



# Spatial patterns of wood traits in China are controlled by phylogeny and the environment

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## ABSTRACT

**Aim** Wood properties are related to tree physiology and mechanical stability and are influenced by both phylogeny and the environment. However, it remains unclear to what extent geographical gradients in wood traits are shaped by either phylogeny or the environment. Here we aimed to disentangle the influences of phylogeny and the environment on spatial trends in wood traits.

**Location** China.

**Methods** We compiled a data set of 11 wood properties for 618 tree species from 98 sampling sites in China to assess their phylogenetic and spatial patterns, and to determine how many of the spatial patterns in wood properties are attributable to the environment after correction for phylogenetic influences.

**Result** All wood traits examined exhibited significant phylogenetic signal. The widest divergence in wood traits was observed between gymnosperms and angiosperms, Rosids and Asterids, Magnoliids and Eudicots, and in Lamiales. For most wood traits, the majority of trait variation was observed at genus and species levels. The mechanical properties of wood showed correlated evolution with wood density. Most of the mechanical properties of wood exhibited significant latitudinal variation but limited or no altitudinal variation, and were positively correlated with mean annual precipitation based on both Pearson's correlation analysis and the phylogenetic comparative method. Correlations at family level between mean annual temperature and wood density, compression strength, cross-section hardness, modulus of elasticity and volumetric shrinkage coefficient became significant after correction for phylogenetic influences.

**Main conclusions** Phylogeny interacted with the environment in shaping the spatial patterns of wood traits of trees across China because most wood properties showed strong phylogenetic conservatism and thus affected environmental tolerances and distributions of tree species. Mean annual precipitation was a key environmental factor explaining the spatial patterns of wood traits. Our study provides valuable insights into the geographical patterns in productivity, distribution and ecological strategy of trees linking to wood traits.

## Keywords

China, climate, geographical variation, phylogeny, phylogenetically comparative method, trees, trait evolution, wood properties.

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## INTRODUCTION

Knowledge of the spatial patterns of wood traits is essential for understanding possible changes in ecosystem functions under different global change scenarios, as wood traits are highly rel-

evant to ecosystem biogeochemistry, tree growth and mortality and plant life-history strategy (van Gelder *et al.*, 2006; Chao *et al.*, 2008; Poorter *et al.*, 2010). For example, previous studies have shown that wood density (WD) is an important variable for reliably estimating the above-ground biomass of tropical

forests (Baker *et al.*, 2004), and a good predictor of leaf area of shrubs in tropical rain forests (Swenson & Enquist, 2008). Climatic change, such as increasing levels of nitrogen deposition and atmospheric carbon dioxide, may result in a decline in the average WD of trees by enhancing radial growth within a forest (Telewski *et al.*, 1999; Stegen *et al.*, 2009). Wood traits also determine decomposition rates of tree biomass, and thus affect carbon and nutrient cycling in forest ecosystems (Chave *et al.*, 2009; Weedon *et al.*, 2009).

It has been shown that some wood traits, such as WD, vary with geographical gradients (Baker *et al.*, 2004; Slik *et al.*, 2010), but it is still ambiguous how they vary with altitude or latitude. For example, several studies have shown that WD decreased significantly with increasing latitude or altitude across Neotropical tree species or at a global scale (Chave *et al.*, 2006; Swenson & Enquist, 2007; Patiño *et al.*, 2009), but Slik *et al.* (2010) found that WD increased with altitude in Bornean forests. The spatial variation in wood traits is probably linked to the spatial patterns of climatic factors and the anatomy of xylem and mechanical strength, which affect the survival and growth of trees under diverse environmental conditions (van Gelder *et al.*, 2006; Chave *et al.*, 2009; Robert *et al.*, 2009). For example, Wiemann & Williamson (2002) found that WD was negatively correlated with mean annual precipitation (MAP) and positively with mean annual temperature (MAT) in North and South American forests, while Patiño *et al.* (2009) found WD to be curvilinearly related to MAP, and showed a maximum at MAP of 2000–3000 mm in Amazonian forests. However, ter Steege *et al.* (2006) suggested that the geographical variation in WD of trees in South America was affected primarily by forest dynamics, which in turn was driven by a gradient of soil fertility and dry season length. Also, there were no significant differences in modulus of elasticity (MOE) and modulus of rupture (MOR) in 32 Australian woody species between low-rainfall and high-rainfall sites (Onoda *et al.*, 2010).

