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Multiple environmental factors regulate the large-scale patterns of plant water use efficiency and nitrogen availability across China's forests

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Abstract

Global changes, e.g., global warming, elevated nitrogen deposition, and shifts of precipitation regime, exert a major influence on forests via affecting plant water use efficiency (WUE) and plant nitrogen (N) availability. Large-scale ecological sampling can help us to better understand variation across regions and provide opportunities to investigate the potential impacts of multiple aspects of global change on forest ecosystem responses. Here, we determine the geographical patterns of key isotopic measures of ecosystem function –plant WUE (calculated from foliar $\delta^{13}C$ values) and plant N availability (assessed by foliar $\delta^{15}N$ values) – across China's forests covering ~ 21 latitude (~22–43° N) and ~28 longitude (~93–121° E) degree, and investigate how a suite of soil, plant, and atmospheric factors regulate them. We found that plant WUE increased but N availability decreased with latitude, while plant WUE and N availability did not vary with longitudinal gradient. Different factors regulate the large-scale patterns in WUE and N availability. The mean annual temperature, atmospheric N deposition, and soil water content exhibit considerable effects on plant WUE over both the north-to-south and east-to-west transects, while the mean annual precipitation, soil potassium content, foliar N, and precipitation seasonality considerably affect the latitudinal patterns of plant N availability. In addition, the east-to-west spatial pattern in plant N availability is associated with the variation in solar radiation. Our results suggest that key forest ecological functions respond to an array of environmental factors, and imply that changes in many different environmental attributes need to be considered in order to successfully assess plant WUE and N availability responses to global changes this century.

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Keywords

Broad-leaved forest, Geographical transect, Foliar carbon and nitrogen isotopes, Nitrogen availability, Precipitation seasonality, Water use efficiency

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Introduction

Geographical transects such as latitudinal and longitudinal gradients provide opportunities to explore not only the current controls on ecosystem function, but also to assess how environmental changes in the future might impact ecosystems. Over such spatial gradients, environmental factors e.g., precipitation, nitrogen (N) deposition, and climatic variability substantially vary with longitude and altitude in China (Li *et al* 2015, Ma *et al* 2019, Willig *et al* 2003,Yu *et al* 2019). Such spatial-environmental changes provide the possibility to explore how ecosystem variables might respond to global or regional change in the future (Niu *et al* 2018).

Plant water use efficiency (WUE) and forest N availability are key measures of how water, carbon, and N are processed (Birami *et al* 2020, Craine *et al* 2018, Elmore *et al* 2016, Hatfield and Dold 2019, Yanni *et al* 2011), which are subject to great geographical and temporal variation in environmental factors (Birami *et al* 2020, Huang *et al* 2016, Liang *et al* 2020). Nitrogen availability is typically assessed by foliar $\delta^{15}N$ values, with high $\delta^{15}N$ values always indicating high N availability in forest ecosystems (Craine *et al* 2009, 2015, 2018, Elmore *et al* 2016, Garten 1993, Hogberg 1997). Atmospheric CO_2 exihbit substantial effects on both plant WUE and N avialibity (Adams *et al* 2020, Craine *et al* 2018, Dusenge *et al* 2020, McLauchlan *et al* 2017, Soh *et al* 2019). Increases in mean annual temperature (MAT) and precipitation (MAP) can lead to decline of plant WUE for increasing stomatal conductance (Kimm *et al* 2020, Matthews and Lawson 2019, Reynolds-Henne *et al* 2010). Increasing N deposition may either increase or decrease plant WUE due to impacts on plant

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photosynthesis and stomatal conductance (Brook and Coulombe 2009, Huang *et al* 2016, Liang *et al* 2020). Forest N availability is negatively correlated with MAP (Craine *et al* 2018, Ma *et al* 2019), but positively correalted with MAT (Craine *et al* 2018) and N deposition (Hietz *et al* 2011), caused by differences between plant N absorption rate, plant growth rate, or soil organic mineralization (Elmore *et al* 2016, Hung Dinh *et al* 2013, Lambers and Poorter 1992). In addition, the climatic variability, e.g., precipitation and temperature seasonality (PS and TS, respectively), are also likely to affect plant WUE and N availability (Li *et al* 2016, Stevens 1989). A number of other climatic factors, such as precipitation regime (Liu *et al* 2013a), wind speed (Cornwell *et al* 2018, Hatfield and Dold 2019; Schymanski and Or 2016), and vapor pressure deficit (VPD, Grossiord *et al* 2020, Shi *et al* 2019, Zhang *et al* 2014) can have individually small but cumulatively substantial impacts on plant WUE and N availability. Furthermore, soil factors and plant traits also affect plant WUE and N availability (Grzebisz et al 2013, Maxwell *et al* 2018), e.g., soil pH may affect plant WUE via changing plant photosynthesis (Cornwell *et al* 2018, Hung Dinh *et al* 2013, Koehler *et al* 2016, Niwayanma and Higuchi 2018). However, more comprehensive assessments of different factors across the soil-atmosphere interface (i.e., spanning ‘traditional’ and other climate variables, soil factors, and plant traits) on plant WUE and N availability are especially lacking.

