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Patterns and determinants of wood physical and mechanical properties across major tree species in China

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The physical and mechanical properties of wood affect the growth and development of trees, and also act as the main criteria when determining wood usage. Our understanding on patterns and controls of wood physical and mechanical properties could provide benefits for forestry management and bases for wood application and forest tree breeding. However, current studies on wood properties mainly focus on wood density and ignore other wood physical properties. In this study, we established a comprehensive database of wood physical properties across major tree species in China. Based on this database, we explored spatial patterns and driving factors of wood properties across major tree species in China. Our results showed that (i) compared with wood density, air-dried density, tangential shrinkage coefficient and resilience provide more accuracy and higher explanation power when used as the evaluation index of wood physical properties. (ii) Among life form, climatic and edaphic variables, life form is the dominant factor shaping spatial patterns of wood physical properties, climatic factors the next, and edaphic factors have the least effects, suggesting that the effects of climatic factors on spatial variations of wood properties are indirectly induced by their effects on species distribution.

wood density, shrinkage coefficient, resilience, geographic pattern, environmental factors

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Wood, the lignified tissues formed by the secondary growth of plants such as trees, shrubs and lianas, are chief component of root and stem in woody plants [1–3]. The physical and mechanical properties of wood can affect the growth and development of woody plants by determining water conduction and mechanical support [4–6], and are closely linked with the morphological structure of individual [7], life-history strategy [8], resource competition [9], community dynamics [10] and the terrestrial ecosystem function of trees [11,12]. Therefore, exploring the physical and mechanical properties of wood and their driving factors can help us to further understand the structure and function of terrestrial ecosystems, and thus provide valuable information for predicting the responses of terrestrial ecosystems to global change. Meanwhile, as the natural polymer materials with heterogeneous, anisotropic characteristics, wood is one of the most widely used material in human society [2,13]. According to the United Nations Food and Agriculture Organization, the log consumption from 2007 to 2011 was about 1.71×10^{11} m^3, among which 45.6% was used for papermaking, board processing and other kinds of industrial production and 54.4% was used as a fuel [14]. The physical and mechanical properties of wood, as one of the basic elements in wood traits evaluation, are the main criteria when

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determining wood usage [15]. Therefore, understanding the patterns and determinants of wood physical properties could provide benefits for forestry management and also provide guidance for wood application and forest tree breeding.

The physical and mechanical properties of wood usually include density, dry shrinkage coefficient, resilience, strength, and hardness. These properties can change with tree species and life form, for example, softwoods are usually looser and softer, while hardwoods are denser and harder [13,16]. Moreover, these wood properties can be affected by climate, soil and other site conditions due to the close association between wood physical and mechanical properties and plant growth [9,17]. Therefore, a comprehensive assessment of the distribution pattern and driving factors of wood physical and mechanical properties are of great importance.

A number of studies have reported the distribution, pattern of wood physical properties and their influencing factors on regional scale [10–12,18,19]. However, these studies generally focus on density and ignore other wood properties such as dry shrinkage coefficient, resilience and strength. Since the growth and development of plants are affected by the combined effect of various wood properties [20–22], consideration of only wood density is insufficient. Moreover, most of these studies were performed in regions of Europe and America which had quite different species composition compared with East Asia, thus the distribution pattern and driving factors of wood properties in China remains elusive. More recently, Chinese colleagues conducted intensive studies on wood physical and mechanical properties of common or important commercial trees [2,23–26], and explored the relationships between those wood properties [27,28]. However, those studies mainly focus on wood physical properties and ignore their driving factors. Although a few recent studies reported wood physical properties as well as their driving factors, the relative contribution of various factors and the influence of edaphic factors on wood properties in China are still unknown [29].

We established a comprehensive database of wood physical and mechanical properties and their influencing factors across major tree species in China. Based on this database, we showed the characteristics of Chinese wood physical and mechanical properties, explored the relationships among those wood physical and mechanical properties, and investigated the influence of life form, climatic and edaphic factors on wood physical and mechanical properties in China.

1 Materials and methods

1.1 Wood physical and mechanical properties database

We collected data based on the principle of more families contained, well-distributed and less values missed. The data were from the literatures (Anatomy and Properties of Chinese Woods, Wood Physical and Mechanical Properties of Main Tree Species in China, Atlas of Gymnosperms Woods of China, Wood Properties of Main Tree Species from Plantation in China) [23–26]. Based on this data, we established a comprehensive database of wood physical and mechanical properties across major tree species in China. The database included 417 species belonging to 80 families and 234 genera. The top five represented families in terms of species numbers were Pinaceae, Fagaceae, Fabaceae, Lauraceae and Taxodiaceae, representing 25.9%, 16.3%, 8.2%, 6.5% and 6.2% of total species numbers in the database respectively. The wood traits in the database include basic density (BD), air-dried density (ADD), radial shrinkage coefficient (RSC), tangential shrinkage coefficient (TSC), volume shrinkage coefficient (VSC), bending strength (MOR), bending modulus of elasticity (MOE), compression strength parallel to grain (CSG), resilience (RES), hardness of transverse section (HES), hardness of radial section (HRS) and hardness of tangential section (HTS). These traits can fully characterize the main wood properties in density, dry shrinkage coefficient, resilience, strength and hardness. The description and definition of those traits are shown in Table 1.

We provide the life form of each species in the database based on the information of *Atlas of Woody Plants in China: Distribution and Climate* [30]. In the present study, there are four types of life forms: evergreen broad-leaved species, deciduous broad-leaved species, evergreen coniferous species and deciduous coniferous species.