Until now, studies of wood traits have focused on wood density, ignoring other important wood traits. Since many wood traits are known to interact with each other to regulate tree hydraulic conductivity, mechanical support, storage of nutrients and water and growth and mortality of trees (King *et al.*, 2006; Stegen *et al.*, 2009; Zhang & Cao, 2009; Zanne & Falster, 2010), it is important to determine how these traits covary along spatial gradients. For example, wood properties such as MOE, MOR and WD that are related to the mechanical strength of trees, are also correlated with xylem cavitation resistance (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005). However, little is known about the spatial patterns of wood traits in China, the only country that hosts a continuous succession from tropical seasonal rain forests, subtropical evergreen broadleaved forests, subalpine conifer forests, temperate deciduous broadleaved forests and boreal forests from 18.0° to 53.3° N latitude. Although it is believed that the physiology, xylem structure and wood traits of a tree can be shaped by phylogeny and the environment (Read & Stokes, 2006; Swenson & Enquist, 2007; Chave *et al.*, 2009), it remains unclear to what extent geographical gradients in wood traits are shaped by each of these two factors. In the present

study, we compiled a national data set of 11 wood properties for 618 tree species from 98 sample sites spread across forests over China, and characterized the effects of phylogeny, temperature and precipitation on wood traits. We hypothesized that wood properties would exhibit significant geographical patterns that are controlled by both environmental and phylogenetic constraints.

