

# Stand Feature Associating With Climate Seasonality Determinate Root-Shoot Ratios of Forest Ecosystems in China

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## Research

**Keywords:** stand age, stand density, environmental factor, root-shoot ratio, Random Forest algorithm

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# Abstract

**Background:** Forest ecosystems play a crucial role in global carbon cycle. Identifying bio- or abio- drivers on forest biomass allocation pattern could improve our understanding in forest carbon sink, stock and cycle across various spatio-temporal scales. Through compiling a dataset (n=1931) of the root-shoot ratio from previous studies, here we implemented the Random Forest algorithm (RF) to elucidate main driven factors on the root-shoot ratio across China forest ecosystems.

**Results:** (1) Forest age and forest density were both contributed mostly to root-shoot ratio variations regardless of forest origins (natural or planted forests). The relative important values (% increase in MSE) for forest density and forest age on the root-shoot ratio were 54.42% and 51.05% in the natural forests, and 74.61% and 117.27% in the planted forests, respectively; (2) Compared to soil variables (soil texture and nutrient status), climatic variables (temperature and precipitation) showed stronger effects on the root-shoot ratio; (3) Partial dependent analysis further demonstrated that root-shoot ratio initially decreased with forest age, but afterwards increased to a relative stable level (the turning point, e.g., ca. 150 yr for natural forests and ca.30 yr for planted forests); (4)The root-shoot ratio increased nonlinearly with an increase of forest density in both forest types. Forest density and precipitation seasonality exerted positively direct effects, while forest age together with temperature seasonality, mean temperature of wettest quarter and precipitation of warmest quarter had negatively effects on the root-shoot ratio of two forest types.

**Conclusions:** The forest age, forest density and climate seasonality contributed mostly to variations of root-shoot ratios in China forest ecosystems. These results would improve our understanding of environmental drivers on forest biomass allocation over a large spatial scale, and to some extent provide a generally practical significance in forest management (e.g., time for timber harvest), although species-specific root-shoot ratio associated with ontogeny should be further investigated in the future.

## Background

Besides substance provision for human society, forest ecosystems provide services such as storing carbon, hosting biodiversity, and regulating climate (Pan et al., 2011; Trumbore et al., 2015). Thus, understanding the process of forest biomass accumulation and allocation strategies responding to currently environmental changes, e.g., climate warming and frequent drought, is crucial for forest management practice (Shestakova et al., 2016; Zhu et al., 2018) and has important implications for the accuracy of global carbon cycle modeling and accounting (Enquist and Niklas, 2002; Jiang and Wang, 2017; Pan et al., 2011). Relative to natural forests, increasing planted forests play more and more important roles in wood supply and ecological services (Chen et al., 2019; Liu et al., 2014). Consequently, elucidating driven mechanism of biomass allocation, especially for planted forests with major cultivated targets for wood production, has important realistic significances.

Natural and planted forests have been found to be distinctly different in terms of carbon stock and water consumption (Yu et al., 2019), drought resistance (Domec et al., 2015), herbivory defense (Schuldt et al., 2015), as well as service function (Cao et al., 2019). The explanations for those disparities were mostly contributed by contrasting species composition and stand structure between two origins. For example, natural forests generally featured with more species richness increase ecosystem carbon storage (Liu et al., 2018), while planted forests had higher productivity and thus higher carbon sequestration rates due to only highly productive species were planted (Guo and Ren, 2014). Root-shoot ratio, a key parameter to describe the biomass allocation between aboveground and belowground, provides a practical tool to estimate belowground biomass (BGB) by relatively easily measured aboveground biomass (AGB) (Marziliano et al., 2015; Mokany et al., 2006; Paul et al., 2019). It not only reflects a plant's specific adaptive responses to its environment (Agathokleous et al., 2019), but also acts as a key descriptor for terrestrial ecosystem carbon modeling (Wang et al., 2008). Previous studies have proved that root-shoot ratio varied with environmental factors, e.g., climate (Matías et al., 2014; Wang et al., 2008), soil texture (Jiang and Wang, 2017; Wang et al., 2014), soil nutrients (Camila Aguetoni et al., 2011; Gedroc et al., 1996; Ma et al., 2019). Among climatic variables, Reich et al. (2014) demonstrated that temperature was a better predictor of biomass allocation than moisture availability because fractional distribution of biomass to roots or foliage was unrelated to aridity, while Guo et al. (2016) revealed that both temperature and precipitation were critical to carbon allocation.

Apart from environmental factors, forest features, such as forest age and forest density, also play important roles in biomass production and thus allocation, e.g., forest age can enhance biomass and productivity via increases in tree size (Barry et al., 2019), and forest density increased forest carbon storage and wood production through higher canopy packing for more light capture (Forrester et al., 2018). The pattern of root-shoot ratio has been proved to vary with forest age and forest density by numerous studies (Fang et al., 2018; Li and Liu, 2014; Peichl and Arain, 2007; Song et al., 2018). For example, King et al. (2007) found that root-shoot ratio of individual trees increased significantly from sapling to mid-mature stage, and then dramatically decreased at the old-stage; while Yang et al. (2019) demonstrated that the ratio of belowground biomass to aboveground biomass of *Quercus acutissima* forests decreased constantly with stand age. Furthermore, Zhang et al. (2016) showed that stand characteristics (tree age and density) had a marked impact on forest biomass accumulation, but it, associated with climate and soil chemistry, exerted no significant effect on biomass allocation, e.g., root-shoot ratio. Therefore, when considering the dependence of biomass allocation on abio- or bio-factors, the relative importance and their interaction of those factors on root-shoot ratio remain unclear, especially at large spatial scales (e.g. national).

