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## **Plant Functional Types rather than Climate or Soil Determine**

### **Leaf Traits in the Forest Biomes of Eastern China**

Zhan Xiaoyun<sup>a</sup>, Yu Guirui<sup>b</sup> & Zhang Tibin<sup>a</sup>

#### **Zhan Xiaoyun**

Email: zhanxiaoyun2005@163.com; Tel: +86 29 87011354

<sup>a</sup> *Institute of Soil and Water Conservation, Northwest A & F University, Yangling 712100, Shaanxi, China*

#### **Yu Guirui**

E-mail: gryu2000@sohu.com; Tel: +86 10 64889432

<sup>b</sup> *Synthesis Research Center of Chinese Ecosystem Research Network, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China*

#### **Zhang Tibin**

Corresponding author, E-mail: zhangtbin@163.com; Tel: +86 29 87012465

<sup>a</sup> *Institute of Soil and Water Conservation, Northwest A & F University, Yangling 712100, Shaanxi, China*

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## **Plant Functional Types rather than Climate or Soil Determine Leaf Traits in the Forest Biomes of Eastern China**

### **ABSTRACT**

Nitrogen (N) has great ecological importance, but the biogeographic pattern across forest biomes in China has only recently been explored. Here we conducted a systematic census of leaf C and N following the same protocol to explore the variations of leaf traits, and their possible responses to plant functional types (PFTs) and environmental factors. Results showed that leaf traits varied substantially across biomes, and the relationships of PFTs to climatic factors were stronger than those of PFTs versus soil nutrient proxies, indicating that plant species composition might be a better predictor of plant species distribution with climate than leaf traits. Soil nutrient proxies explained more variation of leaf traits than climate, which demonstrates that leaf traits reflect important aspects of plant responses to soil nutrients. Importantly, partial general linear models analyses found that PFTs showed the greatest direct influence for leaf traits, and climate and soil affected leaf traits mainly through the change in plant species composition rather than having direct impacts. Hence, we concluded that leaf traits were largely controlled by PFTs rather than climate or soil at the biome scale. The results favoured the species composition hypothesis, indicating that leaf nutrient concentration is mainly determined by plant functional types (PFTs).

### **KEYWORDS**

Biogeochemical hypothesis; forest ecosystem; North-South transect of Eastern China;  
species composition hypothesis; temperature-plant physiological hypothesis

## Introduction

Biogeographic patterns in leaf traits are a challenging issue to both plant physiologists and ecologists (Reich et al. 2003; Chown et al. 2004). Thus, the ability to characterize key leaf traits at regional, continental, or global scales is important for a variety of scientific disciplines, including global biogeography and macroecology (Diaz et al. 2004; Swenson et al. 2012; Leach et al. 2015), as well as for carbon balance and land surface models (Bonan et al. 2003; Sitch et al. 2003). Leaf nitrogen (N) is the determinant of key physiological processes and the major growth-limiting nutrient for northern latitude plant communities (Sterner & Elser 2002; Vitousek 2004; LeBauer & Treseder 2008). Therefore, it is imperative that we begin to focus our attention in the direction of geographically broad variation in leaf N and the factors that may give rise to its trend. Existing publications have synthesized the results of multiple small-scale investigations to examine regional and global patterns of leaf N, and a diverse set of geochemical and ecological factors have been proposed to explain the biogeographic pattern of leaf N (McGroddy et al. 2004; Niklas et al. 2007; He et al. 2014; Sardans et al. 2015). So far, several factors have been proposed to explain the patterns of leaf traits. Among these, climate, soil or plant functional types (PFTs) are thought to be primary factors (Kerkhoff et al. 2005; Niklas et al. 2007; Ordoñez et al. 2009; Sasaki et al. 2010; Han et al. 2011). Therefore, three hypotheses have been put forward to explain geographical patterns of leaf traits. For example, the temperature-plant physiological hypothesis assumes that all plant metabolic processes are temperature sensitive, and high leaf N can compensate for the low efficiency of enzymes and physiological processes at low temperature (Woods et al. 2003; Reich & Oleksyn 2004). In contrast, the biogeochemical hypothesis states that low temperature not only reduces N availability through suppressing decomposition and mineralization of organic matter,