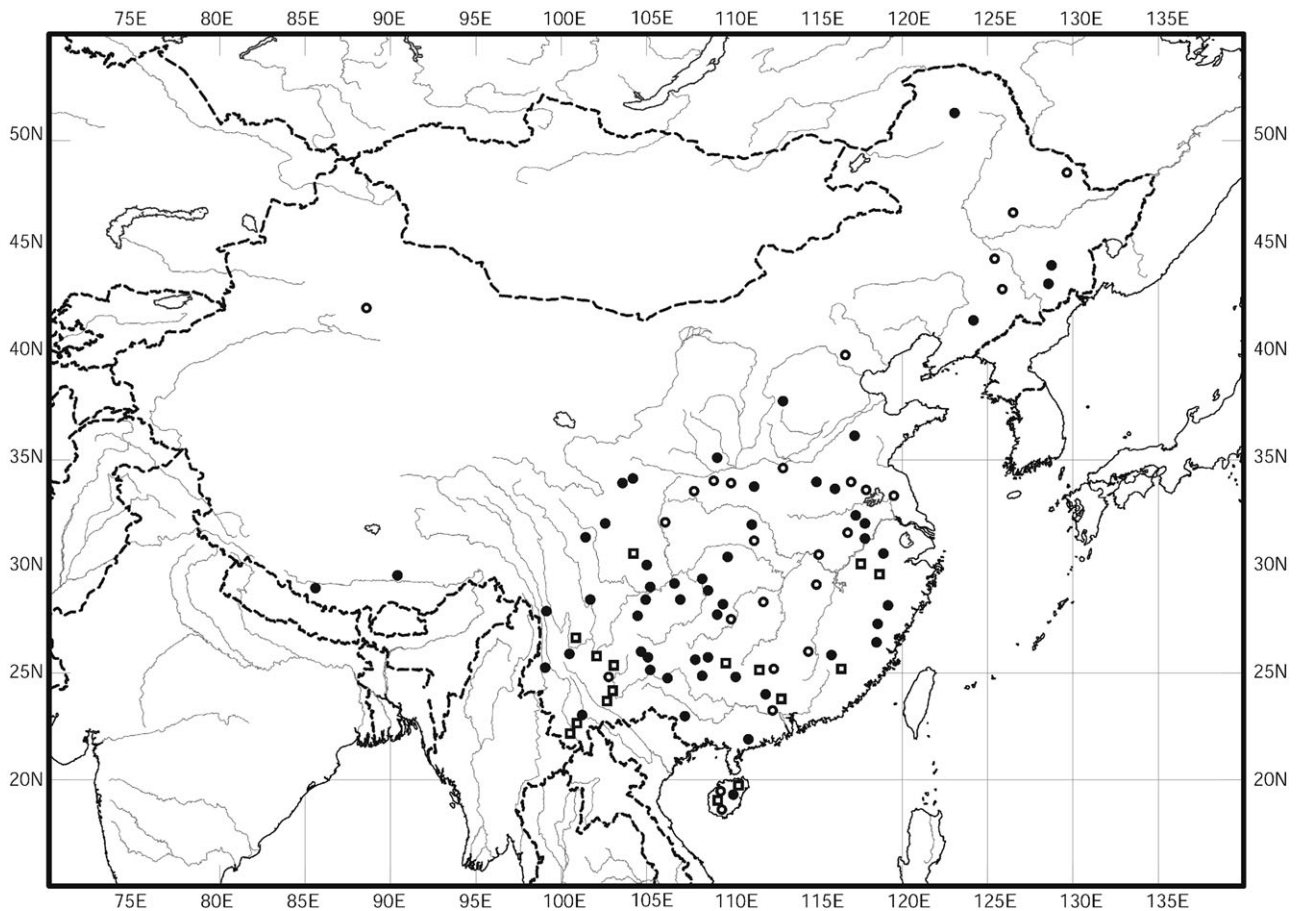
## MATERIALS AND METHODS

Data for 11 wood traits as indicated in Appendix S1 in Supporting Information were compiled from the literature (Cheng, 1985; Cheng *et al.*, 1992; Ye *et al.*, 1999). The data included 618 species (representing *c.* 25% of China's tree species), consisting of 535 angiosperm species and 83 gymnosperm species, from 98 sampling sites (Fig. 1) spanning most woody vegetation types across China. Annual stem radial growth (ARW, mm) was used as a measure of radial growth rate. The mean values of WD ( $\text{g cm}^{-3}$ ), MOR (MPa), compression strength parallel to the grain (CSG, MPa), cross-section hardness (CSH, MPa), MOE (GPa), radial cleavage strength along the grain (RCG, MPa), radial shearing strength parallel to the grain (RSG, MPa), toughness (TN, Pa), tensile strength parallel to the grain (TSG, MPa) and volumetric shrinkage coefficient (VSC, %) were based on the mean of 3–15 trees for each species at the same site (at 15% wood water content).

Altitude, latitude, MAT (°C) and MAP (mm) for each of the 98 sample sites were determined from Google Earth and the China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/shishi/climate.jsp>). The taxonomic assignments of species to division, order and family were based on the APGII system (APG, 2003) and the Angiosperm Phylogeny website (<http://www.mobot.org/MOBOT/Research/APweb/welcome.html>). The 618 species were assigned into 20 orders and 53 families.

The original wood traits of species and the environmental variables were standardized by  $\log_{10}$ -transformation before statistical analysis. To determine how total wood trait variance was partitioned among taxonomic levels, a hierarchical analysis of variance (nested ANOVA) was performed at five taxonomic levels (division/order/family/genus/species) using the 'varcomp' function of the R package 'ape'.

The contribution of focal clades to present-day variation in wood traits was calculated using the method of Webb *et al.* (2008). According the description of Moles *et al.* (2005), the contribution index is calculated by the product of component one times component two, as explained below. The first component is calculated as the ratio of trait variation (sum of squares) attributable to the divergence at the focal node to the variation due to subsequent radiations within the subclades. The second component is the sum of squares of the present-day species in the clade divided by the sum of squares of all the present-day species in the whole tree. The internal node values were calculated using phylogenetically independent contrasts (PIC) (Felsenstein, 1985), after which each variance component was calculated from internal node averages estimated by the 'analysis



**Figure 1** Sampling locations of wood traits in this study. Each circle or square represents one sampling site: ●, number of sampled species  $\leq 3$ ; ○, 4–8 species; □,  $\geq 9$  species.

of traits' module in Phylocom (Webb *et al.*, 2008). The focal clade contribution index was calculated separately for each wood trait.

The variance and correlation analyses were performed in R package 2.9 (R Development Core Team, 2008). We used Pearson's analysis (*cor.test* function) and the 'aov' function to test the correlations and variance components for wood traits and environmental variables without considering phylogeny. A principal components analysis (PCA) was performed using the 'pca' function of the R package 'labdsv' to summarize the joint variation of the 11 wood traits at family level.

The possible evolutionary associations between wood traits and environmental variables at family level were assessed with 'analysis of traits' in PHYLOCOM (Webb *et al.*, 2008), which can be implemented in the 'pic3' function of the R package 'picante'. This program calculates internal node values for continuous traits using the PIC method (Felsenstein, 1985). We used the resolved PHYLOMATIC tree (tree version R20040402) as the backbone for our supertree. The backbone is based on the Angiosperm Phylogeny Group II classification of angiosperms (APG, 2003). For polytomies, daughter nodes were ranked by trait values, and split at the median into two groups. If the number of daughter nodes was odd, the median daughter node

value was assigned to the lower group if its value was lower than the mean across all daughter nodes or to the upper group if its value was higher than the mean. A harmonic mean branch length was calculated for each group, after which the contrast size was calculated as for a dichotomous node (Pagel, 1992; Wright *et al.*, 2007). The correlations among wood traits and between wood traits and environmental variables in gymnosperms, angiosperms and all species were analysed, respectively. Since the gymnosperms only contained one order and five families, the correlation analysis was only performed at species level.