In this study we take a large-scale approach aiming to determine the latitudinal and longitudinal patterns of dominant plant species’ WUE and forest N availability (indicated by foliar δ^{15}N values) across China, and the important environmental factors contributing to

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these patterns. Together, quantifying the large-scale responses of forest WUE and N availability to multiple different environmental factors provides an opportunity to predict the potential changes in forests as they function, which is closely related to water, C, and N cycles of forest ecosystems facing ongoing global changes.

Materials and methods

Sampling and measurement

The sites in this study are conserved locations included in the program "Forest Ecosystem Carbon Project in China" (Tang *et al* 2018), in which the main land of China was divided into 35,800 grid cells based on vegetation diversity, and 4.5% grid cells were selected for investigation (Tang *et al* 2018). From these a total of 2,234 different forest sites has been sampled from across China, from which foliar of dominant forest plants were sampled. Foliar of the several dominant broad–leaved woody species in these broad–leaved forests were collected in 2011-2012. For each dominant species in each forest, at least 10 mature, current-year, fully expanded, and healthy sunlit leaves from mature individuals (breast height greater than 5 cm) were collected per dominant species per forest site. Species were considered dominant based on the criteria described by Tang *et al* (2018).

For this study, we collected foliar samples from 244 sites located in both a latitudinal and a longitudinal transects, including 92 dominant tree or shrub species (**Figure S1**) over the latitudinal and longitudinal gradients. Sampling sites in our study were distributed extensively over the Chinese mainland from within the tropics (22°N) to the cool temperate forest zone at 43°N, and from 93°E to 121°E (**Figure 1**). All foliar samples were dried to a constant weight

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(65°C for 72 h) and ground for analyses. Foliar N concentrations were determined with an elemental analyzer (Isoprime 100, Elementar Isoprime, UK). Foliar $\delta^{13}C$ and $\delta^{15}N$ values were determined using a mass spectrometer (Thermo Finnigan, North Pod Waltham, Massachusetts, USA).

Water use efficiency was calculated from foliar $\delta^{13}C$ values according to Farquhar *et al* (1982) and Ehleringer and Cerling (1995):

$$\Delta^{13}C = \frac{(\delta_a - \delta_p)}{(1 + \frac{\delta_p}{1000})} \quad (1)$$

$$\Delta^{13}C = a + (b - a)\frac{C_i}{C_a} \quad (2)$$

$$WUE = \frac{(C_a - C_i)}{1.6} \quad (3)$$

where: $\Delta^{13}C$ (‰) is carbon (C) isotope discrimination, δ_a and δ_p are $\delta^{13}C$ values for source atmospheric CO_2 and foliar, respectively, $\delta^{13}C$ values of atmospheric CO_2 are about -8.4‰ during 2011-2012; a is the discrimination due to slower diffusion of $^{13}CO_2$ through stomata, and b is fractionation discrimination by Rubisco against $^{13}CO_2$ (b = 27‰, a = 4.4‰) (Farquhar *et al* 1982); C_i is intracellular CO_2 concentration in leaf cells; C_a is atmospheric CO_2 concentration (391.98 ppm); and 1.6 is the ratio of gaseous diffusivity of CO_2 to water vapor (Ehleringer and Cerling 1995).

Nitrogen availability is indicated by foliar $\delta^{15}N$ values, with high $\delta^{15}N$ values showing high N availability in forest ecosystems (Hogberg 1997). The indications of foliar $\delta^{15}N$ values on N availability are now confident (Craine *et al* 2009, 2015, 2018, Elmore *et al* 2016, Garten 1993).