China has by far the largest planted forest area at 91.8 million ha around the world, which account for 23% of the total global forest plantation area (Payn et al., 2015). According to the 9<sup>th</sup> National Forest Inventory, planted forests and natural forests contribute to 36.45% and 63.55% of China's total forest area, respectively (Zhang, 2019). Planted forests in China have undergone a continuous expansion in the past 30 years, which has significantly contributed to an increase in total forest cover and timber supply

as well as other ecosystem services like carbon sequestration (Liu et al., 2014; Xu and Li, 2010; Zhang et al., 2020). Meanwhile, China has diverse climatic zones, ranging from north temperate to tropic. It has a good representation of global biome heterogeneity and environmental gradients, and thus provides an excellent opportunity to explore possible sources of variation in the pattern of root-shoot ratio across forest ecosystems. In the present study, by re-compiling previously published data of root-shoot ratio across China forests, we focus on differences between two forest origins (natural forests vs planted forests), and aim to: (1) identify relative importance of various environmental factors on root-shoot ratio; (2) tease apart indirect and direct effects of environmental factors on the root-shoot ratio. Our results could help to improve our understandings of driven mechanism in the root-shoot ratio or forest biomass allocation strategy over a large spatial scale.

## Methods

### Data collection

Three published datasets were collected in the present study (Fig.1), including 1022 records from Zhang et al. (2015), 418 records from Wang et al. (2014) and 1607 records from Luo et al. (2014). To consistently characterize the climatic and soil conditions presenting at each stand, we used a subset of the 19 bioclimatic variables from the WorldClim database ([www.worldclim.org](http://www.worldclim.org)) with 30-second resolution, and 10 soil variables (~30 cm in depth) from the global dataset ([globalchange.bnu.edu.cn](http://globalchange.bnu.edu.cn)) with 30-second resolution (Table 1), which were extracted according to geographic locations of forest stands provided by three above references using ArcGIS v.10. The procedures used to calculate these climatic and soil variables were fully described in Fick and Hijmans (2017) and Shangguan et al. (2014), respectively.

### Table 1 Environmental variables used in this study

<b>Variable</b>	<b>Explanation and Unit</b>
<b>BI01</b>	Annual Mean Temperature, 0.1°C
<b>BI02</b>	Mean Diurnal Range (Mean of monthly (max temp - min temp)) , 0.1°C
<b>BI03</b>	Isothermality (BI02/BI07) (* 100)
<b>BI04</b>	Temperature Seasonality (standard deviation *100)
<b>BI05</b>	Max Temperature of Warmest Month, 0.1°C
<b>BI06</b>	Min Temperature of Coldest Month, 0.1°C
<b>BI07</b>	Temperature Annual Range (BI05-BI06) , 0.1°C
<b>BI08</b>	Mean Temperature of Wettest Quarter, 0.1°C
<b>BI09</b>	Mean Temperature of Driest Quarter, 0.1°C
<b>BI010</b>	Mean Temperature of Warmest Quarter, 0.1°C
<b>BI011</b>	Mean Temperature of Coldest Quarter, 0.1°C
<b>BI012</b>	Annual Precipitation, mm
<b>BI013</b>	Precipitation of Wettest Month, mm
<b>BI014</b>	Precipitation of Driest Month, mm
<b>BI015</b>	Precipitation Seasonality (Coefficient of Variation)
<b>BI016</b>	Precipitation of Wettest Quarter, mm
<b>BI017</b>	Precipitation of Driest Quarter, mm
<b>BI018</b>	Precipitation of Warmest Quarter, mm
<b>BI019</b>	Precipitation of Coldest Quarter, mm
<b>TN</b>	Total soil N content, g/100g
<b>TP</b>	Total soil P content, g/100g
<b>TK</b>	Total soil K content, g/100g
<b>pH</b>	Soil pH Value (H <sub>2</sub> O)
<b>SOM</b>	Soil organic matter content, g/100g
<b>BD</b>	Soil bulk density, g/cm <sup>3</sup>
<b>POR</b>	Soil porosity, cm <sup>3</sup> /100cm <sup>3</sup>
<b>SA</b>	Soil sand content, g/100g
<b>SI</b>	Soil silt content, g/100g