but also suppresses root nutrient uptake, resulting in low leaf N in cold climate, and hence soil nutrient availability is considered as the main driver of leaf nutrient concentration (McGroddy et al. 2004; Reich & Oleksyn 2004). Whist, the species composition hypothesis argues that leaf nutrient concentration is mainly determined by plant functional types (PFTs) (Vrede et al. 2004; Han et al. 2011). Overall, numerous studies have tested these hypotheses above, and confirmed that climate, soil or PFTs are the primary driving forces of leaf traits. For example, Sardans et al. (2015) reported that different species had their own fixed foliar elemental compositions, but retained some degree of plasticity to the current climatic and competitive conditions. Nonetheless, these syntheses above suffer from the difficulties in standardizing sampling methods and measurements. Additionally, comprehensive information about the variation of leaf traits in Chinese forests across a wide geographical region following the same protocol is lacking, and there are still large gaps in the knowledge of controls on leaf traits.

In this study, a large body consisting of 310 observations of leaf carbon (C) and N for 102 plant species has been accumulated, and information on PFTs, climate (mean annual temperature, MAT and mean annual precipitation, MAP) and soil (soil N and soil C:N ratio) were used to present a more comprehensive assessment of leaf traits in Chinese forests. The main objective is to explore the large-scale patterns of leaf N and leaf C:N ratio and the associated driving forces. The comprehensive analysis and interpretation of those with specific emphasis on Chinese forest leaf traits is powerful for the existing three hypotheses mentioned above. Quantification of the relationships of leaf traits to PFTs, climate and soil is of prime importance for understanding of the biogeographic scaling of vegetation chemistry, and offers promise for the eventual development of new modelling frameworks that could be used to study the effects of future climate change.

## **Material and methods**

### ***Site descriptions***

Located in the heavily forested area, the North-South Transect of Eastern China (NSTEC) spans large gradients of climate, soil substrate materials and plant compositional variations (Zhang & Yang 1995). It thus provides a good representation of wide biome heterogeneity to examine the biogeographic patterns of leaf traits. The NSTEC was formally established as an International Geosphere and Biosphere Program (IGBP) terrestrial transect in 2000, and this study was conducted at 112 forest sites along the NSTEC (Figure. 1). The NSTEC extends from Hainan Island to China's northern border, with a spatial distance of more than 3700 km, ranging from 108° E to 118° E for latitude below 40° N and from 118° E to 128° E for latitude above 40° N (Figure 1). The transect includes 25 provinces, and covers nearly 1/3 of China's territory (Figure 1). Due to the influence of the East Asian monsoon, the climate of the NSTEC displays obvious latitudinal gradients for temperature and precipitation, with MAT and MAP decrease from 22°C and 1800 mm in the south to 1°C and 500 mm in the north, respectively. The great spatial variations from north-south gradient in climate, as well as variations in geomorphology and soil substrate materials, are the primary drivers for the diverse distribution of forest ecosystems along the transect (Peng et al. 2002). Along the NSTEC from north to south, zonal forest ecosystems include cold-temperate coniferous forest, temperate mixed forest, warm-temperate deciduous broadleaved forest, subtropical evergreen broad-leaved forest, and tropical monsoon rainforest (Zhang & Yang 1995).

**[Figure 1]**

### ***Leaf traits and soil nutrient measures***

We selected research sites which were subjected to minimal anthropogenic disturbances, and then sample collection and measurements were conducted during the growing season (June to September, mostly July and August). At each forest site, only the dominant species were selected, and then sun-exposed and newly matured leaves from five individuals of each plant species were collected. After the removal of above-ground litter, soil samples were collected from 0-20 cm of soil using a 3 cm diameter soil auger. To ignore within-site error, eight sub-samples were pooled to one composite soil sample at each site.