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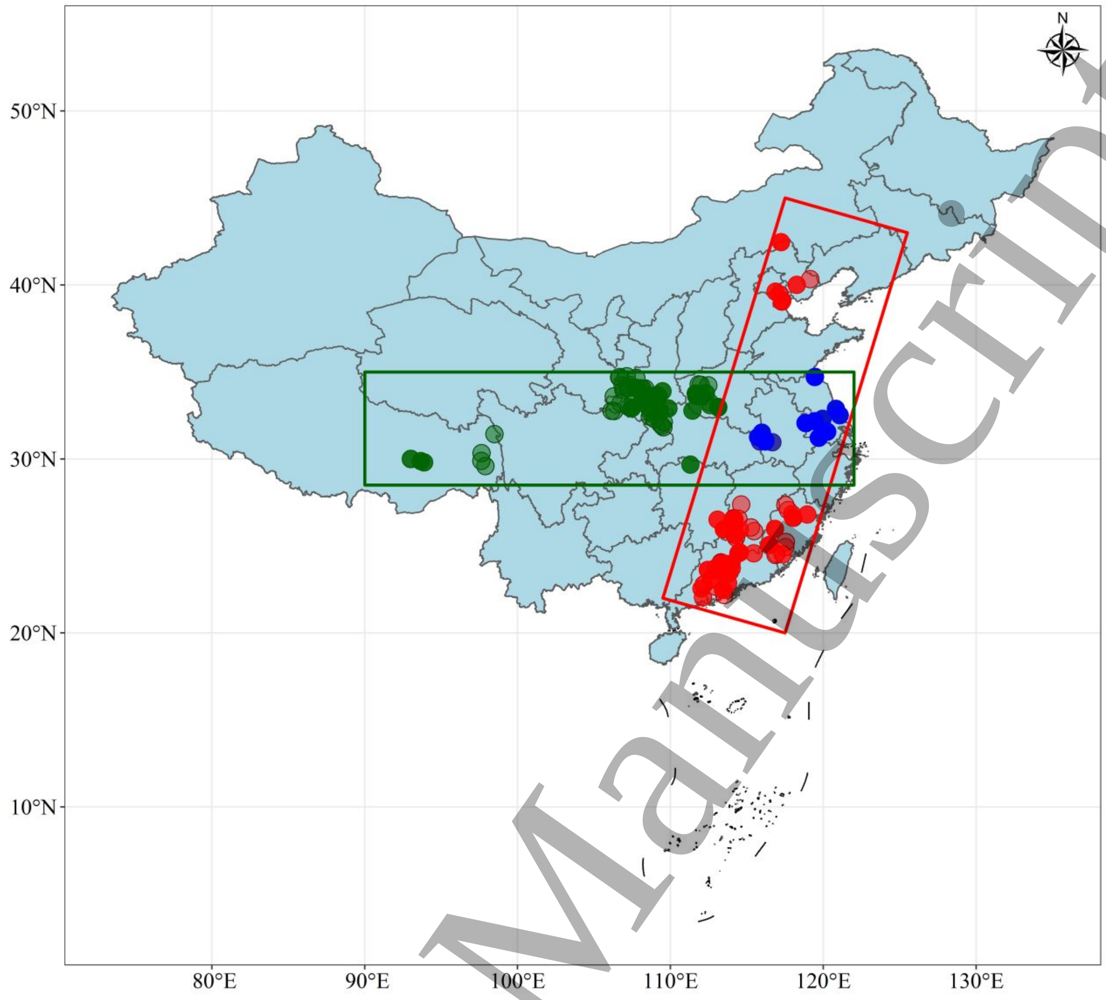

Figure 1. Locations of the 244 sample sites (broad-leaved forests) in the current study. Dark-green sites collectively provide a longitudinal forest transect spanning nearly 3,000 km; red sites provide a latitudinal forest transect of 2,500 km; blue sites are included in both the latitudinal and the longitudinal transects.

Variables related to soil-atmosphere interface

Mean annual temperature, MAP, TS, and PS were directly extracted from the standard (19) WorldClim Bioclimatic variables for WorldClim version 2 (1 km^2), and mean annual solar

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radiation (Solar), wind speed (Wind), and water vapor pressure (VAP) were indirectly calculated by monthly data (1 km^2) extracted from WorldClim version 2 (Fick and Hijmans 2017). The VPD was calculated from temperature and VAP (Grossiord *et al* 2020). Data for monthly potential evapotranspiration (PET) were extracted from Trabucco and Zomer (2019a). The monthly soil water content (SWC) and actual evapotranspiration (AET) were extracted from Trabucco and Zomer (2019b). Total N deposition (Ndep) was estimated based on Jia *et al* (2019), and soil pH, cation exchange capacity of soil (CEC), clay content (Clay), silt content (Silt), organic carbon (SOC) for 0-300 mm depth was derived from SoilGrids250m (Hengl *et al* 2017). Soil N, phosphorus (P, soil P), and potassium (K, soil K) contents (~30 cm in depth, g/100g) were extracted from the global soil dataset (globalchange.bnu.edu.cn) with 30-second resolution (Shangguan *et al* 2013), according to the geographic locations of the sampling sites using ArcGIS 10.3 for Desktop (v.10.3.0.4322). The unit of each environmental factor see **Table S1**.

Data analysis

All environmental factors were standardized via Equation (4) to a mean of 0 and standard deviation of 1 to reduce the magnitude and multicollinearity (Du *et al* 2020) by function scale in R base package (R Core Team 2019).

$$\text{Standardized value} = \frac{\text{Original value} - \text{mean value}}{\text{standard deviation}} \qquad (4)$$

In order to detect the influence of phylogenetic development on foliar $\delta^{13}C$ and $\delta^{15}N$ values of the dominant species in this study, an ultrametric phylogenetic tree was pruned using

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phylo.maker function in V.PhyloMaker R package (**Figure S1,** Jin and Qian 2019**)**. We tested phylogenetic signals of plant WUE and foliar $\delta^{15}N$ values based on Pagel's lambda (λ) and Bolmberg's K statistic (K) calculated by phylosig function in phytools R package (**Table S3**). A value of λ and K closing to 1 ($P < 0.05$) suggests strong phylogenetic signal (Hao *et al* 2014).