## Statistical analysis

All the statistical analyses were implemented in R statistical software (RStudio 1.1.463 with R version 3.5.2). Firstly, outliers of root-shoot ratios in the recompiled dataset were removed by recognizing with four times standard deviations. And to more clearly demonstrate the dependent variables (root-shoot ratio) responding to environmental factors (climatic and soil variables), we used correlation analysis to exclude four non-significantly independent variables (BD, TN, SOM, SI) (Fig.S1), and then used the variance inflation factor (VIF,  $r > 0.7$ ) to remove strongly multi-collinear variables with R package “usdm”, which would severely distort model estimation (Dormann et al., 2013). The left variables included 5 bioclimatic variables (BIO3, BIO4, BIO8, BIO15 and BIO18), 5 soil variables (pH, POR, TP, TK, SA), and together with 2 stand variables (forest age, yr and forest density, number/ha<sup>-1</sup>) were further proceeded with VSURF function (package “VSURF”) (Genuer et al., 2015) to identify and remove the least important variables based on the importance of predictive variables. And Random Forest (RF) machine learning algorithm (Breiman, 2001) was then used to run and assess the relative importance (VIMP) of commonly selected variables on the root-shoot ratio for full, natural and planted forests, separately. The VIMP used in the present study was based on the percentage increase in the mean squared prediction error (% IncMSE). A large VIMP value indicates that incorrect specification detracts from the variable predictive accuracy in the forest, a VIMP close to zero indicates that the variable contributes nothing to predictive accuracy, and negative values indicate that the predictive accuracy improves when the variable is not correctly specified (Breiman, 2001). RF builds several regression trees based on bootstrap resamples of training data, then retrieves the relative importance of each variable by averaging estimates from all regression trees, which increases tolerance for collinearity effects from multiple variables (Dormann et al., 2013) and minimizes spatial autocorrelation problems (Crane et al., 2012). To assess the predictive ability and the performance of RF models, we conducted the 10-fold repeated cross-validation, as each model was refitted 10 times using 90% of the data and predictions derived from the fitted models were compared with observations of the remaining 10%, by using the R package “rfUtilities” (Evans and Murphy, 2015). Cross-validated estimates of root-mean-square error (RMSE), Mean Absolute Error (MAE) and median percentage of explained variation ( $R^2_{\text{pseudo-median}}$ ) were reported for 1000 cross-validations. The significance of the importance of driving variables was assessed with R package “rfPermute” (Archer, 2016), and the selected variables’ contributions to the root to shoot ratio were also illuminated by partial dependent analysis with partialPlot function of the package “randomForest” (Liaw and Wiener, 2002).

Given that the predictive variables might also be correlated, Structural Equation Models (SEMs) were further constructed to tease apart indirect and direct effects of environmental factors on the root-shoot ratios with a multivariate approach using R package “lavaan” (Rosseel, 2012). SEM is a powerful tool to analyze the relationships among causally linked inter-correlated variables. Each single-headed arrow in an SEM represents a hypothesized causal relationship where the variable at the tail of the arrow is a

direct cause of the variable at the heard (Ma et al., 2020). Goodness-of-fit index (GFI), comparative fit indexes (CFI), root MSE of approximation (RMSEA) and standardized root mean square residual (SRMR) are used for evaluation of global fit as a good fit when GFI/CFI > 0.95, RMSEA < 0.08, SRMR < 0.06 (Hu and Bentler, 1999). In addition, due to some variables were not normal, we confirmed the fit of the model using the Bollen-Stine bootstrap test (P value >0.10 for good fit) (Schermelleh-Engel et al., 2003).

## Results

### Root-shoot ratio varied between two origins

The re-compiled dataset covered a large range of environmental variations, e.g., annual mean temperature ranged from -5.7 °C to 24.9°C, and annual precipitation ranged from 25 mm to 3354 mm (Table S1). The root-shoot ratios varied between forest origins (Fig.S1), as the ratios of the natural forests (mean±se,  $0.243 \pm 0.003$ , n = 653) was marginally significantly higher than that of planted forests ( $0.236 \pm 0.002$ , n =1278) ( $p = 0.073$ ). For the natural forests, root-shoot ratio ranged from 0.057 to 0.620 with median value as 0.237; while for the planted forests, it ranged from 0.033 to 0.588 with median value as 0.225.

### Relative importance of variables on root-shoot ratio

The six variables (forest age, forest density, BIO4, BIO8, BIO15 and BIO18) were finally identified as most important factors affecting the root-shoot ratio of forest ecosystems in China. With these variables, RF models performed moderately well on variations of the root-shoot ratio, e.g., they explained 28.35 % (RMSE = 1.87%, MAE = 1.11%), 33.18 % (RMSE = 1.59%, MAE = 0.76%) and 33.42 % (RMSE = 1.34%, MAE = 0.68%) variations of the root-shoot ratio in the natural, planted and full forest stands, respectively (Table 2, Fig. 2). Relative importance value (VIMP) and order of the selected environmental factors on the root-shoot ratio varied with forest origins (Table 2, Fig. S2), but forest age or forest density was generally contributed to the most importance in the root-shoot ratio variations regardless of forest origins. For the full dataset, the forest age (133.80%), BIO18 (108.74%) and forest density (102.31%) accounted for the top three important variables on the root-shoot ratios (Table 2, Fig. 2a). For the natural forests, VIMP with the decreasing order was forest density (54.42 %), forest age (51.05%), BIO4 (48.97%), BIO8 (48.95%), BIO18 (47.05%), BIO15 (38.95%) (Table 2, Fig. 2b); for the planted forests, the largest VIMP was forest age (117.27 %), followed by BIO18 (99.45%), BIO4 (79.54%), BIO15(77.21%), BIO8 (75.35%) and forest density (74.61%) (Table 2, Fig. 2c). Significantly linear relationship occurred between the RF-based predicted root-shoot ratio (RS) and the field observed RS across forest origins (Fig.2 d-f).