Leaf samples were dried for 24 h at 60 °C upon returning to the laboratory. Soil samples were air-dried at room temperature and then passed through a 2 mm sieve to remove roots, gravel and stones. All samples were ground into fine powder with a planetary mill and then oven-dried at 70 °C for 24 h before analysis. Total C and N concentration were determined using an elemental analyzer (2400 II CHNS/O Elemental Analyzer, Perkin-Elmer, USA) with a combustion temperature of 950 °C and a reduction temperature of 640 °C. Leaf C and N values were expressed herein per unit of dry biomass ( $\text{mg}\cdot\text{g}^{-1}$ ).

#### ***Climate data and plant functional types***

In this study, synchronous climate data were collected at meteorological stations, and for the sites with missing climate data, we used a raster product with a 10-day-0.1° spatial-temporal resolution, which built from 730 meteorological stations in China from 1951 to 2000 (Tao et al. 2007). In order to analyse the climatic controls on the biogeographic patterns of leaf traits, site climate was described in terms of MAT and MAP.

PFTs classifications were generally based on similar morphological and life-history characteristics (Chapin et al. 1996; Gitay & Noble 1998). All plant species in the dataset



were primarily classified into five groups according to their respective PFTs, and they were grasses (G), deciduous shrubs (SD), evergreen shrubs (SE), deciduous trees (TD), and evergreen trees (TE).

### ***Statistical analyses***

To meet normality and homogeneity assumptions for analysis of variance and regression analysis, leaf N and C:N ratio data were  $\log_{10}$ -transformed before analyses, as was commonly done in analysis of variance (McGroddy et al. 2004; Wright et al. 2004). The differences in leaf traits among different PFTs and the relationships between PFTs-climate and PFTs-soil were tested using one-way analysis of variance (ANOVA), followed by Fisher's least significant difference (LSD) comparisons when the differences were significant. Bivariate analysis of trait-climate and trait-soil relationships and multivariate analysis of the combined effects of climate and soil on leaf traits were quantified using linear regression models or dynamic curve fit. By comparing the distribution of the scatter diagram and  $R^2$ , we selected the better-fit functions that had a higher  $R^2$  value. Analogous to ANOVA, the predictive power of climate versus soil was compared in terms of F-values to account for differences in sample size.

To demonstrate the relative effects of PFTs, climate and soil on leaf traits, partial general linear models analyses were conducted, using leaf traits as dependent variables, and PFTs, climate and soil as predictors. As a first step, within climate (MAT and MAP) and soil variables (soil N and soil C:N), stepwise selection of variables was performed to exclude variables that did not contribute significantly ( $P < 0.01$ ) to the explained variation. Then, the partial regressions divide the variation in response variable explained by several predictor variables into independent components (representing the independent effects of an individual explanatory variable when controlling effects of the

other explanatory variables) and joint components (usually representing the collinearities between explanatory variables). The variation partitioning with three explanatory matrices leads to the identification of seven fractions in this study, i.e., independent effects of PFTs, climate, and soil; interactive effects of PFTs and climate, PFTs and soil, climate and soil, and the interactive effect of all variables (Heikkinen et al. 2005). The significance of effects was tested with the F-ratios between mean squares of effects and residuals.

The partial regressions were performed with SAS statistical software package version 9.2 and other analyses were conducted by SPSS 16.0 statistical software (SPSS Inc., Chicago, IL, USA), and also the graphs were performed by Simplot 13.0 software.

## **Results**

### ***Leaf traits versus PFTs***

Considerable differences of leaf traits among PFTs were observed. The average of leaf C, leaf N and leaf C:N ratio was  $495.7 \text{ mg} \cdot \text{g}^{-1}$ ,  $17.6 \text{ mg} \cdot \text{g}^{-1}$ , and 31.3, respectively (Figure 2). On average, the highest leaf C and leaf N were found both in deciduous trees, while the lowest values were appeared in evergreen shrubs (Figure 2(a), 2(b)). In terms of stoichiometry ratio, evergreen trees were richest in leaf C:N ratio, and deciduous trees had the lowest leaf C:N ratio, while the other PFTs (grasses and shrubs ) were not different from each other and were intermediate to the others (Figure 2(c)). Among these traits, the variability (coefficient of variation, CV) in leaf N (33.8%) and leaf C:N ratio (34.1%) were sharply greater than that in leaf C (10.6%). Therefore, leaf C was not mentioned in the following presentation, due to its relative stability.