## RESULTS

### Geographical variations in wood traits

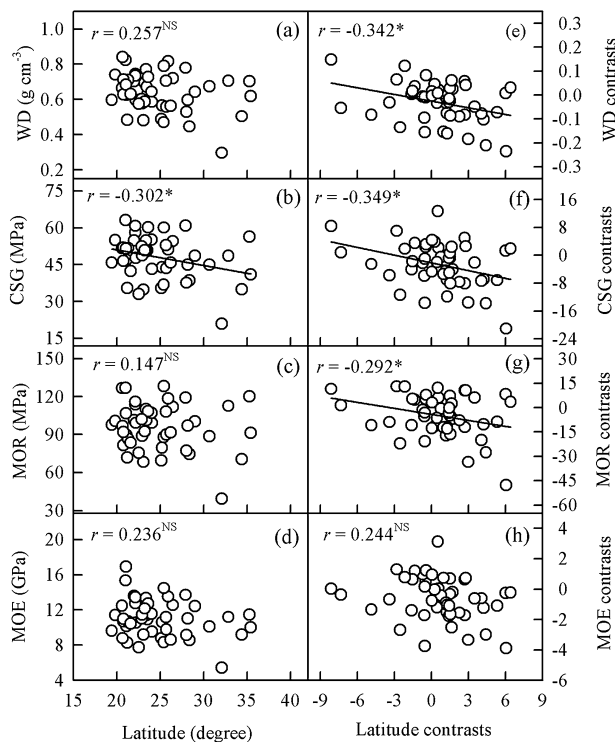
In gymnosperms, at the species level, WD, CSH and ARW were negatively correlated with latitude, while VSC was positively correlated with altitude and RSG and ARW negatively correlated with altitude. In angiosperms, most wood traits varied with latitude, while only RSG and TN varied with altitude (Fig. 2; Appendix S2). Below 1000 m above sea level, neither WD nor MOR were related to altitude, but they decreased at altitudes higher than 1000 m (Appendix S2).

At the family level, only CSG in angiosperms decreased with increasing latitude (linear regression), and none of the wood traits were correlated with altitude. After phylogenetic correction, however, the correlations of WD, VSC, CSG, MOR and CSH with latitude and TN with altitude became significant (Fig. 2; Appendix S2). When treating angiosperms and gymnosperms as one group, WD, VSG, CSG, MOR and CSH were correlated with latitude after phylogenetic correction, but no wood trait varied with altitude (Appendix S2). TSG did not show geographical variation at any taxonomic scale.

### Climatic effects on wood traits

For gymnosperms, at the species level, WD, RSG, CSH and ARW were positively correlated with MAP, while CSH was positively related and VSC negatively related to MAT (Appendix S2). In angiosperms, WD, VSC, CSG, MOR, MOE, RSG and CSH were positively correlated with both MAP and MAT. ARW and TSG were also positively correlated with MAP. Across all angiosperm and gymnosperm species, TN was significantly correlated with both MAP and MAT (Appendix S2).

At the family level, WD, VSC, CSG, MOR, MOE and CSH were positively correlated with MAP (Fig. 3), while WD, CSG and CSH were correlated positively with MAT. MOR was also



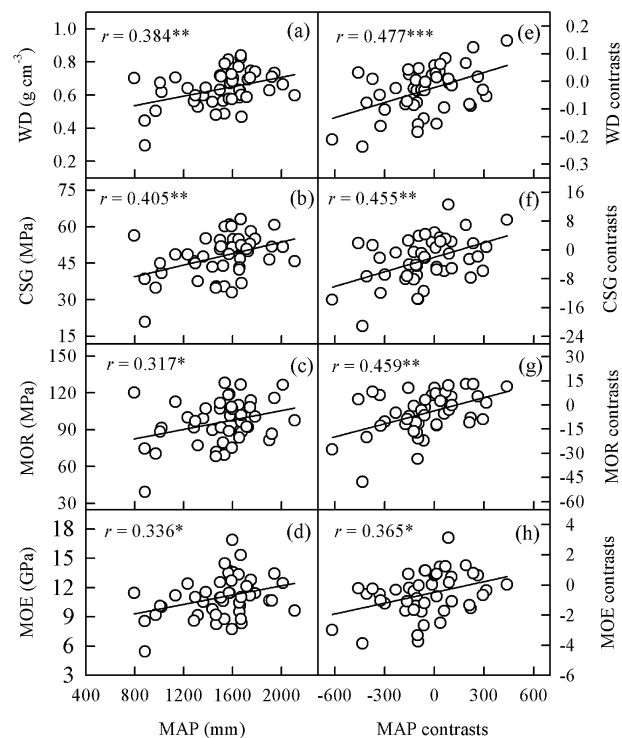
**Figure 2** Relationships between wood traits and latitude for angiosperm tree species at family level: (a)–(d) Pearson's correlation between wood traits and latitude; (e)–(h) phylogenetically independent contrast correlation between wood traits and latitude. WD, wood density; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity. NS,  $P > 0.05$ ; \* $P < 0.05$ .

positively correlated with MAT after correction for phylogeny (Fig. 4; Appendix S2). However, RSG, TSG, RCG and ARW were not significantly correlated with MAP and MAT based on both Pearson's and PIC correlations.

### Phylogenetic variation in wood traits

Among the 618 tree species from 53 families, the most represented families in terms of species numbers were Pinaceae and Fagaceae, while the most represented orders were Pinales, Fagales and Malpighiales. All wood properties exhibited significant phylogenetic signal (Fig. 5; Appendices S3 & S4). The highest wood density and stem mechanical property values were found in Fagales and Myrtales, while the lowest values were found in Apiales and Pinales. WD, CSG, MOR, TSG and MOE varied about three-fold among families, while TN, RCG, CSH and RSG varied from four- to seven-fold. The variation in ARW was relatively large, varying up to 15.9-fold (Appendix S3).