**Table 2 Relative importance of the variables selected by the VSURF function on the root-shoot ratios in forest ecosystems of China.  $R^2_{\text{pseudo}}$  and  $\text{MSE}_{\text{fitted}}$  were calculated from model predicted against observed values; RMSE and MAE derived from media cross-validation;  $R^2_{\text{pseudo-median}}$  was median permuted percent variance explained.**

Variables	Full data		Natural forest		Planted forest	
	%IncMSE	<i>P</i>	%IncMSE	<i>P</i>	%IncMSE	<i>P</i>
Forest age	133.80	0.020	51.05	0.020	117.27	0.020
Forest density	102.31	0.020	54.42	0.020	74.61	0.020
BIO4	90.49	0.020	48.97	0.020	79.54	0.020
BIO8	91.22	0.020	48.95	0.020	75.35	0.020
BIO15	86.80	0.020	38.95	0.020	77.21	0.020
BIO18	108.74	0.020	47.05	0.020	99.45	0.020
Model performance						
$R^2_{\text{pseudo}}$ , %	34.42		28.35		33.18	
$\text{MSE}_{\text{fitted}}$ , %	0.44		0.57		0.41	
RMSE, %	1.34		1.87		1.59	
MAE, %	0.68		1.11		0.76	
$P_{\text{value}}$	<0.001		<0.001		<0.001	
$R^2_{\text{pseudo-median}}$ , %	97.12		94.30		95.97	

### Partial dependent of root-shoot ratio on environmental variables

Overall, root-shoot ratio decreased with increase of forest age for both forest origins. However, after initial decrease it turned to increase to a relative stable level (the turning point, e.g., ca. 150yr occurring for natural forests and ca.30yr for planted forests) (Fig.3-a, g). The root-shoot ratio increased nonlinearly with forest density in both forest origins (Fig.3). The ratios decreased with temperature seasonality (BIO4) until to ~50°C (natural) and ~70°C (planted), and then increased. The ratios responding to mean temperature of wettest quarter (BIO8) was opposite between two origins when  $\text{BIO8} < 15^\circ\text{C}$ , as presenting increasing trend for natural forest while with decreasing trends for planted forests. Interestingly, root-shoot ratios responded to precipitation seasonality (BIO15) with cosine-like trend in the natural forest, while with inverse parabolic trend in the planted forest. Specially, both origins initially decreased with BIO15 toward the bottoms (~ 60 mm for natural and ~75mm for planted forest) and then rebound, but only descend again in the natural forest (vertex value: ~ 90 mm). Finally, consistent trends were also observed in the response of root-shoot ratio to precipitation of warmest quarter (BIO18) for two forest origins, as initially sharply decreasing but after  $\text{BIO18} \approx 500\text{mm}$ , both turning to slightly increase afterwards.

## Direct and indirect effects of environmental factors on root-shoot ratio

SEMs explained a few variations of root-shoot ratio (Fig.4), e.g., 16.5% for natural forest and 4.9% for planted forest, which maybe contributed mostly by strongly non-linear correlation between dependent and independent variable as revealed by above partial analysis (Fig.3), but still providing to some extent information about the direct and indirect effects of variables on the root-shoot ratio studied. Consistently, four variables (forest age, BIO4, BIO8 and BIO18) had direct negative effects on root-shoot ratio of both origins, and their standardized direct effects were -0.108, -0.094, -0.092 and -0.229 in the natural forests, and -0.080, -0.015, -0.099 and -0.092 in the planted forests, respectively (Table S2). Two variables (forest density and BIO15) had direct positive effects on root-shoot ratio, and their standardized direct effects were 0.177 and 0.165 in the natural forests, and 0.096 and 0.099 in the planted forests. Meanwhile, only two variables (forest age and BIO15) exerted significantly indirect negative effects on root-shoot ratio through forest density, and their indirect effects were -0.080 and -0.014 in the natural forests, and -0.033 and -0.011 in the planted forests (Fig.4, Table S2).

## Discussions

### The effects of stand feature on root-shoot ratios

We found that the natural forests showed slightly higher root-shoot ratio than planted forests (Fig.S1), which was consistent with other studies (Luo et al., 2012; Mokany et al., 2006; Wang et al., 2008). The discrepancy in the root-shoot ratio between two forest origins could be explained by the optimal partitioning theory (OPT), which suggesting that plants preferentially allocate biomass to the organ that acquires the limiting resources (Bloom et al., 1985; Eziz et al., 2017; Reich, 2002). For instance, compared to natural forests, planted forests are generally established in areas with fertile and moist soils associated with site preparation activities, leading to enhanced aboveground biomass at the cost of belowground biomass. The initially decreasing trends observed for root-shoot ratio responding to forest age (Fig.3) were in accordance with other studies (Guo and Ren, 2014; McConnaughay and Coleman, 1999; Mokany et al., 2006; Peichl and Arain, 2007), and could be regarded as a natural consequence of plant ontogeny, leading to the accumulation of aboveground biomass as a stand develops. However, the turning points occurred in this study may suggest that the trees allocate more biomass into below-ground once the stands reach up to quantitative maturity. For example, Zhu et al. (2018) found that the aboveground biomass accumulates rapidly at young stand age and gradually saturates at later stages. Meanwhile, planted forests were generally cultivated with fast-growing species associated with more intensive management activities, which would account for the differences in the age estimated of the turning point between the two forest origins. The root-shoot ratio increased nonlinearly with an increase of forest density in both forest types, which was consistent with most previous reports (Mokany et al., 2006). The increased density caused more intensive competition within stands, leading trees to invest more biomass into below-ground parts.