ANOVA analysis showed that all climatic factors and soil nutrient proxies were closely related to the occurrence of the various PFTs (Figure 3). Specifically, evergreen shrubs and evergreen trees corresponded to high MAT, while deciduous shrubs and

deciduous trees occurred in cold climate with low MAT (Figure 3(a)). The ranking was generally similar when MAP was examined for PFTs individually (Figure 3(b)). On average, deciduous trees appeared at the highest soil N, and evergreen shrubs occurred at the lowest soil N (Figure 3(c)), while the trend was opposite in analyses using soil C:N ratio for PFTs (Figure 3(d)). Additionally, the strength of the relationships of PFTs to climatic factors ( $F = 46.9$  for MAT and  $42.8$  for MAP) was stronger than that of PFTs versus soil nutrient proxies ( $F = 17.7$  for soil N and  $23.1$  for soil C:N), which suggesting that climate, rather than soil nutrient plays a vital role in shaping PFTs in this region.

**[Figure 2]**

**[Figure 3]**

#### ***Leaf traits versus climatic factors***

Leaf N and leaf C:N ratio for all species pooled together along the NSTEC were significantly correlated with both MAT and MAP (all  $P < 0.001$ , except MAT for leaf C:N ratio, Figure 4). On average, MAT and MAP accounted for 7.7% and 14.0% of variation in leaf N, and explained 2.1% and 8.6% of variation in leaf C:N ratio, respectively (Figure 4, model 1 and 2 in Table S1). Generally, there was a consistent and significant shift from species with high leaf N in cold climate with low MAT and MAP towards species with low leaf N in high MAT and MAP conditions (Figure 4(a), 4(b)). In contrast, leaf C:N ratio increased linearly with MAT and MAP, which was in the opposite direction to leaf N (Figure 4(c), 4(d)).

**[Figure 4]**

#### ***Leaf traits versus soil nutrient proxies***

We documented soil N and soil C:N ratio to address their relationships with leaf traits along the NSTEC. Our data demonstrated a general positive linear correlation between

leaf N and soil N for all plant species ( $R^2 = 0.18$ ,  $P < 0.001$ ) (Figure 5(a)), and the response to soil C:N ratio were opposite in direction for leaf N (Figure 5(b)). In contrast, leaf C:N ratio was also significantly related to soil nutrient measures, but in the opposite direction to leaf N (Figure 5(c), 5(d)). When conducted binary linear regression analysis, we found that the models including soil N and soil C:N ratio jointly explained 18% and 11% of variations in leaf N and leaf C:N ratio, respectively, marginal improvements over soil N or soil C:N ratio alone (model 6 in Table S1). Across all bivariate analyses above,  $R^2$ -values and F-values of soil nutrient proxies for leaf traits were almost always higher than those of leaf traits versus climatic factors, illustrating that soil nutrient proxies determine leaf traits more strongly than climate.

**[Figure 5]**

***Combined influences of PFTs, climate and soil on leaf traits***

General linear models analyses showed that the overall models including PFTs, climate and soil could account for 50.8% and 42.6% biogeographic variations in leaf N and leaf C:N ratio, respectively (Figure 6). PFTs accounted for the largest explained fraction of the variations for leaf traits, interpreting 35.9% of the total variation for leaf N and 31.8% for leaf C:N ratio (Figure 6). However, significant collinearities between these factors could potentially obscure their true roles (Table 1). In order to assess their independent and joint effects, partial general linear models regressions were used to examine their relative causality in the control of the variations in leaf traits. Specifically, PFTs, climate and soil explained independently 15.6%, 2.3% and 6.9% of the variation in leaf N, respectively; the interactive effects of PFTs and climate (ab), PFTs and soil (ac), climate and soil (bc), and PFTs, climate and soil (abc) represented 7.9%, 5.6%, 5.7% and 6.8%, respectively (Figure 6(a)). As for leaf C:N ratio, the independent effects of PFTs, climate and soil were 13.7%, 1.4% and 4.8%, respectively, and the total of their

interactive effect was 5.6% (Figure 6(b)). Performing the partial general linear models indicated that the effects of PFTs were much larger than those of climate and soil for both leaf N and leaf C:N ratio.