Linear mixed effects models (LMEM) were used to determine the patterns of plant WUE and foliar $\delta^{15}N$ values along geographical transects, with geographical gradient as fixed effect and with altitude as random effect (Crawley 2007). We determined variance explained of tree species, geographical gradients, altitude, and sampling site by calcVarPart function in variancePartition R package after creating models with formual as Variable ~ 1 + Latitude + Altitude + (1|Species) + (1|Site) and Variable ~ 1 + Longitude + Altitude + (1|Species) + (1|Site), because linear mixed effect model is more accurately in estimation variance component than ANOVA due to set a Gaussian prior on variables modeled as random effects (Hoffman and Schadt 2016, Nakagawa and Schielzeth 2013).

We used step and lmer function in lmerTest R package to select and established best fit models based AICc of each model to find out which and how environmental factors and foliar N control the geographical patterns of plant WUE and foliar $\delta^{15}N$ values, with species, and sample sites as random effects. The collinearity of fit models was assessed through variance inflation factors (VIF) (Marchand *et al* 2020), and VIF of each variable lower than 5 indicated negligible collinearity (Hovenden *et al* 2019).

We used structural equation models (SEM) to test the causes that plant WUE and foliar

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$\delta^{15}N$ values varied with geographical gradient from the perspective of environmental factors. We added the correlations between latitude or longitude and environmental factors on the basis of best models mentioned above and built an a *priori* model. We ran the a *priori* model, then removed all non-significant paths, and reran the new model. A goodness-of-fit of model was assessed by the ratio of χ^2 to degrees of freedom ($\chi^2/df \leq 2$, $P > 0.05$), and comparative fit index (CFI ≥ 0.95) (Schermelleh-Engel *et al* 2003). Significance was set at $P < 0.05$. All statistical analyses were performed using the R software platform (R Core Team 2019).

Results and discussion

Latitudinal and longitudinal patterns of plant WUE and foliar $\delta^{15}N$ values

Plant WUE and foliar $\delta^{15}N$ values significantly varied along latitudinal, while did not vary along longitudinal gradient, with WUE and foliar $\delta^{15}N$ values increased and decreased, respectively, with latitude (**Figure 2a, b; 3, Table S2**). Overall, ~ 32.2% and 2.0% of the variance for plant WUE and foliar $\delta^{15}N$ values, respectively, could be explained by latitude, but 0.1% and 1.2% of the variance, respectively, by longitude ($P > 0.05$, **Figure 2, 3**). In addition, 0.7~9.4% and 1.0~8.5% of the variance for plant WUE and foliar $\delta^{15}N$ values, respectively, were explained by altitude, and 26.3 ~ 51.2% and 38.0 ~ 64.9% of variance for plant WUE and foliar $\delta^{15}N$ values, respectively, were explained by sampling site in this study (**Figure 3**).

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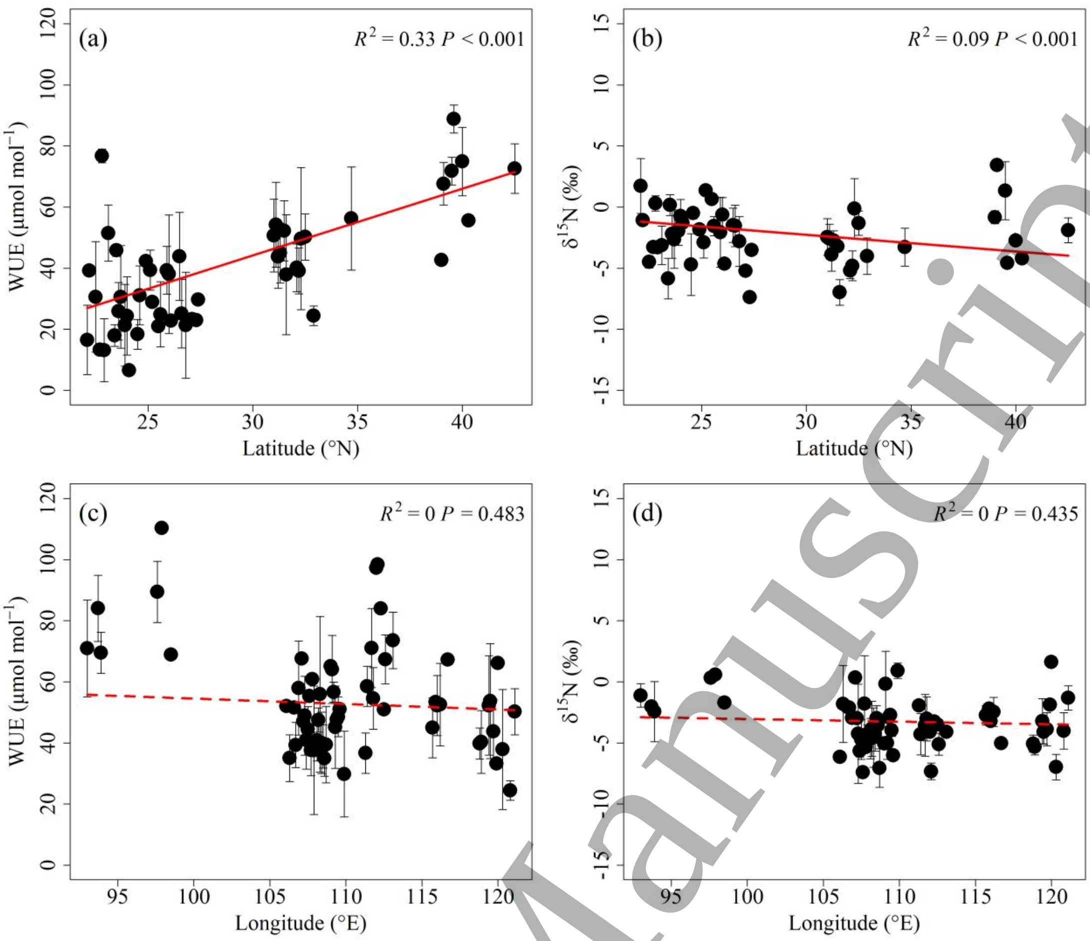