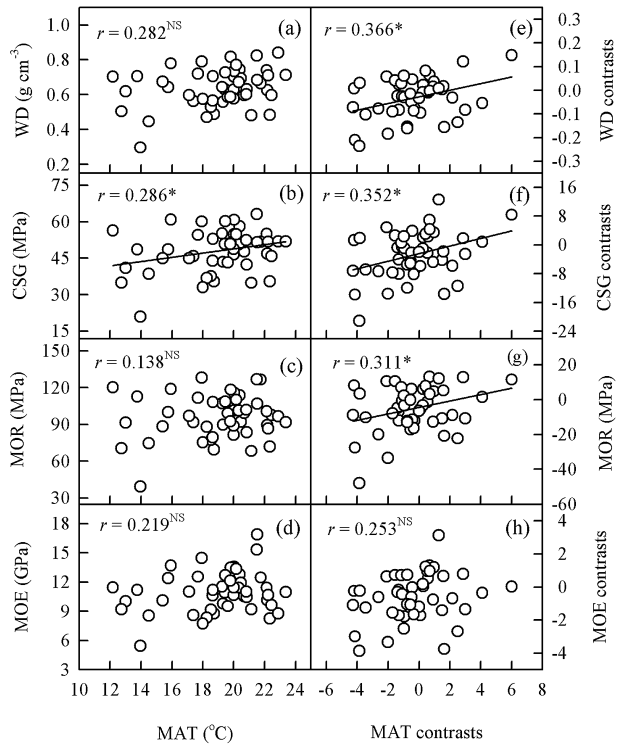
The proportion of variance for the 11 wood traits was significantly different at various taxonomic levels (Table 1). For example, the proportion of variance in RCG at division level accounted for 63.3% of the total RCG variance, while the proportions of variance in MOE, MOR and TSG at this same taxonomical level were less than 0.01%. More than 90% of total



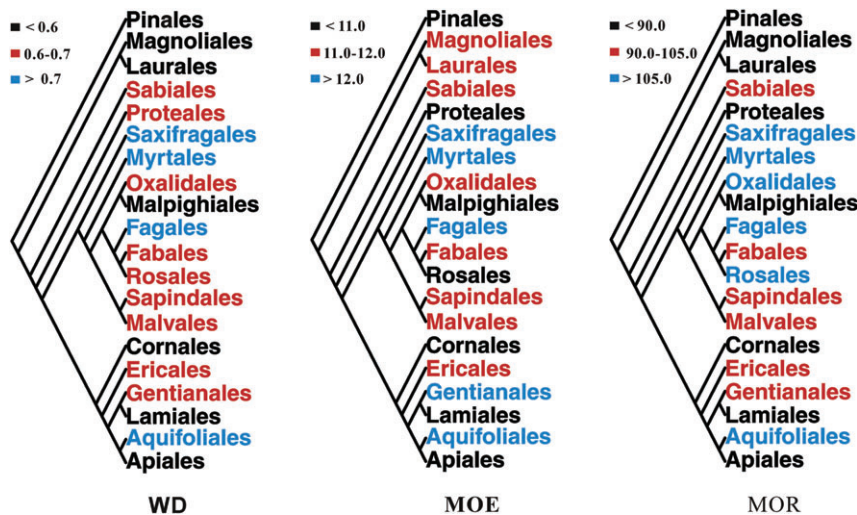
**Figure 3** Relationships between wood traits and mean annual precipitation (MAP) for angiosperm tree species at family level: (a)–(d) Pearson's correlation between wood traits and MAP; (e)–(h) phylogenetically independent contrast correlation between wood traits and MAP. WD, wood density; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



variance in WD, VSC, CSH, MOR, MOE, TN, CSG, ARW and TSG was found at family, genus and species levels combined, while the largest proportion of variance in RSG was observed at division level.



**Figure 4** Relationships between wood traits and mean annual temperature (MAT) for angiosperm species at family level: (a)–(d) Pearson's correlation between wood traits and MAT; (e)–(h) phylogenetically independent contrast correlation between wood traits and MAT. WD, wood density; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity. NS,  $P > 0.05$ ; \* $P < 0.05$ .



**Figure 5** The mean values of wood traits for each order. The phylogeny is based on the Angiosperm Phylogeny Group II classification. WD, wood density ( $\text{g cm}^{-3}$ ); MOE, modulus of elasticity (GPa); MOR, modulus of rupture (MPa).

The contribution indices of key clades to present-day variation in wood traits are given in (Table 2). For the majority of wood traits, the widest divergence was observed between gymnosperms and angiosperms, Rosids and Asterids, Magnoliids and Eudicots, and in Lamiales. The contribution indices of Rosids I versus Rosids II and Asterids I versus Asterids II were relatively small.