[Table 1]

[Figure 6]

## Discussion

### *Variations in leaf traits*

Leaf N in the present study was, on average,  $17.6 \text{ mg}\cdot\text{g}^{-1}$  (Figure 2), which was higher than that measured in Chinese grasslands ( $2.8 \text{ mg}\cdot\text{g}^{-1}$ ) (He et al. 2006), but lower than the average value found in global ( $20.1 \text{ mg}\cdot\text{g}^{-1}$ ) (Reich & Oleksyn 2004). Leaf C:N ratio for all species along the transect was 31.3 (Figure 2), which falls between that of Chinese grasslands (17.9) (He et al. 2006) and global forests (37.1) (McGroddy et al. 2004). We also found that both leaf N and leaf C:N ratio varied among PFTs (Figure 2). Specifically, compared with evergreen trees, deciduous trees had higher leaf N, but lower leaf C:N ratio (Figure 2), which was consistent with the result reported by Wright et al. (2004). Our findings are also supported by the growth rate hypothesis proposed by Elser et al. (2003) and Vrede et al. (2004): deciduous trees with short leaf lifespan have higher growth rate, therefore are rich in N and have higher photosynthetic rates than do evergreen trees.

Moreover, the occurrence of the various PFTs was correlated to both climatic factors and soil nutrient proxies, but the differences among PFTs in relation to soil were weaker than the strength of the correlations among leaf traits and soil (Figure 3, Figure 5).

Together, this might imply that to characterize plant responses to soil nutrient, leaf traits might perform better than PFTs. In contrast, PFTs were strongly affected by climatic factors (Figure 3). These offsets according to PFTs in combination with the fact the

different PFTs have different trait values may explain the low explanatory power of climate and soil in predicting leaf traits (Wright et al. 2005; Reich et al. 2007). Hence, we infer that the change according to PFTs do not interfere with trait-soil relationships, due to the minor effects of soil nutrient proxies on distribution of PFTs.

### ***Driving forces for leaf traits***

Leaf traits are the result of long-term interaction between plant and the environment, reflecting the adaption of plant to minimize the negative influence of harsh environment (Bonan 2002). In recent years, several studies about leaf key functional traits and the driving forces have been performed across regional and global scales (Niklas et al. 2007; Townsend et al. 2007; Peñuelas et al. 2008; Yu et al. 2010; He et al. 2014).

The present study identified one geographically broad trends in leaf traits, and found that leaf traits were related to climatic factors and soil nutrient proxies (Figure 4, Figure 5), of which PFTs, climate and soil accounted for a substantial part of the biogeographic variations in leaf traits (Figure 6). The results were in agreement with the previous studies conducted for the various PFTs and in different geographical regions (Chen et al. 2013; He et al. 2014). Specifically, we found that leaf N decreased with increasing MAT, it is mainly due to MAT has stronger effects on plant growth than on soil N mineralization (Aerts et al. 2007), thus leading to N dilution in mature green leaves (Reich & Oleksyn 2004; Wright et al. 2004). Welker et al. (2005) also reported that warming reduces N concentrations in green leaves in long-term warming experiments, whereas, Aerts et al. (2007) found that the lack of response in short-term warming experiments. The difference between the Aerts et al. (2007) findings and ours could also be explained by the fact that Aerts et al. (2007) used temperature manipulations on a single plant community, whereas our results reflect the combined effects of large environmental gradients and many different plant communities. The pattern may also

reflect the effect of MAP on soil N (Vitousek 2004), which could drive the changes in leaf N. Therefore, our findings suggest that the combination of PFTs, temperature and precipitation-related physiology and soil substrate-related N is responsible for the observed patterns of leaf traits, and also reflects pervasive geographic patterns in the structure and function of forest ecosystems (Hedin 2004; Wright et al. 2004).