Figure 2. Patterns of plant water use efficiency (WUE, a, c) and foliar N isotope (δ^{15}N values, b, d) along latitudinal and longitudinal gradients tested by the linear mixed effects model, with longitude or latitude as fixed effect, and with species and altitude as random effects (**Table S2**). Solid and dashed lines indicate plant WUE and foliar δ^{15}N values varied with geographical gradients significantly or non-significantly, respectively, at $P < 0.05$ level.

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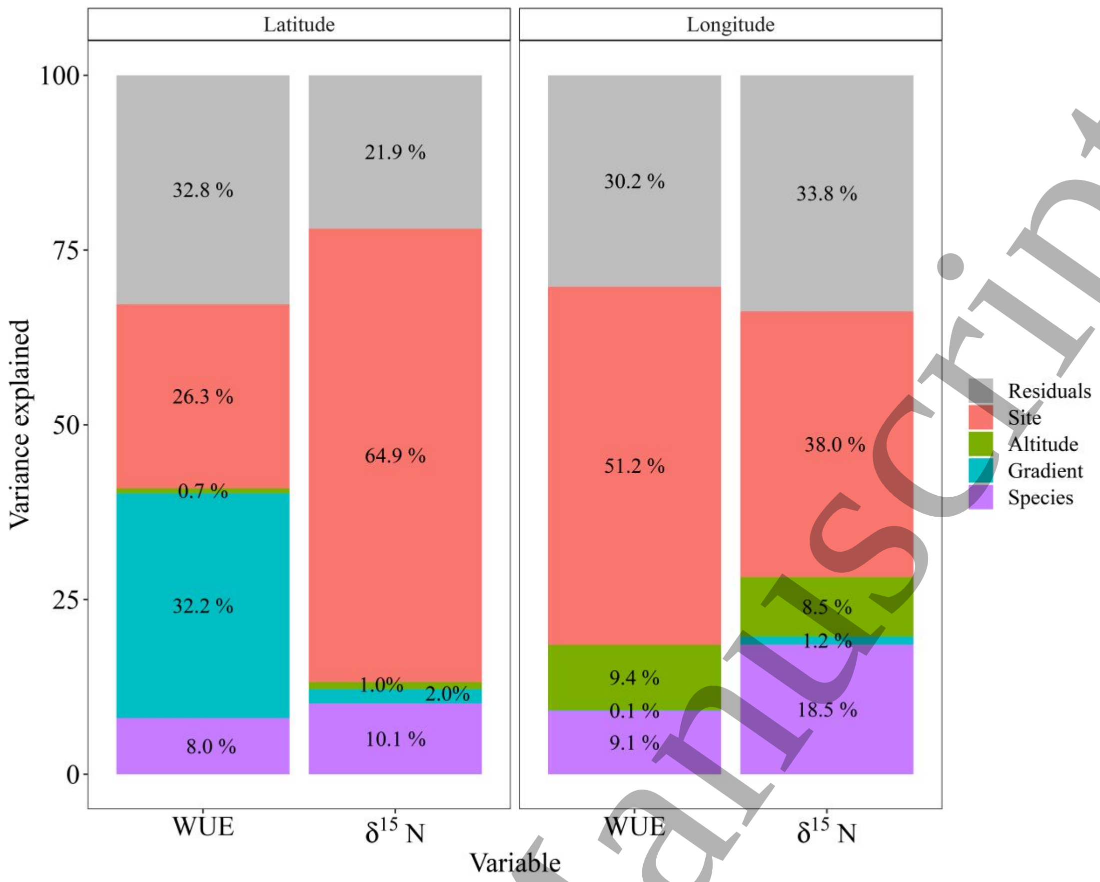

Figure 3. Variance explained of plant water use efficiency (WUE) and foliar nitrogen isotopes values ($\delta^{15}N$ values), explained by geographical gradients, species, sampling site, and altitude. Variance derived from calcVarPart function in variancePartition R package with formula as Variable ~ Latitude + Altitude + (1|Species) + (1|Site) and Variable ~ Longitude + Altitude + (1|Species) + (1|Site), respectively, for latitude and longitude. "Gradient" indicates latitude and longitude, respectively, in left and right panel.