1.2 Climatic and edaphic data

The climatic indices used in the present study were annual mean temperature (MAT) and annual precipitation (MAP). These data were obtained from the world climate data information website (http://www.worldclim.org) with spatial resolution of 0.0083 (about 1 km^2 in place near the equator) [31,32].

The soil indices included soil organic carbon density, total soil nitrogen density and soil pH. The data of soil organic carbon density came from Yang [33], total soil nitrogen density came from Yang [34] and the pH value of soil came from soil of China [35].

Cokriging interpolation methods were used to obtain the climatic and edaphic data of each sampling site. We established a comprehensive database of wood physical properties and life form of the species as well as environmental factors of each sampling site.

1.3 Data analysis

Among 12 wood physical and mechanical traits, resilience and three hardness-related indices show logarithmic normal distribution (Figure 2); therefore, we used logarithmic transformation of those four indices before analysis. If not specified, data of all other traits were normally transformed

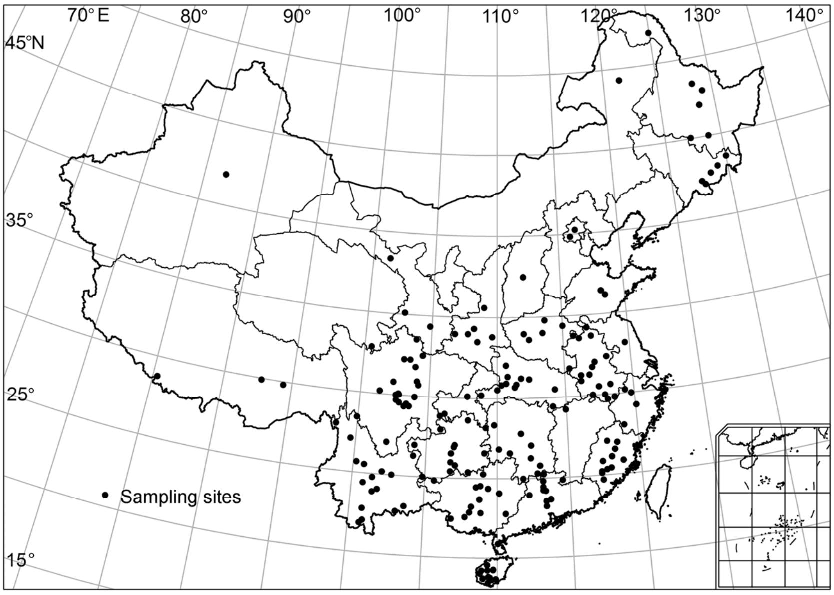

Figure 1 Sampling sites of wood physical and mechanical properties across China.

Table 1 Description and definition of wood physical and mechanical traits

Wood physical and mechanical traits	Units	Definition
Basic density (BD)	g cm^{-3}	The mass of oven dried wood per unit of fresh volume. Basic density=oven dry mass/green volume.
Air-dried density (ADD)	g cm^{-3}	The mass of air-dried wood per unit of air-dried volume. Generally air-dried density has a moisture content of about 12% by weight. Air-dried density=Air-dried mass/Air-dried volume.
Radial shrinkage coefficient (RSC)	%	The volumetric shrinkage across the radial plane. Generally expressed as the percentage of volumetric shrinkage when moisture content reduced 1%.
Tangential shrinkage coefficient (TSC)	%	The percentage of volumetric shrinkage across the tangential plane when moisture content reduced 1%.
Volume shrinkage coefficient (VSC)	%	Expressed as the percentage of the shrinkage coefficient of wood changing from its green to oven-dried state.
Bending Strength (MOR)	Mpa	The highest stress experienced within the wood at its moment of rupture. It is measured use the size of curvature radius (R). R=(3F×L)/(2b×h^2); F is the fracture load, L is the span, b is the width, h is the thickness.
Bending modulus of elasticity (MOE)	Gpa	The strength that deformations produced by low stress are completely recoverable after loads is removed. It reflects the elasticity and stiffness of wood.
Compression strength parallel to grain (CSG)	Mpa	Maximum stress sustained by a compression parallel-to-grain specimen.
Resilience (RES)	J cm^{-2}	Defined as the capacity of wood to absorb energy when it is deformed elastically and then, upon unloading to have this energy recovered. In other words, it is the maximum energy per volume that can be elastically stored. It reflects the capacity to resist deformation and rapture.
Hardness of transverse section (HES)	kgf cm^{-2}	Generally defined as resistance to indentation using a modified Janka hardness test, measured by the load required to embed a 11.28-mm ball to one-half its diameter in transverse plane.
Hardness of radial section (HRS)	kgf cm^{-2}	Generally defined as resistance to indentation using a modified Janka hardness test, measured by the load required to embed a 11.28-mm ball to one-half its diameter in radial plane.
Hardness of tangential section (HTS)	kgf cm^{-2}	Generally defined as resistance to indentation using a modified Janka hardness test, measured by the load required to embed a 11.28-mm ball to one-half its diameter in tangential plane.

before analysis in this paper.

We used the Pearson correlation analyses to examine correlations among 12 wood physical indices. Principal component analysis (PCA) was used to reduce the dimensionality of the data, and choosing the wood physical indices with the greatest contribution in principal component as the representative indices. Based on these representative indices, prediction equations for other wood physical traits were established through stepwise regression.

We then used life form, climatic and edaphic variables as independent variables and assessed the relative contribution of each variable to the variation of wood physical and mechanical properties using the General Linear Model. Considering that life form, climatic and edaphic variables may have colinearity correlation, we further performed partial regression analysis to distinguish the contribution of each variable.