However, it is not clear whether these trends result from the direct effect of climate and soil or from the indirect effects through the change in plant species composition. Partial general linear models analyses showed that PFTs explained independently more than 10.0% of the total variations for both leaf N and leaf C:N ratio, while climate explained independently less than 2.5% , and soil represented between 4.8 and 6.9% of the variations in leaf traits (Figure 6). Moreover, the interactive effects of PFTs and climate, PFTs and soil were larger than the effects of climate or soil alone for leaf traits (Figure 6). Hence, PFTs were more important than climate and soil in shaping the biogeographic patterns of leaf traits, and climate and soil affected leaf traits mainly through the change in plant species composition rather than via themselves. The importance of PFTs could also be illustrated by the relationships between the deciduous percentage and the leaf traits in woody species (deciduous trees vs. evergreen trees) along the latitudinal gradient (Figure S1). Species that tended to have high leaf N, such as deciduous trees (relative to evergreen trees), were more proportionately distributed in northern than southern regions, while the trend was opposite for leaf C:N ratio (Figure S1). The results above suggest that the geography of leaf traits was largely controlled by plant species composition, favouring the species composition hypothesis (Ågren 2004; Reich & Oleksyn 2004; Reich et al. 2010). Thus, future efforts should focus on identifying the role of PFTs more precisely on biome-spanning patterns of leaf traits.

#### ***Uncertainty of explanatory power for leaf traits***

Even though the climate-trait and soil-trait relationships discussed above were statistically significant, the relationships still showed considerable scatter around the fitted lines (Figure 4, Figure 5). Climate and soil combined could explain just only 23.9% for leaf N and 18.0% for leaf C:N ratio (model 7 in Table S1). Taking PFTs into account, the partial general linear models analyses showed that from the total variability that was not captured by PFTs, climate and soil parameters, on average 49.2% of the variation in leaf N, and 57.4% for leaf C:N ratio (Figure 6). The great deal variability for leaf traits might be ascribed to various causes: species variation within functional types, suitable meteorological elements, soil substrate, etc (Westoby & Wright 2006; Durán et al. 2010). Physiological variability within each functional type could be an important factor contributing to the low explanatory power. A wide range of meteorological elements, including average diurnal range of temperature (DRT), annual precipitation seasonality (ASP), and growing season length (GSL) might also exert a major control of leaf traits (Mediavilla & Escudero 2003; Han et al. 2011; Borer et al. 2013). However, due to the currently unavailable data for these climatic factors, the possible effects of these factors on leaf traits need to be kept in mind when the climate based regression equations are applied in future work. Further, soil total N is the most commonly used proxy of N supply, which gives an indication of the size of the soil N pool, but how much of this pool is actually available for plant uptake is still unknown (Vitousek & Howarth 1991). Our findings showed the inadequacy of soil total N, to characterize soil nutrient in relation to leaf traits, therefore, paucity of information on soil N available hindered the estimation of the effect of soil on leaf traits. Also, soil substrate age has been shown to influence soil nutrient availability and leaf traits, with lower levels in very young and old soils than in young to intermediate age soils (Hedin et al. 2003). Perhaps, natural selection and evolutionary adaption play a vital role in



shaping the observed regional patterns in leaf traits distribution. For example, to a degree, the existence of geographically broad pattern in strategies of plant nutrient investment offers evidence of top-down feedbacks between ecosystem-scale nutrient economic and natural selection of individual within local environment. The information generated in this study stresses the importance of reporting adequate site information in ecological studies involving leaf traits. This is critical for expanding the current analysis and including other plant traits related to more environmental factors. Though it is most challenging to quantify precisely all controls of leaf traits, we spare no effort to analyse the relative effects of PFTs, climate and soil on spatial patterns of leaf traits of forests in eastern China. The spatial patterns of leaf traits were influenced by PFTs, climate, soil and their interactions and generally, PFTs has a stronger influence than soil and climate. The findings demonstrate that leaf traits are determined by climate and soil mainly via the shifts in PFTs, and this analysis is crucial for reliable calibration of models designed to predict vegetation shifts with climate change.