Interestingly, forest density had the most important effects on the root-shoot ratio of natural forests, while forest age acted the decisive role on the root-shoot ratio of planted forests in the present study. This discrepancy was mostly contributed by the features of both origins. For the natural forests, competition for space (either belowground or aboveground) was crucial for individuals' survival and growth, e.g., competition for soil water or nutrient at the belowground and for light resource at the aboveground; meanwhile, compared to the planted forests, higher competition intensity at the understory of the natural forests suggest more consumption for soil water and nutrients by neighbors, leading to more biomass investment into roots to acquire resources from deeper soil; while for the planted forests, the densities were generally arranged according to the space requirement of the planted species and sometimes associated with thinning operations along the development of stands; therefore, tree age (a proxy of size) accounted for the most important factor on root-shoot ratio in the planted forests (Ledo et al., 2018). In addition, compared to monospecific stands of the planted forests, mixed-species stands occurred in natural forests generally led to more production partitioning belowground in all stand ages due to increased fine root production (Ma et al., 2019).

### **The role of climatic variables in determining root-shoot ratios**

The root-shoot ratio decreased with temperature of growing season (especially when BIO8 >15°C), which was partially in accordance with (Reich et al., 2014; Wang et al., 2014). The negative relationship between root-shoot ratio and temperature could be explained by the factor that less biomass is allocated into roots at higher temperatures because the increasing temperature enhances water and nutrient availability, leading to less water and nutrients demanded by roots to maximize tree growth rate (Luo et al., 2012). On the other hand, the root-shoot ratio presented a decreasing trend with precipitation of growing season (when BIO18 < 500mm), which was consistent with most of previous studies (Fang et al., 2018; Luo et al., 2012; Qi et al., 2019). Mokany et al. (2006) demonstrated that root-shoot ratio was negatively correlated with precipitation for forests and woodlands worldwide. As prediction from the optimality theory, root biomass fraction would increase with the decrease of precipitation (Fang et al., 2018). When precipitation increases, water supply would become sufficient and trees could allocate less biomass to roots for soil water uptake; but when the increasing precipitation exceeds the threshold of forest water demands (here BIO18≈500mm for both forest origins), forests may be limited by soil nutrient rather than by water availability, causing more biomass allocated into roots for more nutrient uptake from the soil.

We also found that precipitation seasonality had significantly direct effects on stand density, thus exerted indirect effects on the root-shoot ratio. It may suggest that climate variables may mediate the effects of forest density on root-shoot ratio, through influencing rate of carbon accumulation and inducing self-thinning of stands (Panayotov et al., 2016; Xu et al., 2019). Soil variables had no significant effects on root-shoot ratio of both forest origins in the present study, which was contradict to other studies (Jiang and Wang, 2017; Wang et al., 2014). For example, Wang et al. (2014) found that soil texture altered the response of root-shoot ratio to climatic factors, and lower water and nutrient availability from sandy soil may be responsible for the larger root-shoot ratio. Ma et al. (2019) found that both aboveground production and its partitioning to aboveground increased significantly with the availability of soil

nutrients. This inconsistency would be contributed by two reasons. Firstly, over a large scale, climate could over-whelm the effect of soil variables on root-shoot ratio, due to development of soil feature generally associate with specific climate (Luo et al., 2017); secondly, the soil variables used in this study were interpolated instead of field data (Shangguan et al., 2014), which to some extent would blur the specific soil characteristics of stands studied. Soong et al. (2020) demonstrated recently that soil properties contributed to explain tree growth and mortality, but not biomass across tropical forests. Finally, the interspecific and intraspecific variations of biomass allocation responding to environmental factors (Shao et al., 2019; Veresoglou and Peñuelas, 2019) were not taken into account for the pattern of root-shoot ratio in the present study, which would be deserved to address the biomass allocation strategy of trees in the future study.

## Conclusions

This study separately evaluated the relative importance of climatic variables, soil properties, stand age and density on the root-shoot ratio of natural and planted forests across China. We found that forest age and forest density were both contributed mostly to root-shoot ratio variations regardless of forest origins. The turning point (age) in the relationship between root-shoot ratio and forest age, to our best knowledge, was first time to be uncovered for both forest origins (e.g., ca. 150yr for natural forests and ca.30yr for planted forests). Compared to soil variables, climatic variables showed stronger effects (direct and indirect through stand features) on the root-shoot ratio. Although more efforts should be made for species-specific pattern of root-shoot ratio over large spatial scale, our result to some extent improve our understanding of forest biomass allocation against forest origin and forest age.

## Declarations

### Authors' contributions

J. Liu devised the main theoretical framework and proof outline. F. Kang and J. Liu performed the model simulations, and both took the lead in writing the manuscript. A. Yu and M. Guo processed the climate/soil data and provided technical support for the research. Q. Wang, Z. Jiang and W. Xiao provided significant feedback and helped improve the research and manuscript. The author(s) read and approved the final manuscript.

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### Availability of data and materials

The datasets used and/or analyzed in this study are available from the corresponding author on request.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

All authors have no conflict of interest.