It is already known that both plant WUE and foliar $\delta^{15}N$ values can differ significantly among tree species, functional types, and environmental gradients (Ma *et al* 2019, Soh *et al* 2019, Soolanayakanahally *et al* 2009, Tang *et al* 2014). In this study, plant species exhibit effects on plant WUE (8.0~9.1%) and foliar $\delta^{15}N$ values (10.1-18.5%) (**Figure 3**), however,

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significant phylogenetic signals were not found (λ< 1, $P > 0.05$, **Table S3**). Thus, the interpretation of geographical gradients and in particular sampling site on the variation of plant WUE and foliar $\delta^{15}N$ values imply that both plant WUE and N availability are associated with the environmental factors, in particular along the latitude (**Figure 2**) where environmental factors, e.g., temperature, vary significantly from the south to the north of China (Li *et al* 2016). Our findings differ from Wei *et al* (2019) who found instead that plant WUE decreased with increasing latitude. The pattern of plant WUE decreased but not significantly with increasing longitude is also inconsistent with Li *et al* (2016) who found the WUE of invasive herbs declines toward the east in China.The differences between previous studies and our study might result from the different ecosystems (broad-leaved forest ecosystems in this study *vs* arid shrub ecosystems in Wei *et al* 2019), vegetation types (shrubs and trees in this study *vs* herbs and shrubs in Li *et al* 2016 and Wei *et al* 2019), and geographical regions (covering 22–43°N, 93–121°E in this study *vs* 35–55°N, 47–85°E in Wei *et al* 2019). These findings suggest that exhibiting of high WUE for tree species growing at high latitudes (north) may be one of adaptive strategies to the dry and cold conditions.

Our results also showed that foliar $\delta^{15}N$ values decreased with increasing latitude although the foliar samples at higher latitude is relatively less than at lower latitude, but were invariant with longitude (**Figure 2b, d**). Numerous studies have revealed that plant growth is more likely to be limited by soil N at higher latitudes (e.g., Du *et al* 2020). Based on the efficiency of foliar $\delta^{15}N$ values indicating plant N availability (Craine *et al* 2018, Elmore *et al* 2016), the broad-scale patterns of foliar $\delta^{15}N$ values shown in this study support the inference

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that low N availability characterizes high-latitude forests due to low rate of mineralization (Liu *et al* 2016). However, it is bear noted that there are relatively higher foliar $\delta^{15}N$ values in 37~45°N than those in 30~35°N, which might result from high N deposition (Yu *et al* 2019) but lower net primary production of temperature forest than (sub)tropical forests (Zhuang *et al* 2009), leading to less consumption of soil available N.

Factors regulating the variation of plant WUE and foliar $\delta^{15}N$ values

Two models were established to determine which and how environmental factors and foliar N affect plant WUE and foliar $\delta^{15}N$ values along the geographical gradients (**Table 1, Figure S2**). Mean annual temperature, Ndep, and SWC explained 37% variations of plant WUE, with significantly negative correlations between MAT, SWC and plant WUE, while positive ones between Ndep and plant WUE (**Table 1**). Foliar $\delta^{15}N$ values were positively correlated with MAP, PS, solar radiation, soil K, and foliar N, but negatively with TS (**Table 1**). 21% variance of foliar $\delta^{15}N$ values could be explained by the above factors (**Table 1**).

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Table 1 Summary of the best-fitted models for determining the relationships between independent variables and plant WUE and foliar $\delta^{15}N$ values. All independent variables were standardized. The abbreviations of each variable can be found in **Table S1**. R^2_m: R^2 of fixed effects only; R^2_c: R^2 of both fixed and random effects. All VIF of variables in each model are lower than 5 (**Table S4**).

Variable							
Dependence	**Independence**	**Estimate**	**SE**	**df**	**t value**	***P*** **(>|t|)**	***R²***
WUE	Intercept	46.25	1.48	97.52	31.21	<0.001	$R^2c = 0.74$
	MAT	-8.84	1.47	146.42	-6.02	<0.001	$R^2m = 0.37$
	Ndep	4.63	1.48	115.36	3.13	0.002	
	SWC	-8.09	1.43	139.46	-5.67	<0.001	
$\delta^{15}N$	Intercept	-2.81	0.19	106.82	-15.01	<0.001	$R^2c = 0.76$
	MAP	0.71	0.27	141.65	2.66	0.009	$R^2m = 0.21$
	TS	-0.63	0.23	128.43	-2.76	0.007	
	PS	0.61	0.22	124.32	2.73	0.007	
	Solar radiation	0.47	0.18	133.34	2.59	0.011	
	Foliar N	0.62	0.10	278.37	6.51	<0.001	
	Soil K	0.47	0.17	186.72	2.72	0.007	