All statistical analyses were performed using R package

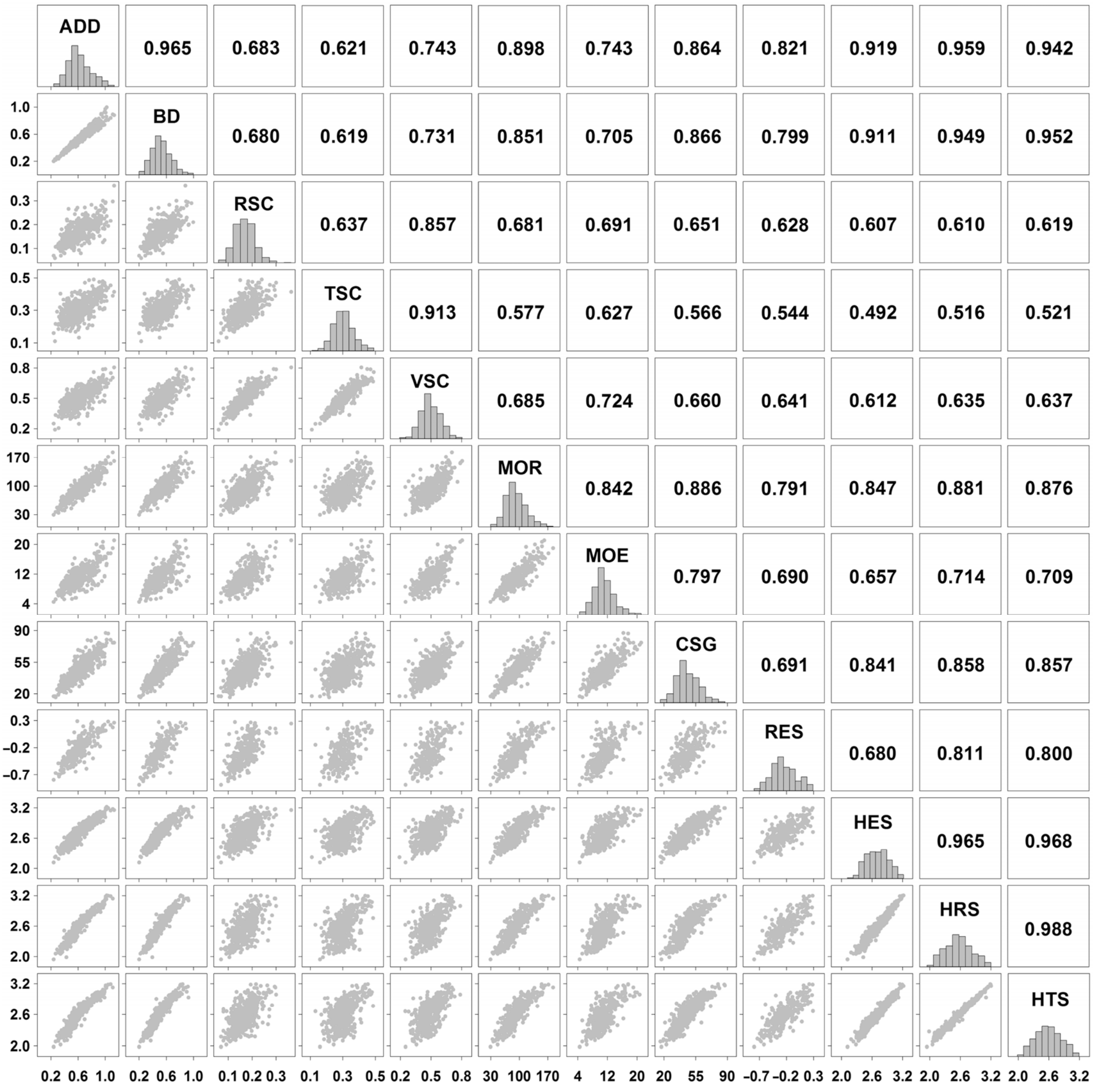

Figure 2 Correlations among 12 wood physical and mechanical properties. Above diagonal line is the distribution pattern of each wood trait, the upper right part shows the correlation coefficient, and the bottom left shows the scatter diagram. All correlations are significant (P<0.001).

3.0.2 software [36], and PCA was performed using FactoMineR package [37].

2 Results

2.1 General characteristics of wood physical traits

In general, the values of wood physical and mechanical traits varied dramatically among different species. For example, the indices of hardness and resilience varied about 13–20 times among species, whereas indices of density, dry shrinkage coefficient and the strength only showed five times variation among species (Table 2).

We showed the top five species with the maximum or minimum value in wood physical and mechanical properties (Table S1 in Supporting Information). The top five species with the maximum value in wood physical and mechanical properties were all broad-leaved species: the top five species with the maximum value in hardness and compression strength parallel to grain were all evergreen broad-leaved species (*Litchi chinensis*, *Amesiodendron chinense*, *Cyclobalanopsis neglecta*, etc.), those with the maximum value in resilience were all deciduous broad-leaved species (*Salix matsudana*, *Pteroceltis tatarinowii*, *Excentrodendron tonkinense*, etc.), and those with the maximum value in density and dry shrinkage coefficient and strength index were mostly deciduous broad-leaved species (*Hopea hainanensis*, *Mesua ferrea*, etc.). Except few species such as *Ochroma lagopus*, the top five species with the minimum value were mostly deciduous broad-leaved or evergreen coniferous species (*Spondias pinnata*, *Paulownia fargesii*, *Cunninghamia lanceolata*, *Cryptomeria japonica* var. *sinensis*, etc.).