### Correlations among wood traits

PCA showed that the mechanical properties of wood loaded strongly on the first axis of the PCA, explaining 58.5% of variation in the 11 tested traits at family level, while ARW loaded on the second axis, which explained 23.4% of the total variation in wood traits (Fig. 6).

Pearson's correlation analysis confirmed the findings of the PCA analysis, with positive correlation of WD with all mechanical properties in both angiosperms and gymnosperms (Appendix S5). ARW was negatively correlated with all the mechanical properties of wood except TN for angiosperms and with WD, VSC, CSG, MOR, MOE and TSG for gymnosperms. With the exception of VSC versus RSG, CSH, RCG and RSG versus MOE, TSG, the correlations among other wood traits were statistically significant at the species level for gymnosperms, while all mechanical properties of wood were significantly correlated for angiosperms. All correlations among mechanical properties of wood at family level for angiosperms were significant according to both Pearson's analysis and PIC method (Appendix S5). However, ARW was only significantly related to TSG and RCG.

### DISCUSSION

It has been found that wood density significantly varies with geographical and environmental gradients in Neotropical and Bornean forests (Chave *et al.*, 2006; Swenson & Enquist, 2007;

Wood traits	No. of species	Division	Order	Family	Genus	Species
WD	618	8.9	< 0.1	19.2	45.2	26.7
VSC	490	13.3	< 0.1	17.8	35.5	33.4
CSG	576	1.7	< 0.1	17.0	41.9	39.5
MOR	540	< 0.1	< 0.1	14.2	32.0	53.8
MOE	489	< 0.1	2.5	19.1	39.3	39.2
RSG	317	15.2	10.5	< 0.1	43.6	30.7
TSG	247	< 0.1	< 0.1	26.6	42.4	31.0
TN	406	8.6	2.2	15.9	38.6	34.7
CSH	528	6.7	< 0.1	19.5	43.3	30.5
RCG	312	63.3	0.7	5.4	15.3	15.2
ARW	280	13.3	< 0.1	23.3	25.5	37.8

WD, wood density; VSC, volumetric shrinkage coefficient; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity; RSG, radial shearing strength parallel to the grain; TSG, tensile strength parallel to the grain; TN, toughness; CSH, cross-section hardness; RCG, radial cleavage strength along the grain; ARW, annual stem radial growth.

**Table 1** Proportions of variance in wood traits at different taxonomic levels.

**Table 2** Contribution indices of key clades to present-day variation in wood traits.

WD	VSC	CSG	MOR	MOE	TN	CSH	RCG	RSG	TSG	ARW	Clades involved
<b>0.32</b>	<b>0.40</b>	<b>0.45</b>	<b>0.22</b>	<b>0.09</b>	<b>0.19</b>	<b>0.40</b>	<b>0.35</b>	<b>0.10</b>	0.05	<b>0.04</b>	Gymnosperms versus Angiosperms
<b>0.17</b>	<b>0.26</b>	<b>0.24</b>	<b>0.24</b>	<b>0.34</b>	<b>0.31</b>	<b>0.12</b>	0.04	<b>0.09</b>	<b>0.51</b>	0.01	Rosids versus Asterids
<b>0.11</b>	0.09	<b>0.14</b>	<b>0.12</b>	<b>0.12</b>	0.02	<b>0.13</b>	<b>0.05</b>	<b>0.13</b>	<b>0.25</b>	<b>0.05</b>	Lamiales, Oleaceae versus Bignoniaceae, Lamiaceae and Paulowniaceae
0.03	<b>0.11</b>	0.09	0.07	0.02	< 0.01	0.12	<b>0.09</b>	0.05	<b>0.19</b>	<b>0.12</b>	Magnoliids versus Eudicots
0.03	0.04	0.04	0.01	0.02	<b>0.12</b>	0.02	< 0.01	< 0.01	< 0.01	0.01	Malpighiales, Ixonanthaceae versus Clusiaceae, Euphorbiaceae, Euphorbiaceae and Salicaceae
0.02	< 0.01	0.04	0.04	0.02	0.01	0.03	< 0.01	< 0.01	0.01	0.04	Fagales, Fagaceae versus Betulaceae, Casuarinaceae, and Juglandaceae
0.01	0.01	0.01	0.01	0.02	< 0.01	0.01	< 0.01	< 0.01	0.01	< 0.01	Pinales, Cephalotaxaceae versus Cupressaceae, Pinaceae, Podocarpaceae and Taxaceae
0.01	< 0.01	0.03	0.08	0.02	0.03	0.05	0.05	0.07	0.10	< 0.01	Ericales, Myrsinaceae, Ebenaceae and Sapotaceae versus Styracaceae, Symplocaceae and Theaceae
0.01	0.01	0.01	0.02	0.01	< 0.01	0.02	< 0.01	0.02	< 0.01	< 0.01	Sapindales, Anacardiaceae and Burseraceae versus Meliaceae, Rutaceae, Sapindaceae and Simaroubaceae
0.01	< 0.01	0.04	0.02	< 0.01	0.01	0.03	0.03	0.02	0.01	0.01	Rosales, Rhamnaceae versus Cannabaceae, Moraceae and Ulmaceae
< 0.01	0.01	< 0.01	0.01	< 0.01	0.03	< 0.01	0.06	0.01	< 0.01	< 0.01	Rosids I versus Rosids II
< 0.01	0.04	< 0.01	< 0.01	0.10	0.01	< 0.01	< 0.01	0.01	0.01	–	Asterids I versus Asterids II

The three largest contribution indices for each wood trait are shown in bold.