Apparently, plant WUE and foliar $\delta^{15}N$ values in this study were affected by different variables as shown by the best-fitted models. The correlations between environmental factors and plant WUE are consistent with previous studies (Cornwell *et al* 2018, Matthews and Lawson 2019). The adverse impacts of temperature on stomatal regulation (Liu *et al* 2018, Matthews and Lawson 2019, Urban *et al* 2017) and photosynthesis (Hebbar *et al* 2020) of plants explained the significantly negative relationships between MAT and plant WUE. The

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result implies that WUE of forest plants might be declined under future global warming. High SWC could increase evapotranspiration, transpiration (Matthews and Lawson 2019, Xue *et al* 2016, Schymanski and Or, 2016, Zhang *et al* 2019) and leaf water potential (Liu *et al* 2013b), leading to low WUE. The relationship between SWC and WUE contribute to the changes in plant WUE in this study. The enhancement of plant photosynthesis caused by increasing N deposition (Brooks and Coulombe 2009) might explain the positive relationships between N deposition and WUE in this study. This result supports that increasing N deposition can enhance WUE of forest plants (Lu *et al* 2014).

The effects of plant (traits) on foliar $\delta^{15}N$ values suggest that the floristic composition of the community itself may be a critical factor when considering how changing N availability will impact forest ecosystems (Craine *et al* 2018). We found that foliar $\delta^{15}N$ values were significantly correlated with foliar N, which is consistent with Craine *et al* (2018), indicating that high N availability enhances plant N absorption. We also found that TS, PS, MAP, soil K, and solar radiation substantially affected foliar $\delta^{15}N$ values, showing their substantial impacts on N availability. Frequent and high precipitation may shorten plant photosynthesis, decrease N absorb, resulting high N availability in forest with high MAP and PS as shown in this study, which are inconsistent with previous studies showing N declines with MAP (Craine *et al* 2018, McLauchlan *et al* 2017). Temperature variability (i.e., TS) exhibits considerable influence on leaf senescence and N input (Asseng *et al* 2011), soil microbial activities, and litter decomposition (Gremer *et al* 2018; Schimel *et al* 1999), which lead to the negative relationships between TS and foliar $\delta^{15}N$ values in this study. In addition, increases

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286 of solar radiation at lower level may benefit to plant growth and increases plant N storage (Pu *et al* 2020), but can also enhance soil N mineralization due to increase soil temperature (Grzebisz *et al* 2013, Guntiñas *et al* 2012, Xue *et al* 2016), resulting in high N availability.

Possible mechanisms for latitudinal and longitudinal patterns of WUE and foliar $\delta^{15}N$ values

Considering the effects of factors on plant WUE and foliar $\delta^{15}N$ values (**Figure 4, S3-S5**), we identified that MAT, SWC (negatively, -), and atmospheric N deposition (positively, +) drove the patterns of plant WUE (**Figure 4a, Figure S3**), while MAP (-), PS (+), foliar N (+) and soil K (+) drove the ones of foliar $\delta^{15}N$ values, over the latitude (**Figure 4b, Figure S3**). Along the longitudinal gradient, changes in plant WUE were attributed to MAT, N deposition, and SWC (+) (**Figure 4c, Figure S4**), while changes in foliar $\delta^{15}N$ values were associated with MAP (+), solar (+), and foliar N (+), and soil K (-) (**Figure 4d, Figure S4**).