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## Figures

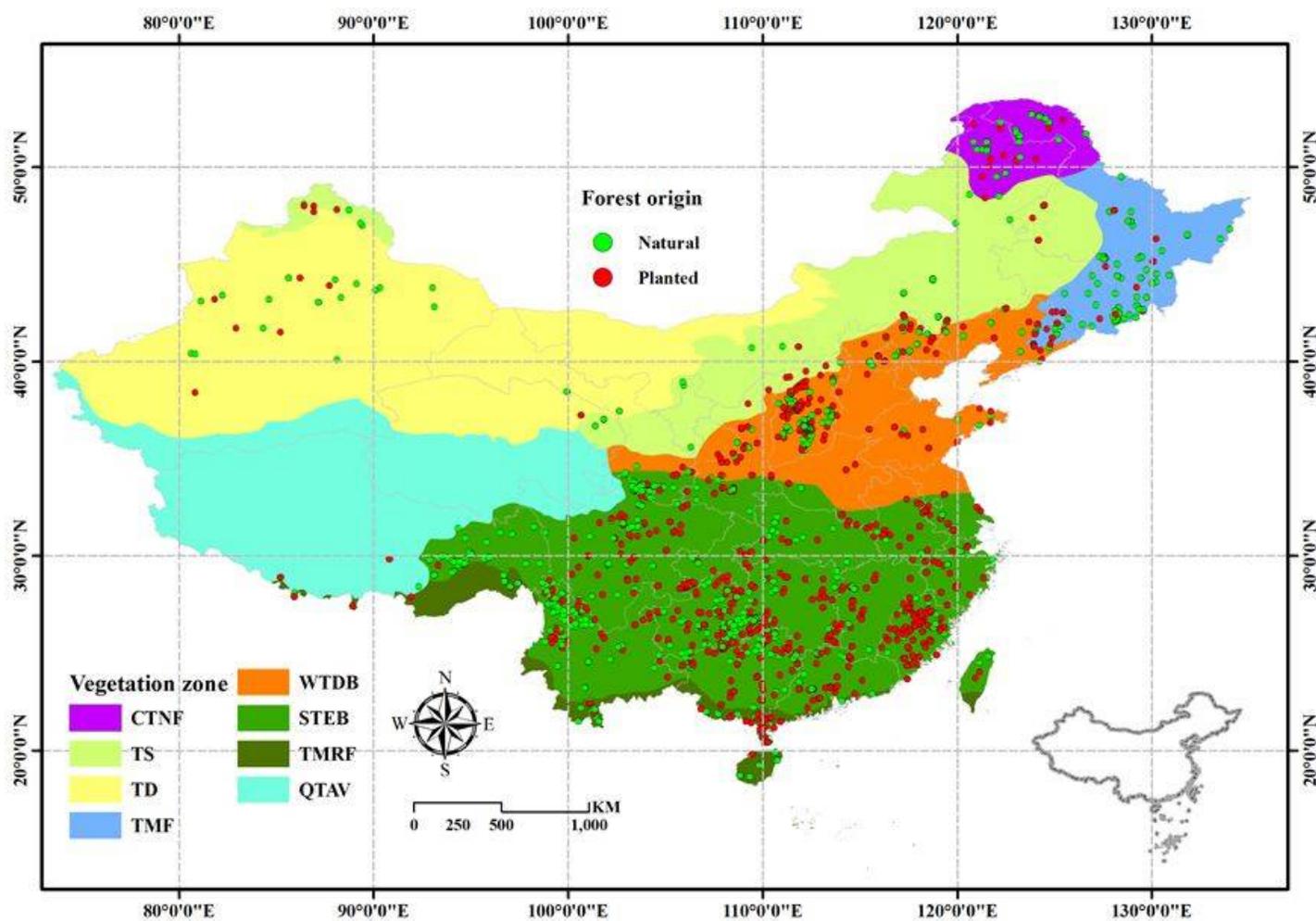
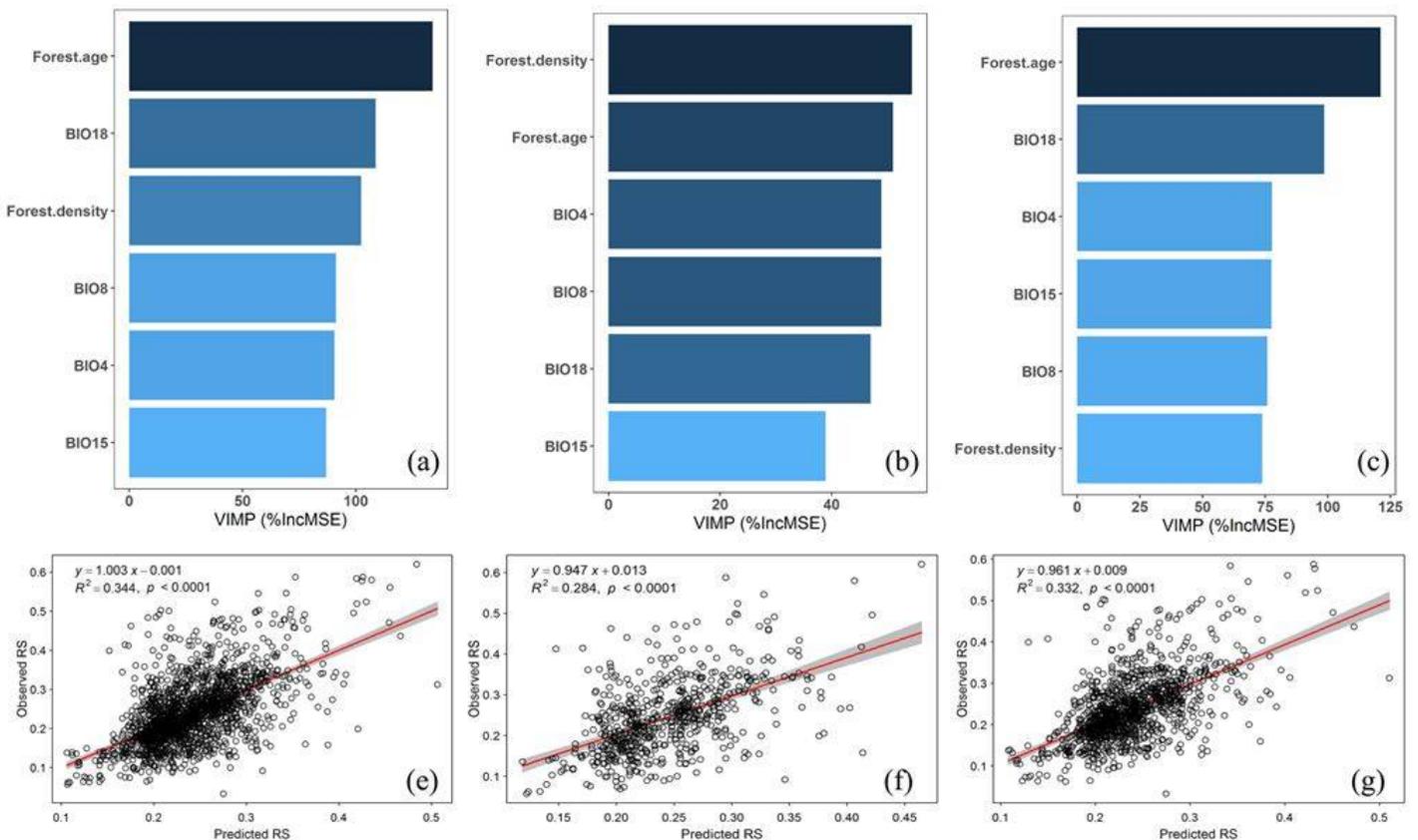