#### **Disclosure statement**

No potential conflict of interest was reported by the authors.

#### **Supporting information**

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

**Table S1.** Bivariate and multivariate linear regressions of leaf traits on climatic factors and soil nutrient proxies.

**Figure S1.** Latitudinal trends in leaf traits of deciduous trees vs. evergreen trees.

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**Table legends:**

**Table 1.** Correlation matrix of independent variables. MAT, mean annual temperature; MAP, mean annual precipitation; Soil N, soil total N; Soil C:N, soil total C:N ratio; \*\*,  $P < 0.01$ .

Variables	MAT	MAP	Soil N	Soil C:N	Leaf N
MAT	1				
MAP	0.88**				
Soil N	-0.61**	-0.51**			
Soil C:N	0.62**	0.60**	-0.85**		
Leaf N	-0.27**	-0.36**	0.43**	-0.41**	
Leaf C:N	0.15**	0.28**	-0.30**	0.30**	-0.87**



**Figure captions:**

**Figure 1.** Spatial distributions of monitoring sites (solid triangles). The region between the two lines represent the area of the North-South Transect of Eastern China (NSTEC).

**Figure 2.** Box plots of leaf C, N, and C:N ratio by qualitative plant functional types (PFTs) that separate species into five groups (G, grasses; SD, deciduous shrubs; SE, evergreen shrubs; TD, deciduous trees; TE, evergreen trees). The box plots summarize the distribution of points for each variable and group. Box plots indicated interquartile ranges (box area), medians (horizontal line in the box), 25th and 75th percentiles (lower and upper box margins), 10th and 90th percentiles (lower and upper error bars) and individuals in the lower 10th percentiles (solid circles for each group).

**Figure 3.** Distributions of plant functional types (PFTs) in relation to climatic factors and soil nutrient proxies. Different letters above bars indicate significant differences among PFTs, determined by Fisher's least significant difference (LSD) comparisons ( $P < 0.05$ ). G, grasses; SD, deciduous shrubs; SE, evergreen shrubs; TD, deciduous trees; TE, evergreen trees; N, numbers of species.

**Figure 4.** Trends in leaf traits along climatic gradients. Leaf N versus mean annual temperature (MAT) (a), leaf N versus mean annual precipitation (MAP) (b), leaf C:N ratio versus MAT (c), and leaf C:N ratio versus MAP (d). N, numbers of species; All leaf traits were  $\log_{10}$ -transformed.

**Figure 5.** Trends in leaf traits along soil nutrient measures. Leaf N versus soil N (a), leaf N versus soil C:N ratio (b), leaf C:N ratio versus soil N (c), and leaf C:N ratio versus soil C:N ratio (d). N, numbers of species; All leaf traits were  $\log_{10}$ -transformed.

**Figure 6.** Variation partitioning ( $R^2$ ) of factors in accounting for the variations in leaf N (a), and leaf C:N ratio (b). Plant functional types (PFTs): grasses (G); deciduous shrubs