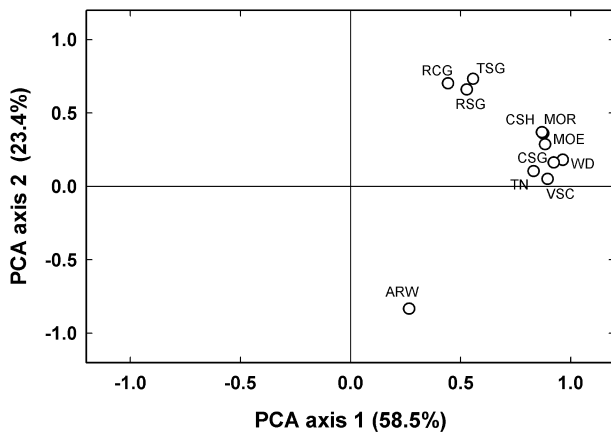
WD, wood density; VSC, volumetric shrinkage coefficient; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity; TN, toughness; CSH, cross-section hardness; RCG, radial cleavage strength along the grain; RSG, radial shearing strength parallel to the grain; TSG, tensile strength parallel to the grain; ARW, annual stem radial growth.

Slik *et al.*, 2010). Little is known about the geographical patterns and environmental influences on other wood traits. In the present study, we characterized the latitudinal and altitudinal variation in 11 wood traits of 618 angiosperm and gymnosperm tree species across China, and showed that these spatial patterns were controlled by both the environment and phylogeny.

### Geographical variation in wood traits

Most wood traits, such as WD, CSG, MOR, MOE and CSH showed significantly decreasing values with increasing latitude,

while only TN, RSG and RCG showed limited altitudinal gradients (Fig. 2; Appendix S2). Our results were in contrast to the findings on decreasing WD with altitude in the Neotropical forests (Chave *et al.*, 2006; Swenson & Enquist, 2007) and the positive correlation between WD and altitude across tropical tree species in Borneo (Slik *et al.*, 2010). However our results supported the negative correlation between WD and latitude as found across Neotropical tree species (Chave *et al.*, 2006; Swenson & Enquist, 2007), and the lack of relationship between WD and altitude for Douglas fir in north-western America reported by Acuna & Murphy (2006). These contradictory



**Figure 6** Principal components analysis (PCA) of 11 wood traits from 53 families. WD, wood density; VSC, volumetric shrinkage coefficient; CSG, compression strength parallel to the grain; MOR, modulus of rupture; MOE, modulus of elasticity; TN, toughness; CSH, cross-section hardness; RCG, radial cleavage strength along the grain; RSG, radial shearing strength parallel to the grain; TSG, tensile strength parallel to the grain; ARW, annual stem radial growth.

results could be caused by regional differences in species composition that are related to different biogeographic histories or regional differences in environmental changes along latitudinal and altitudinal gradients.

Our study showed that MAP was more important than MAT in explaining the spatial variation in wood traits of trees across China (Figs 3 & 4; Appendix S2). This was in line with the finding on stronger correlation of wood density with precipitation than with temperature for the forest trees in North and South America (Martínez-Cabrera *et al.*, 2009). In China, MAT decreases with increasing latitude and altitude, while MAP is curvilinearly related with altitude, increasing up to mid-altitudes but decreasing with further increase in altitude towards mountain tops (Appendix S2). This could explain why at species level neither WD nor MOR were significantly correlated with altitude below 1000 m elevation, but decreased with altitude above 1000 m (Appendix S2), and most wood properties exhibited significant latitudinal variation but limited or no altitudinal variation.