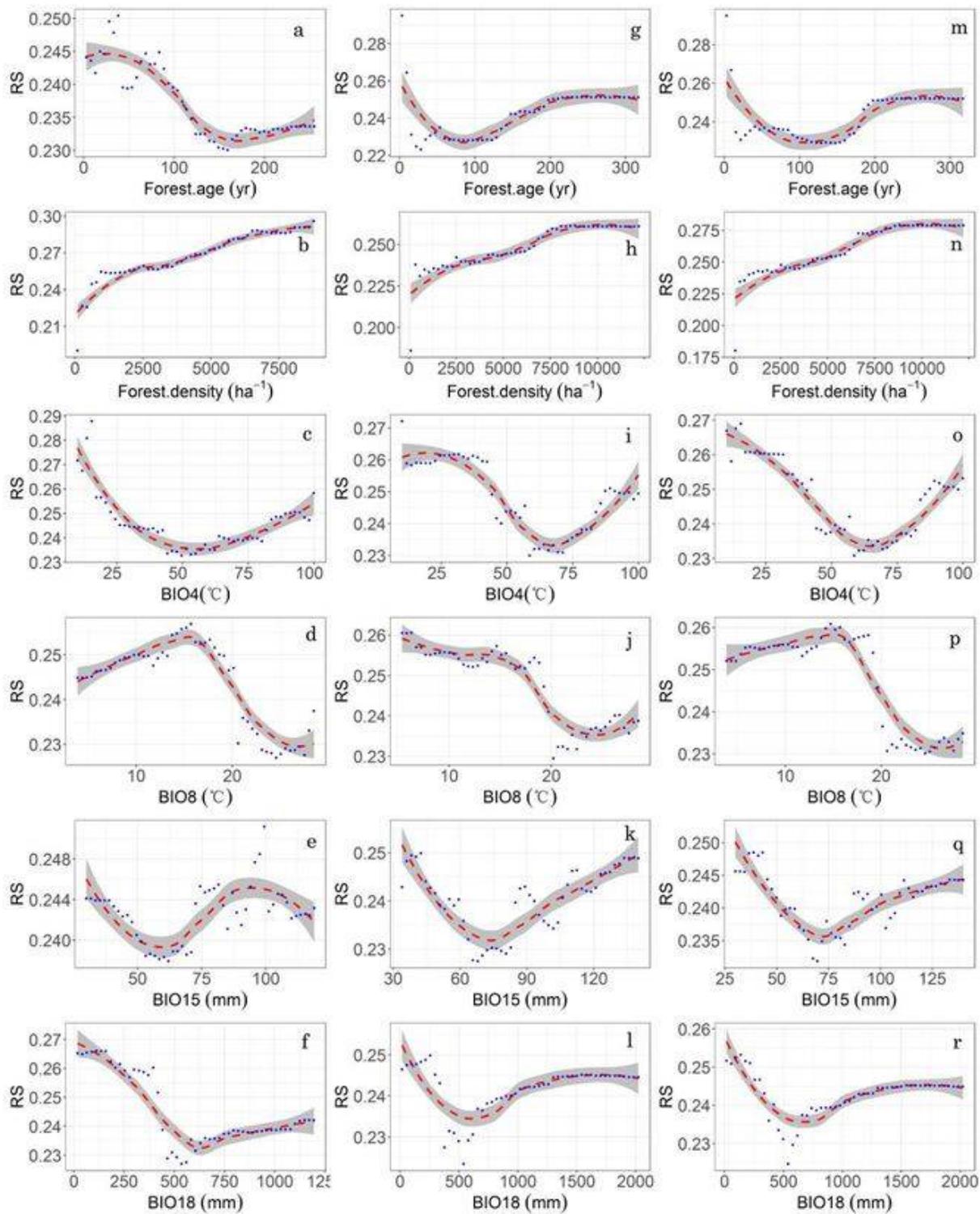
Figure 1

The spatial distribution of forest stands involved in the compiled dataset of root-shoot ratio in China forest ecosystem (vegetation zone: CTNF, cold temperate needle forest; TS, temperate steppe; TD, temperate desert; TMF, temperate needle and deciduous broadleaf mixed forest; WTDB, warm temperate deciduous broadleaf forest; STEB, subtropical evergreen forest; TMRF, tropical monsoon forest. The vegetation dataset is provided by Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (RESDC, <http://www.resdc.cn>)). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