We found significant positive correlations among all wood physical and mechanical indices (P<0.001, Figure 2). Among these correlations, two hardness indices (hardness of radial section and tangential section) had the largest correlation coefficient of 0.99, density and hardness had the largest correlation coefficient of more than 0.90 among the indices that represent different physical properties, whereas tangential shrinkage coefficient and hardness of transverse section showed the lowest correlation coefficient of 0.49.

2.2 Empirical prediction models between wood physical and mechanical properties

PCA was conducted on 12 wood physical and mechanical indices. The first, second and third axis of PCA can explain a combined 84.2% of the variation (Table 3), which is enough to reflect the majority of information of wood physical and mechanical properties.

For the first axis of PCA, density, hardness, strength of compression and bending all have high explanation rate, and ADD has the most. For the second axis, only RSC, TSC and VSC have high explanation rate, and TSC has the most. For the third axis, most indices except RES show small contributions. Overall, ADD, TSC and RES can reflect the basic information of wood physical and mechanical properties.

Therefore, we choose ADD, TSC and RES as independent variables, and use stepwise regression method to establish prediction equations for the other nine wood physical traits (Table 4). The empirical equations can match well with measurements. For BD, MOR, CSG, HTS, HES and HRS, the R^2 of regression equations were all higher than 0.75. Among them, the HRS had the larger R^2 of 0.94, whereas RSC and MOE had the smallest R^2 of 0.54 and 0.61, respectively.

2.3 Influence of life form and environmental factors on wood mechanical and mechanical properties

Based on life form, one-way ANOVA analyses for ADD, TSC and RES were performed. The results revealed significant variations of ADD, TSC and RES with life form. For example, ADD was highest in evergreen broad-leaved spe-

Table 2 Statistic values of wood physical and mechanical traits[a)]

Wood traits	Sample size	Average	Range	SD
BD	482	0.53	0.20–1.00	0.14
ADD	585	0.62	0.24–1.13	0.17
TSC	572	0.17	0.06–0.32	0.04
RSC	575	0.30	0.11–0.49	0.06
VSC	556	0.50	0.19–0.81	0.10
MOR	538	91.57	29.40–183.10	24.99
MOE	465	11.08	4.50–21.10	2.71
CSG	574	46.17	16.00–87.30	12.39
RES	280	0.66	0.16–1.94	0.37
HES	527	570.89	131.0–1650.0	288.13
HRS	462	444.32	88–1598	280.39
HTS	463	460.89	96–1554	273.22

a) The values of RES, HES, HTS and HRS are logarithmic normal transformed data. See Table 1 for the full names and units of these traits.

Table 3 PCA analyses of 12 wood physical and mechanical properties[a)]

Relative contribution	Wood traits	First axis	Second axis	Third axis	Fourth axis	Fifth axis
Contribution of each traits to principal component (%)	BD	9.01	0.10	10.84	0.19	0.42
	ADD	10.46	0.36	2.93	0.53	0.17
	TSC	7.09	13.18	0.01	0.01	68.00
	RSC	5.83	27.94	0.10	6.17	28.79
	VSC	7.20	25.99	0.04	4.94	0.00
	MOR	9.96	0.50	0.87	12.68	0.15
	MOE	7.31	0.75	13.76	42.19	2.00
	CSG	9.56	0.26	3.47	10.24	0.28
	RES	5.16	2.04	62.94	11.65	0.00
	HES	9.62	7.22	4.83	2.16	0.09
	HRS	9.40	11.19	0.12	4.39	0.03
	HTS	9.41	10.47	0.09	4.84	0.06
Variance contribution rate of principal component (%)		68.27	10.15	5.78	4.33	2.98

a) The relative contribution of top 5 principal components and variance contribution of each principal component are shown.

Table 4 Prediction models of wood physical properties by stepwise linear regression, in which ADD, TSC and RES act as explanatory variables[a)]

Wood physical traits	Prediction model	R^2	Explanatory variable	*P*
BD	0.841×ADD	93.2%	ADD	0.000***
			TSC	–
			RES	–
RSC	0.025+0.119×ADD+0.234×TSC	54.2%	ADD	0.000***
			TSC	0.000***
			RES	–
VSC	0.049+0.148×ADD+1.172×TSC	87.4%	ADD	0.000***
			TSC	0.000***
			RES	–
MOR	14.76+119.97×ADD+27.15×TSC+14.14×RES	84.1%	ADD	0.000***
			TSC	0.053†
			RES	0.003**
MOE	1.495+9.627×ADD+12.372×TSC	61.1%	ADD	0.000***
			TSC	0.000***
			RES	–
CSG	0.276+71.97×ADD-6.199×RES	78.6%	ADD	0.000***
			TSC	–
			RES	0.017*
HES	2.050+1.279×ADD-0.432×TSC	85.4%	ADD	0.000***
			TSC	0.000***
			RES	–
HRS	1.839+1.535×ADD-0.582×TSC+0.0860×RES	94.0%	ADD	0.000***
			TSC	0.000***
			RES	0.003**
HTS	1.865+1.515×ADD-0.594×TSC+0.061×RES	92.5%	ADD	0.000***
			TSC	0.000***
			RES	0.051†

a) The R^2 of each model, the variables entering the model and their significant level are listed. "–" means the variable did not enter the model. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; †, $P<0.1$.

cies and lowest in evergreen coniferous and deciduous conifer species, TSC was higher in evergreen broad-leaved species than in deciduous broad-leaved and evergreen coniferous species, and RES was higher in deciduous broad-leaved and evergreen broad-leaved species than in evergreen coniferous and deciduous conifer species (Figure S1 in Supporting Information).

