</strong></td>
<td>-1.33</td>
</tr>
</tbody>
</table>
Table 3: PERMANOVA on Euclidean distance of 13 functional traits for 33 species (seven deciduous and four evergreen liana species, and 10 deciduous and 12 evergreen tree species). The interaction was not significant. Species data were representative for the 13 traits.

<table>
<thead>
<tr>
<th>Source</th>
<th>Degree of freedom</th>
<th>Sum of square</th>
<th>Mean square</th>
<th>F</th>
<th>$r^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adonis (formula = species data ~ growth form + leaf habit, data = group data, permutations = 1,000,000, method = ‘euclidean’)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth form</td>
<td>1</td>
<td>55.926</td>
<td>55.926</td>
<td>30.507</td>
<td>0.487</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Leaf phenology</td>
<td>1</td>
<td>4.396</td>
<td>4.396</td>
<td>2.397</td>
<td>0.038</td>
<td>0.082</td>
</tr>
<tr>
<td>Residual</td>
<td>29</td>
<td>53.164</td>
<td>1.833</td>
<td></td>
<td>0.475</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32</td>
<td>114.946</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adonis (formula = species data ~ leaf habit + growth form, data = group data, permutations = 1,000,000, method = ‘euclidean’)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf phenology</td>
<td>1</td>
<td>7.290</td>
<td>7.290</td>
<td>4.004</td>
<td>0.063</td>
<td>0.021</td>
</tr>
<tr>
<td>Growth form</td>
<td>1</td>
<td>53.032</td>
<td>53.032</td>
<td>29.126</td>
<td>0.461</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>54.624</td>
<td>1.821</td>
<td></td>
<td>0.475</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32</td>
<td>114.946</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 1
Figure 2

(a) *Rosa longicuspis*

- \(n = 338\)
- \(\text{Mean} = 32.3 \, \mu m\)
- \(\text{CV} = 54\%\)
- \(\text{Skewness} = 1.05\)

(b) *Vaccinium duclouxii*

- \(n = 299\)
- \(\text{Mean} = 24.1 \, \mu m\)
- \(\text{CV} = 27\%\)
- \(\text{Skewness} = 0.09\)
Figure 3

(a) Log $K'$ vs. Log $D_Y$ (um)

Liana $r = 0.91^{**}$
Tree $r = 0.69^{**}$

(b) Log $K''$ vs. Log $VD$ (no mm$^2$)

Liana $r = 0.66^{**}$
Tree $r = 0.54^{**}$

(c) Log $D_Y$ (um) vs. Log $VD$ (no mm$^2$)

Liana $r = 0.90^{**}$
Tree $r = 0.93^{**}$
Figure 4

(a) Log SLA (cm\(^2\) g\(^{-1}\)) vs. Log LDMC (g g\(^{-1}\))
- Liana: \(r = -0.67^{**}\)
- Tree: \(r = -0.43^{*}\)

(b) Log SLA (cm\(^2\) g\(^{-1}\)) vs. Log LD (kg m\(^{-3}\))
- Liana: \(r = -0.77^{**}\)
- Tree: \(r = -0.61^{**}\)

(c) Log LDMC (g g\(^{-1}\)) vs. Log LD (kg m\(^{-3}\))
- Liana: \(r = 0.87^{**}\)
- Tree: \(r = 0.70^{**}\)

(d) Log LT (µm) vs. Log LD (kg m\(^{-3}\))
- Liana: \(r = -0.66^{**}\)
- Tree: \(r = -0.46^{*}\)
Figure 5

(a) Log $D_{vein}$ (mm mm$^{-2}$) vs. Log $D_V$ ($\mu$m)

(Tree $r = 0.50$ *)

(c) Log $K$ (mg g$^{-1}$) vs. Log $D_V$ ($\mu$m)

(Liana $r = 0.63$ *)

(b) Log LT ($\mu$m) vs. Log $D_V$ ($\mu$m)

(Tree $r = -0.49$ *)

(d) Log LDMC (g g$^{-1}$) vs. Log $K$ (kg m$^{-1}$ s$^{-1}$ MPa$^{-1}$)

(Liana $r = -0.61$ *)
Figure 6

(a) Log LT (μm) vs. Log VD (no mm⁻²)

(b) Log N (mg g⁻¹) vs. Log VD (no mm⁻²)

(c) Log K (mg g⁻¹) vs. Log VD (no mm⁻²)

(d) Log LD (kg m⁻³) vs. Log WD (g cm⁻³)

(e) Log N (mg g⁻¹) vs. Log WD (g cm⁻³)

(f) Log P (mg g⁻¹) vs. Log WD (g cm⁻³)

Tree $r = 0.51^*$

Tree $r = 0.50^*$

Tree $r = -0.59^{**}$

Tree $r = -0.45^*$

Tree $r = -0.44^*$

Tree $r = -0.55^{**}$