Variable importance ranking based on OOB error (the percent increase in mean square error, %IncMSE) of the predicted variables selected by the VSURF function (a-c); and the linear regression for the RF-based predicted root-shoot ratio (RS) and the field observed RS, the red solid line is the prediction curve, the gray solid line indicates the 95% confidence intervals and the shaded confidence area for the predictions (e-g). Overall forest plots: a, e; natural forests: b, f; planted forests: c, g.



**Figure 3**

Partial dependent analysis between root-shoot ratio (RS) and six factors (forest age, forest density, BIO4, BIO8, BIO15, BIO18) (natural forests, a-f; planted forests, g-l; full plots, m-r). The blue points were data points, the red dashed line and grey area were fitted models by method “loess” with 95% confidence interval.

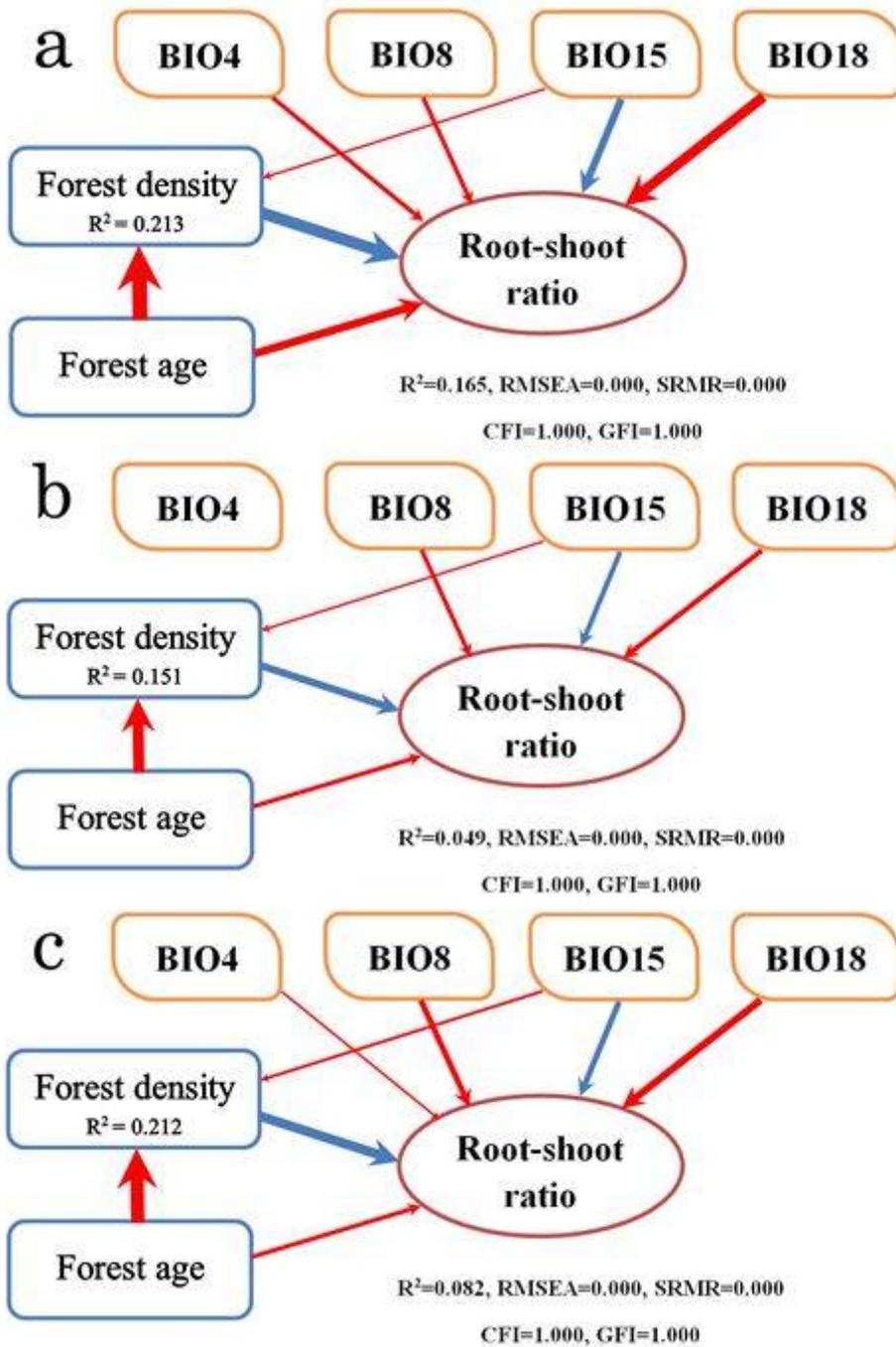


Figure 4

Structural equation models (SEMs) depicting direct and indirect effects of environmental factors on root-shoot ratio (a: natural; b: planted; c:full). All line width corresponds to parameter size with red for negative and blue for positive value ( $p < 0.05$ ). R2 denotes the proportion of variation explained. More details were listed in Table S2.

## Supplementary Files

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