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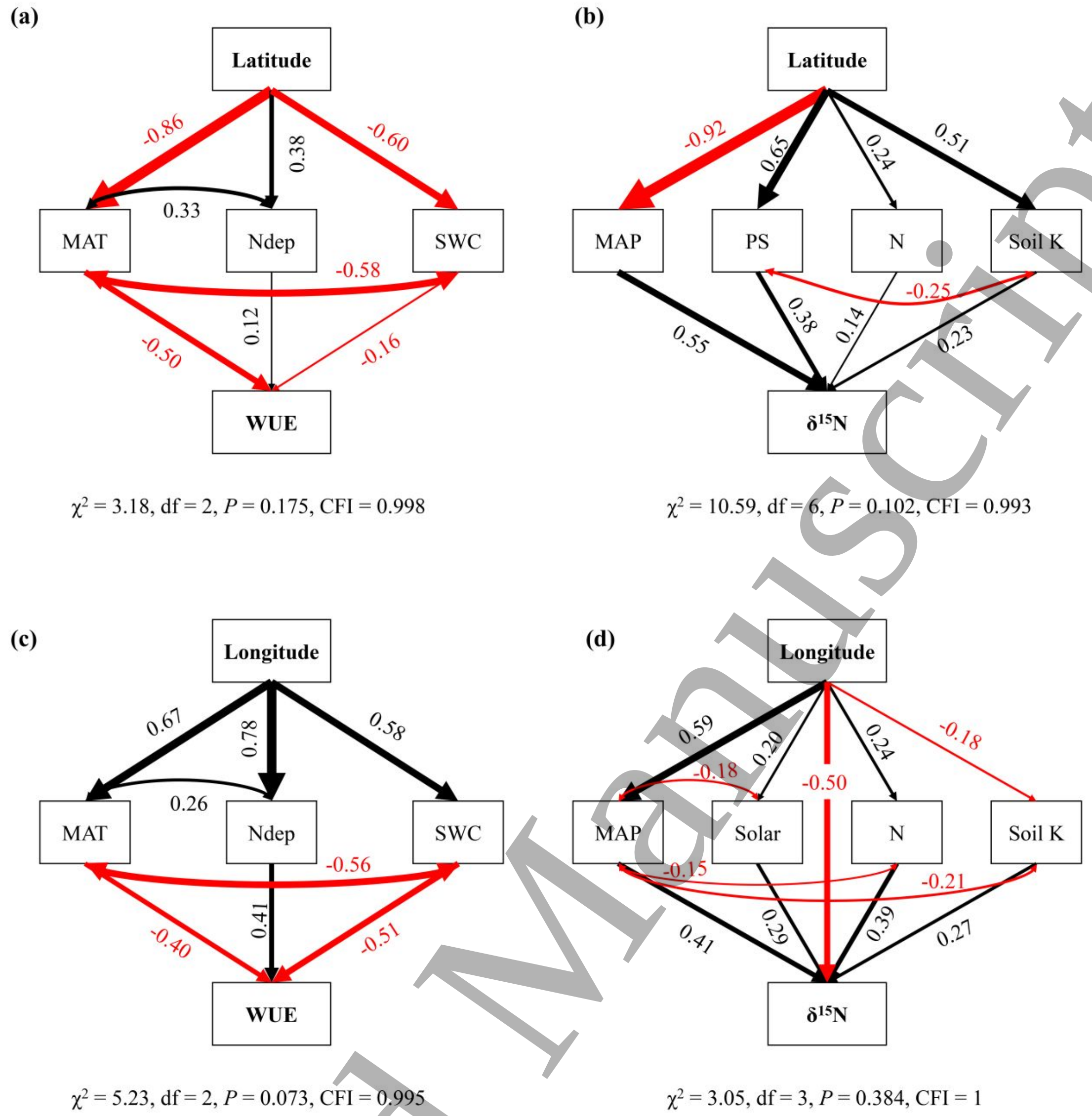

Figure 4. Pathways of the effects of longitude and latitude on plant WUE and foliar $\delta^{15}N$ values assessed by structural equation models. Arcs between independent variables indicate the covariance between relevant two variables. Line width corresponds to parameter size. The red and black lines indicate significantly negative and positive effects ($P < 0.05$) respectively

Given the significant variations of plant WUE and foliar $\delta^{15}N$ values with latitude but not with longitude, there were extremely complicated influences for environmental factors and foliar N on plant WUE and foliar $\delta^{15}N$ values in longitude as shown by the SEM (**Figure 4**). The possible reasons for the latitudinal pattern of plant WUE are the declines of MAT and

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307 SWC but increases of N deposition along the latitude. The decline of N availability along latitude is likely caused by the decline of MAP, but most of declines can be offset by the effects of PS, foliar N, and soil K on N availability. In contrast, the longitudinal patterns of plant WUE and N availability might be contributed to the offsets between the negative and positive effects, e.g., the negative effects of MAT and SWC but the positive effects of N deposition on plant WUE. In addition, the lower variations of climate, e.g., MAT and MAP, (**Figure 4**), but larger difference of N deposition, along longitude than along altitude (Yu *et al* 2019) led to the differences in the controlling factors to WUE and foliar $\delta^{15}N$ values. Our results suggest that the effects of longitude on plant WUE and N availability are also important to reveal how environmental factors control the functions and processes of forest ecosystems. The large-scale geographical patterns and the driving factors of plant WUE and N availability in the forests across China address our second aim, concerning which environmental factors contribute to the spatial gradients in plant WUE and N availability and how their influence may differ depending on the environmental context. Our results suggest that more environmental factors including solar radiation and climate seasonality should be taken into consideration in predicting the status of plant WUE and N availability under global changes.

Conclusions

We analyzed an extensive gradient of Chinese broad-leaved forests, and found that the water use efficiency of dominant tree species increased from south to north, while N availability declined over latitudinal gradients. Neither plant WUE nor N availability varied with

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longitude. Multiple factors and leaf traits regulate the geographical patterns of WUE and N availability. Specifically, mean annual temperature, N deposition, and soil water content drive the north-south variation in plant WUE, instead there are more factors - mean annual precipitation, precipitation seasonality, soil K content, and foliar N concentration – which drive N availability over longitudinal gradients. Overall, this large-scale analysis of contemporary variations in isotopic C and N indicators of Chinese forests' ecological functions reveal not only that a wide range of environmental factors are influential, but also that the impact of each is highly context-dependent. This suggests that through this century, changes in multiple aspects of the soil-plant-atmosphere system are likely to have significant, but regionally differing, impact on forest ecological functions.

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Data availability

The data that support the findings of this study are available upon reasonable request from the authors.

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