The present study revealed the significant and positive correlation of WD, MOR, MOE and CSH with MAP and MAT (Figs 3 & 4; Appendix S2). Our results confirmed the findings of a positive correlation between WD and MAT in South America reported by Wiemann & Williamson (2002) and Patiño *et al.* (2009). However, they contradicted the findings of a negative association between WD and MAP in tropical trees of South America (Wiemann & Williamson, 2002; Swenson & Enquist, 2007), and the lack of association of WD with rainfall in South America (Muller-Landau, 2004). Onoda *et al.* (2010) found that WD was higher in low-rainfall sites than high-rainfall sites in Australia, but MOE and MOR were not. Patiño *et al.* (2009) observed a positive correlation between WD and MAP below

3000 mm, but a negative correlation when MAP exceeded 3000 mm in Amazon forests. The positive correlation of WD with temperature could be linked to wood development by decreasing vessel size and density and increasing cell wall thickness with increasing temperature due to reduction in water viscosity in xylem water pipes (Roderick & Berry, 2001; Thomas *et al.*, 2004, 2007). In contrast to the consistent correlation of WD with MAT, there was a strong discrepancy in the relationship between WD and rainfall among studies. This discrepancy may be explained in part by differences in environmental factors, such as soils and temperatures, among the sampling sites. In our study, WD decreased with the increasing latitude (Fig. 2), while latitude was negatively correlated with MAP ( $r = 0.722$ ,  $P < 0.0001$ ; Appendix S2). The positive correlation between WD and MAP found by the present study may therefore be a result of the wide latitudinal range covered by our study which includes a continuous succession of forest ecosystems ranging from tropical seasonal rain forests to boreal forests. Most of other studies such as those cited above include fewer types of forest ecosystems and a much smaller latitudinal range.

The geographical variation in wood mechanical traits is also related to the ecological strategy and evolutionary history of trees. Stem structure and architecture are greatly influenced by resource supply and environmental stress. Plants can adapt to these stresses over evolutionary time through the adjustment of stem structure and architecture (Read & Stokes, 2006); however, species with different wood structures will occupy different habitats due to environmental filtering (Martínez-Cabrera *et al.*, 2009). For instance, from tropical to temperate climates, vessel element lengthen and vessel diameter decrease, while the incidence of scalariform perforations and tracheids increases (Jansen *et al.*, 2004; Wheeler *et al.*, 2007). In our study, some relationships between wood traits, latitude and altitude became significant after PIC, indicating that evolutionary constraints due to phylogenetic conservatism affect the environmental tolerances of tree species and thus their latitudinal and altitudinal ranges. Patterns of wood traits across China supported the idea that species are not randomly distributed across sites but follow the ‘habitat tracking’ hypothesis (Ackerly, 2003).

### Evolution and correlation of wood traits

The present study showed that all of the examined wood properties exhibited a strong phylogenetic signal. Most variance in wood traits was found at genus and species level (Appendix S3). Only RCG exhibited the largest proportion of variance at division level, being the most phylogenetically conservative trait among the wood traits studied (Table 1). The present study and previous studies have consistently shown that WD is phylogenetically conserved at different taxonomic levels (Baker *et al.*, 2004; Chave *et al.*, 2006; Preston *et al.*, 2006; Slik, 2006; Swenson & Enquist, 2007). The strong phylogenetic conservatism in almost all of the studied wood traits is likely to be related to their basic and interrelated functions as they all influence and contribute to stem water transport, stem water and nutrient storage

and mechanical support of the tree (Pratt *et al.*, 2007; Poorter *et al.*, 2010). Changes in one trait directly influence other trait values which, in concert, influence tree performance under different environmental conditions. For example, if a plant has to develop thicker xylem conduit walls and smaller conduit diameters to increase the resistance of conduit cavitation under negative pressure, such changes may increase xylem construction cost and decrease hydraulic conductivity (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005). Overall, the strong interdependence of different wood traits is confirmed by the fact that most wood traits in the present study were correlated with each other, especially at species and family levels. As a result, one of the most studied wood traits, WD, can be used as a proxy for the overall mechanical strategy of the tree.

The largest divergences in wood traits were found between angiosperms and gymnosperms and between Rosids and Asterids due to the large difference in stem structure (Table 2). Previous studies have shown that wood anatomy contains a significant phylogenetic signal, especially at the ordinal level (e.g. Baas *et al.*, 2000). Evolution of wood traits in trees can be accompanied by a change in xylem anatomy, since WD is significantly correlated with the proportion of parenchyma cells in the stem cross-section, fibre-cell wall thickness and vessel or tracheid size, which is related to the ecological strategies by controlling the proportion of carbon invested per unit volume of stem (Martínez-Cabrera *et al.*, 2009; Poorter *et al.*, 2010).

## CONCLUSION

The spatial variations in wood traits were shaped by environment and phylogenetic constraints that limit the environmental adaptability of tree species. MAP was more important than MAT in explaining the spatial patterns of wood traits in trees across China. Wood traits were highly evolutionarily conservative and WD showed correlated evolution with mechanical properties. The present results indicate that climate change, such as increasing temperature and altered precipitation regime, is likely to affect ecosystem functions, carbon storage and nutrient turnover in different forest ecosystems in the future.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Wood traits and environmental variables of 618 species in China.

**Appendix S2** Correlations between wood traits and climatic variables.

**Appendix S3** Wood traits of 53 families.

**Appendix S4** Wood traits of 20 orders.

**Appendix S5** Correlation coefficients among wood traits.

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