Correlation analysis was conducted for three chosen wood indices and two climatic variables and three edaphic variables (Table S2 in Supporting Information). ADD had significant positive correlation with climatic factors ($P<0.01$), had significant negative correlation with soil pH ($P<0.05$), and had weak negative correlation with total soil nitrogen density ($P<0.1$). TSC had no significant correlation with annual mean temperature, annual precipitation, total soil nitrogen density and soil pH, but had weak positive correlation with soil organic carbon density ($P<0.1$). RES had significant positive correlation with annual mean temperature and soil pH ($P<0.05$), had weak negative correlation with total soil nitrogen density ($P<0.1$), and had no significant correlation with other climatic and edaphic variables.

Furthermore, we chose life form, climatic and edaphic variables as independent variables, and used the general linear model to analyze the relative contribution of each variable to the variation of three wood representative indices. The models were all statistically significant ($P<0.001$) despite different explanation rate, which was 23.0%, 30.6%, and 7.2% for ADD, RES, and TSC, respectively. Among the three independent variables, life form had the highest contribution ($P<0.001$), with explanation rate of 21.11%, 4.06% and 25.36% for ADD, TSC and RES, respectively (Table 5). The explanation rate of climatic and edaphic variables on the three wood representative indices differed greatly after removing the influence of life form. For ADD, annual mean temperature and soil pH had the contribution rate of 1.34% and 0.46%; for TSC, annual mean temperature and total soil nitrogen density had the contribution rate of 2.06% and 0.60%; and for RES, annual precipitation, annual mean temperature and soil pH had the contribution rate of 1.62%, 2.00% and 1.49%, respectively.

As life form, climatic and edaphic variables may have collinearity correlation, partial regression was performed to distinguish the contribution of each variable (Figure 3). The results revealed that life form had the highest explanation

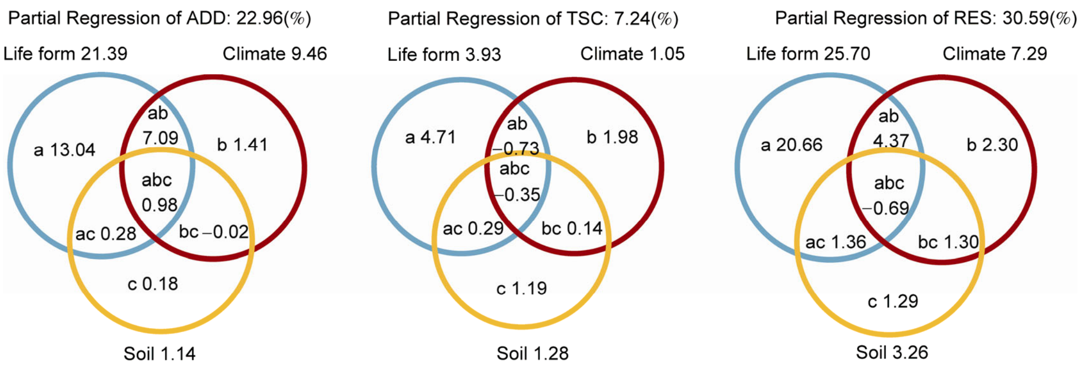

Figure 3 Partial regression analysis of ADD,TSC and RES. Letters indicate significant levels of $P<0.05$, the values of RES are untransformed original value because they would be negative after logarithmic transformation.

Table 5 GLM analysis of ADD, TSC and RES by using life form, climatic and edaphic variables as explanatory variables[a)]

Response	Term	Df	MS	F	P	%SS
ADD						
	Life form	3	1.13	52.52	<0.001***	21.11
	MAP	1	0.01	0.30	0.587	0.04
	MAT	1	0.21	10.00	0.002**	1.34
	SOCD	1	0.00	0.01	0.908	0.00
	TSND	1	0.00	0.02	0.879	0.00
	SPH	1	0.07	3.45	0.068†	0.46
	Residuals	575	0.02			77.04
TSC						
	Life form	3	0.09	8.23	<0.001***	4.06
	MAP	1	0.04	12.50	<0.001***	2.06
	MAT	1	0.00	0.07	0.798	0.01
	SOCD	1	0.01	1.86	0.174	0.31
	TSND	1	0.01	3.64	0.057†	0.60
	SPH	1	0.00	1.29	0.256	0.21
	Residuals	564	2.03			92.76
RES						
	Life form	3	1.22	32.77	<0.001***	25.36
	MAP	1	0.23	6.29	0.013**	1.62
	MAT	1	0.29	7.73	0.006**	2.00
	SOCD	1	0.02	0.47	0.494	0.12
	TSND	1	0.00	0.00	0.991	0.00
	SPH	1	0.21	5.76	0.017**	1.49
	Residuals	564	0.04			69.41

a) MAT, annual mean temperature; MAP, annual precipitation; SOCD, soil organic carbon density; STND, total soil nitrogen density; SPH, soil pH. Df, degree of freedom; MS, mean square; %SS, explanation rate. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; †, $P<0.10$.

rate for ADD, TSC and RES, being 13.04%, 4.71% and 20.66%, respectively; while the explanation rate of climatic and edaphic variables were less than 2.30%. In the large-scale pattern of ADD and RES, the explanation rates of climatic or edaphic variables alone were lower than those of these variables combined with life form, suggesting that the effects of climatic or edaphic variables on spatial variations of wood properties were overridden by life form.

3 Discussion

3.1 Characteristics of wood physical and mechanical properties across major tree species in China and their practical significance

Comparison of wood physical and mechanical properties across major tree species in China shows that the values of main wood properties in hardwood are higher than those in softwood, suggesting that hardwood could meet more practical needs and has wider usage, while softwood normally is more suitable for some special needs. This is in consistent with contemporary Chinese timber source and usage, for instance, the species of commonly used wood such as Oak, Manchurian ash and birch are broad-leaved species [2].

Investigation on three representative wood traits (ADD, TSC and RES) further indicates that the influence of life form varied with wood traits. For RES, the value in hardwood is higher than in softwood; for TSC, hardwood and softwood have no significant difference. Since the usage of wood is not simply determined by density, dry shrinkage coefficient and elasticity, our results suggested that when one wood trait was critical compared to other wood traits, there was no need to choose the timber having higher values in all wood traits. For instance, furniture instruments usually require wood with small dry shrinkage coefficient and pay little attention to resilience. Therefore, we can use softwood with small dry shrinkage coefficient instead of hardwood.

3.2 Improvement of wood physical and mechanical properties prediction model

Wood physical and mechanical properties include density, dry shrinkage coefficient, elasticity, strength, hardness, etc. These properties serve as crucial basis and reference in estimate of wood quality and wood usage [3,15]. Since wood physical and mechanical properties have various indices, the assessment of wood properties based on few critical indices seems very necessary.

It is normally considered that wood density is crucial in determining wood strength, elasticity and hardness. Since wood density is the most readily obtained index, researchers usually establish correlations between wood density and other wood physical and mechanical indices to predicate the value of other wood indices. For instance, on global scale, wood density has significant positive correlation with modulus of elasticity and modulus of rupture, and has power exponent correlation with RES [38]. Zhao et al. [27] analyzed the wood physical properties of Chinese trees and demonstrated that density had a significant linear positive relationship with tensile strength, bending strength and compression strength, while density had power exponent correlation with resilience. Comparison of these empirical models shows that using density alone as predictive variable is inaccurate and insufficient for some wood traits such as bending modulus of elasticity and dry shrinkage coefficient.

The results of PCA indicate that the first axis contributed 68.3% of variation, and the second and third axis contributed another 15.9%. Therefore, only considering the first axis is not enough. Moreover, for wood physical properties except basic density, especially for MOE and dry shrinkage coefficient, empirical models with ADD, TSC and RES as the evaluation index of wood physical properties provided more accuracy and higher explanation power than traditional linear model or power exponent model (Table S3 in Supporting Information). Our results demonstrate that traditional methods of determining wood application or predicting other wood traits based on density [39–41] are debatable. Although wood density is easy to acquire, some other variables such as dry shrinkage coefficient should be taken into account. Our results also implied that despite significant correlations among wood physical traits, certain degree of independence occurs between different wood physical traits.

3.3 Factors controlling geographical pattern of Chinese wood physical properties

Wood is formed by the secondary growth of woody plants [2,3,13]; therefore wood traits are affected by genetic characteristics of woody plants themselves, and are closely associated with the evolutionary status of woody plants [9,12]. Our results indicate that life form exhibits the largest explanation rate for large-scale spatial patterns of ADD, TSC and RES. Since life form can comprehensively reflect the evolution process of plants [42], the results of our study imply that evolution process might be the dominant factor shaping spatial patterns of wood physical properties.

On the other hand, since the growth and development of trees are affected by environmental factors, wood physical traits are inevitably affected by climatic and edaphic factors [17,18,43]. Analyses of GLM indicated that the relationships between climatic factors and wood physical properties were inconsistent after removing the effect of life form: wood density was more affected by temperature, dry shrinkage coefficient was more affected by precipitation, whereas resilience was affected by both temperature and precipitation. In addition, edaphic factors had little effect on wood physical properties after removing the effect of life form.

A number of studies have reported the effect of climatic factors on wood physical properties, especially on wood density, but the conclusions varied with studies. For instance, a study in Mexico stated that wood density had negative correlation with precipitation [44]; a study in Amazon regions with precipitation less than 3000 mm a^{-1} showed significant positive relationship between wood density and precipitation [45], and a study in America revealed positive correlation between wood density and temperature [46]. A global synthesis of 4,667 woody species indicated temperature had stronger effect on wood physical properties than precipitation [9]. In contrast, Zhang et al. [29] reported that both temperature and precipitation had significant relationship with wood physical properties, and the effect of precipitation was stronger than that of temperature.

The results of partial regression analysis indicated that for ADD and RES, the explanation rate of climatic variables and life form combined was much higher than that of climatic variables alone, which implied that the effects of climatic factors on spatial variations of wood properties were indirectly induced by their effects on species distribution. Previous studies demonstrated that factors determining species distribution varied with regions. For instance, species distribution was mainly affected by energy in America [47] and by the lowest temperature of winter in Eastern Asia [48], but was more randomly distributed in Amazon forest [49]. Therefore, the difference of correlations between climatic factors and wood physical properties in these studies may be due to the different effects of climatic factors on species distribution. As to the effect of climatic factors on wood physical properties, Zhang et al. [29] showed that precipitation had a stronger effect on wood density than temperature. However, our results indicated that temperature had a stronger effect on wood density than precipitation.

Other than influencing the pattern of wood physical properties by altering species distribution, environmental factors can affect the physiological process of plant growth and development and thus influence wood physical properties. For instance, a study of *Abies alba* and *Picea abies* found that rising temperature can lead to water deficiency and slow down tree growth and increase wood density [50]. Additionally, edaphic factors can increase soil fertility, impact tree growth and wood chemical composition, and alter wood physical properties [19,51]. In the present study, both GLM and partial regression analysis indicated that climatic and edaphic factors played little role in shaping spatial patterns of wood physical properties. Therefore, environmental factors shape spatial patterns of wood physical properties mainly through species distribution, rather than physiological processes.

Both GLM and partial regression analysis indicated that life form and environmental factors had different explanation rate for ADD, TSC and RES. This result can provide evidence for above statement that certain degree of independence exists in different wood physical properties.

The explanation rate of all factors in our model was lower than 50%, which may be due to two main reasons. First, our study area covered the whole country and had large spatial scale, but the data came from the literatures. These literatures did not report accurate data of environmental factors (climate and edaphic variables) for each site, and we had to use Cokriging interpolation to estimate these data for each site at a low spatial resolution based on the geographical coordinates provided in the literatures. Second, although life form can act as the comprehensive index of genetic evolution, it cannot fully reflect all the information of genetic evolution. Therefore, improvement of the model is needed in further studies.

4 Conclusion

Based on a database of wood physical properties and environmental factors, we explored the spatial patterns and driving factors of wood properties across major tree species in China. Our results showed that (i) certain degree of independence exists between different wood physical properties. Compared with wood density, air-dried density, tangential shrinkage coefficient and resilience provided more accuracy and higher explanation power when used as the evaluation index of wood physical properties. (ii) Among life form, climatic and edaphic variables, life form is the dominant factor shaping spatial patterns of wood physical, climatic factors the next, and edaphic factors have the least effects. This result suggests that the effects of climatic factors on spatial variations of wood properties in China are indirectly induced by their effects on species distribution.

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1 Hickey M, King C. The Cambridge Illustrated Glossary of Botanical Terms. Cambridge: Cambridge University Press, 2000
2 Cheng JQ.Wood Science. Beijing: Forestry Publishing House, 1985
3 Wu R. Microstructural study of sanded and polished wood by replication. Wood Sci Technol, 1998, 32: 247–260
4 Roderick ML, Berry SL. Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. New Phytol, 2001, 149: 473–485
5 Ter Steege H, Hammond DS. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. Ecology, 2001, 82: 3197–3212
6 Larjavaara M, Muller-Landau HC. Rethinking the value of high wood density. Funct Ecol, 2010, 24: 701–705
7 Sterck FJ, Bongers F, Newbery DM. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. Plant Ecol, 2001, 279–292
8 Van Gelder H, Poorter L, Sterck F. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. New Phytol, 2006, 171: 367–378
9 Swenson NG, Enquist BJ. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. Am J Bot, 2007, 94: 451–459
10 Chao KJ, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama A, Martinez RV. Growth and wood density predict tree mortality in Amazon forests. J Ecol, 2008, 96: 281–292
11 Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol, 2004, 10: 545–562
12 Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecol Appl, 2006, 16: 2356–2367
13 Bergman R, Cai Z, Carll CG, Dietenberger MA, Falk RH, Frihart CR, Glass SV, Hunt CG, Ibach RE, Kretschmann DE, Lebow ST, Rammer DR, Ross RJ, Stark NM, Wacker JP, Wang XP, Wiedenhoeft AC, Wiemann MC, Zelinka SL. Wood Handbook: Wood as an Engineering Material. Madison, Wisconsin: US Department of Agriculture, Forest Service, Forest Products Laboratory, 2010
14 FAO. FAO Yearbook of Forest Products 2011. 2013
15 Bowyer JL, Shmulsky R, Haygreen JG. Forest Products and Wood Science: An Introduction. Ames, IIowa: Blackwell Publishing, 2007
16 Carlquist S. Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood. Springer, 2001
17 Quesada CA, Phillips OL, Schwarz M, Czimczik CI, Baker TR, Patino S, Fyllas NM, Hodnett MG, Herrera R, Almeida S, Davila EA,

Arneth A, Arroyo L, Chao KJ, Dezzeo N, Erwin T, di Fiore A, Higuchi N, Coronado EH, Jimenez EM, Killeen T, Lezama AT, Lloyd G, Lopez-Gonzalez G, Luizao FJ, Malhi Y, Monteagudo A, Neill DA, Vargas PN, Paiva R, Peacock J, Penuela MC, Cruz AP, Pitman N, Priante N, Prieto A, Ramirez H, Rudas A, Salomao R, Santos AJB, Schmerler J, Silva N, Silveira M, Vasquez R, Vieira I, Terborgh J, Lloyd J. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences, 2012, 9: 2203–2246

18 Briffa K, Schweingruber F, Jones P, Osborn T, Shiyatov S, Vaganov E. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature, 1998, 391: 678–682

19 Muller-Landau HC. Interspecific and inter–site variation in wood specific gravity of tropical trees. Biotropica, 2004, 36: 20–32

20 Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. Towards a worldwide wood economics spectrum. Ecol Lett, 2009, 12: 351–366

21 Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SE, Coomes DA. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. Am J Bot, 2010, 97: 207–215

22 Poorter L, McDonald I, Alarcón A, Fichtler E, Licona JC, Peña-Carlos M, Sterck F, Villegas Z, Sass-Klaassen U. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol, 2010, 185: 481–492

23 Cheng JQ, Yang JJ, Liu P. Anatomy and Properties of Chinese Woods. Beijing: Forestry Publishing House, 1992

24 Research Institute of Wood Industry, Chinese Academy of Forestry. Wood Physical and Mechanical Properties of Main Tree Species in China. Beijing: Forestry Publishing House, 1982

25 Jiang XM, Cheng YM, Yin YF. Atlas of Gymnosperms Woods of China. Beijing: Science Press, 2010

26 Bao PC, Jiang ZH. Wood Properties of Main Tree Species from Plantation in China. Beijing: Forestry Publishing House, 1998

27 Zhao CR, Dong YK. Synthetical analysis of physical and mechanical properties of wood (ii)—correlation analysis. J Northeast Forest Univ, 1989, 17: 45–54

28 Zhao CR, Dong YK. Synthetical analysis of physical and mechanical properties of wood (i)—principal component analysis. J Northeast Forest Univ, 1988, 16: 105–118

29 Zhang SB, Slik J, Zhang JL, Cao KF. Spatial patterns of wood traits in China are controlled by phylogeny and the environment. Global Ecol Biogeogr, 2011, 20: 241–250

30 Fang JY, Wang ZH, Tang ZY. Atlas of Woody Plants in China: Distribution and Climate. Beijing: Higher Education Press, 2009

31 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol, 2005, 25: 1965–1978

32 Ma WH, He JS, Yang YH, Wang XP, Liang CZ, Mohammat A, Zeng H, Fang JY, Schmid B. Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites. Global Ecol Biogeogr, 2010, 19: 233–243

33 Yang YH, Mohammat A, Feng JM, Zhou R, Fang JY. Storage, patterns and environmental controls of soil organic carbon in China. Biogeochemistry, 2007, 84: 131–141

34 Yang YH, Ma WH, Mohammat A, Fang JY. Storage, patterns and controls of soil nitrogen in China. Pedosphere, 2007, 17: 776–785

35 Xiong Y, Li J. Soil of China. Beijing: Science Press, 1986

36 R Development Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austrilia: 2014

37 Lê S, Josse J, Husson F. Factominer: an r package for multivariate analysis. J Stat Softw, 2008, 25: 1–18

38 Armstrong J, Skaar C. The effect of specific gravity on several mechanical properties of some world woods. Wood Sci Technol, 1984, 18: 137–146

39 Chen R, Tong FP, Li G, Liu ZH, Zhang H, Tang J. Longitudinal variation patterns of timber wood material property, chemical composition and calorific value of *Castanopsis fissa*. Chin Agricult Sci Bull, 2013, 16: 24–28

40 Ji KS, Wang ZR, Qiu JQ, Chen YB, Lin WJ. Selection, propagation and cultivation of *Pinus massoniana* clones for pulp use. Sci Silvae Sin, 2004, 40: 64–69

41 Guan N, Liu ZX, Pan ZG. Variation of wood basic density and tracheid lengthof different provenances loblolly and slash pines. Forest Res, 1993, 6: 235–241

42 Feng Y, Xu HL, Zhou B. Florae and their ecological characteristics in the lower reaches of Tarim River. Acta Bot Boreali-Occident Sin, 2005, 25: 2285–2288

43 Beets P, Gilchrist K, Jeffreys M. Wood density of radiata pine: effect of nitrogen supply. Forest Ecol Manag, 2001, 145: 173–180

44 Barajas-Morales J. Wood specific gravity in species from two tropical forests in Mexico. IAWA Bull, 1987, 8: 143–148

45 Patiño S, Lloyd J, Paiva R, Baker TR, Quesada CA, Mercado LM, Schmerler J, Schwarz M, Santos AJB, Aguilar A, Czimczik CI, Gallo J, Horna V, Hoyos EJ, Jimenez EM, Palomino W, Peacock J, Sarmiento C, Sota A, Turriago JD, Villanueva B, Vitzthum P, Alvarez E, Arroyo L, Baraloto C, Bonal D, Chave J, Costa ACL, Herrera R, Higuchi N, Killeen T, Leal E, Meir P, Monteagudo A, Neil D, Pitman N, Priante Filho N, Prieto A, Panfil SN, Rudas A, Silva N, Silveira M, Soares deAlmeida S, Torres-Lezama A, Vásquez-Martínez R, Vieira I, Malhi Y, Phillips OL. Branch xylem density variations across the Amazon basin. Biogeosciences, 2009, 6: 545–568

46 Wiemann MC, Williamson GB. Geographic variation in wood specific gravity: effects of latitude, temperature, and precipitation. Wood Fiber Sci, 2002, 34: 96–107

47 Currie DJ. Energy and large-scale patterns of animal-and plant- species richness. Am Nat, 1991, 27–49

48 Wang Z, Fang J, Tang Z, Lin X. Patterns, determinants and models of woody plant diversity in China. P Roy Soc B: Biol Sci, 2011, 278: 2122–2132

49 Chave J. Neutral theory and community ecology. Ecol Lett, 2004, 7: 241–253

50 Barber VA, Juday GP, Finney BP. Reduced growth of alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature, 2000, 405: 668–673

51 Novaes E, Kirst M, Chiang V, Winter-Sederoff H, Sederoff R. Lignin and biomass: a negative correlation for wood formation and lignin content in trees. Plant Physiol, 2010, 154: 555–561

Supporting Information

Table S1 General statistical characteristics of main wood physical properties

Table S2 Relationships between ADD, TSC, RES and climatic and edaphic factors, showing the correlation coefficient and significance level

Table S3 Goodness of fit for linear model and power exponent model of other wood physical properties by using air-dried density as explanatory variable.

Figure S1 Comparison of ADD (A), TSC (B) and RES (C) among different life forms. Different letters mean significant difference level at $P<0.05$.

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