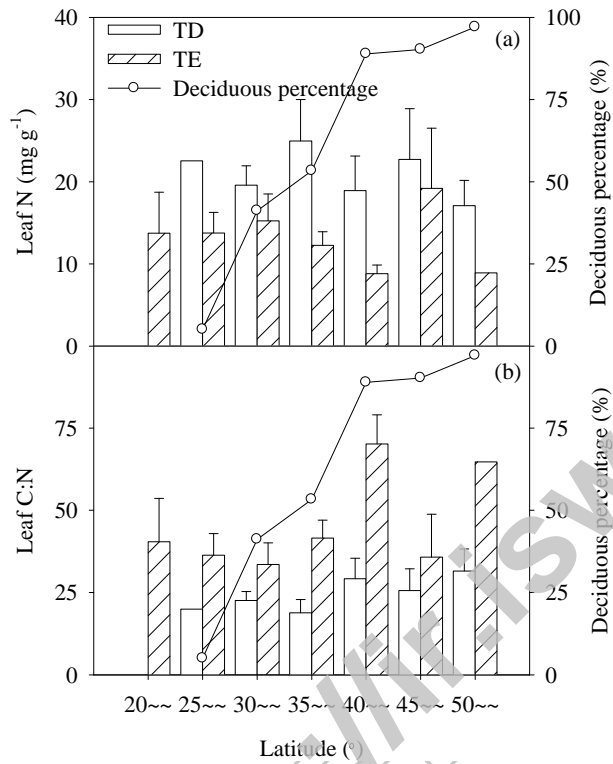
(SD); evergreen shrubs (SE); deciduous trees (TD) and evergreen trees (TE); Climate: mean annual temperature (MAT) and mean annual precipitation (MAP); Soil: Soil N and Soil C:N ratio. The symbols a, b and c represented the independent effects of PFTs, climate, and soil, respectively; ab, the interactive effect of PFTs and climate; ac, the interactive effect of PFTs and soil; bc, the interactive effect of climate and soil; and abc, the interactive effect of PFTs, climate and soil. Full model involved all of the three factors.

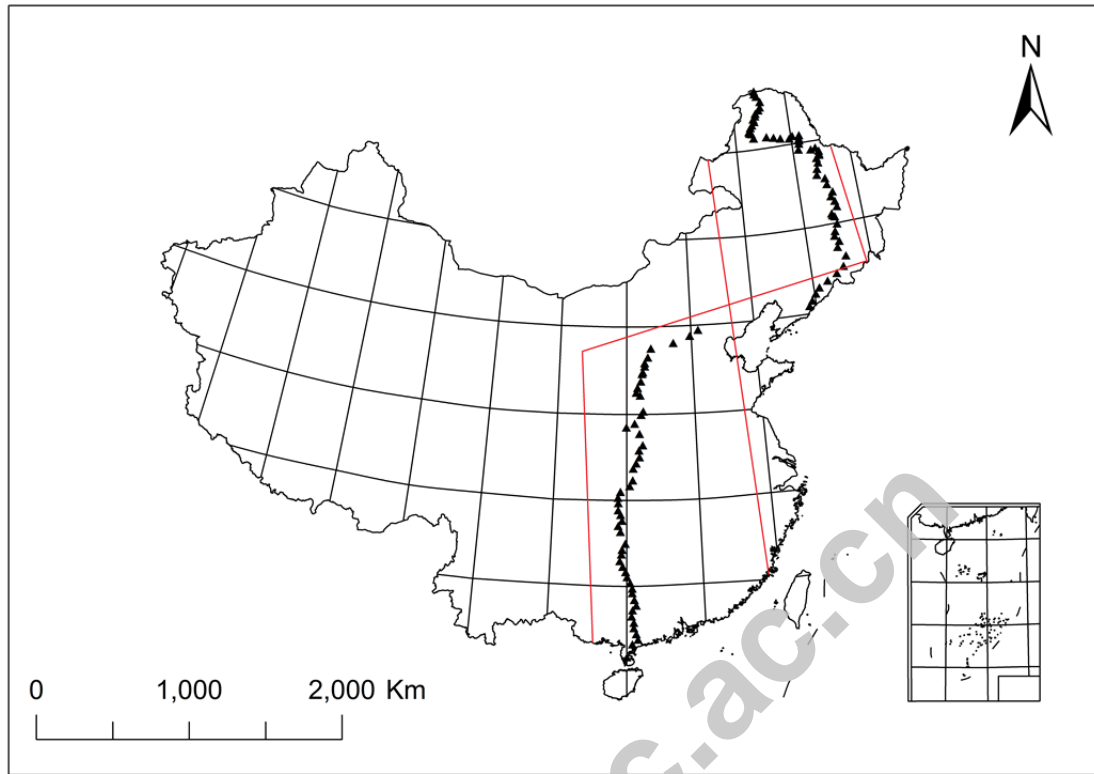
## Supporting information:

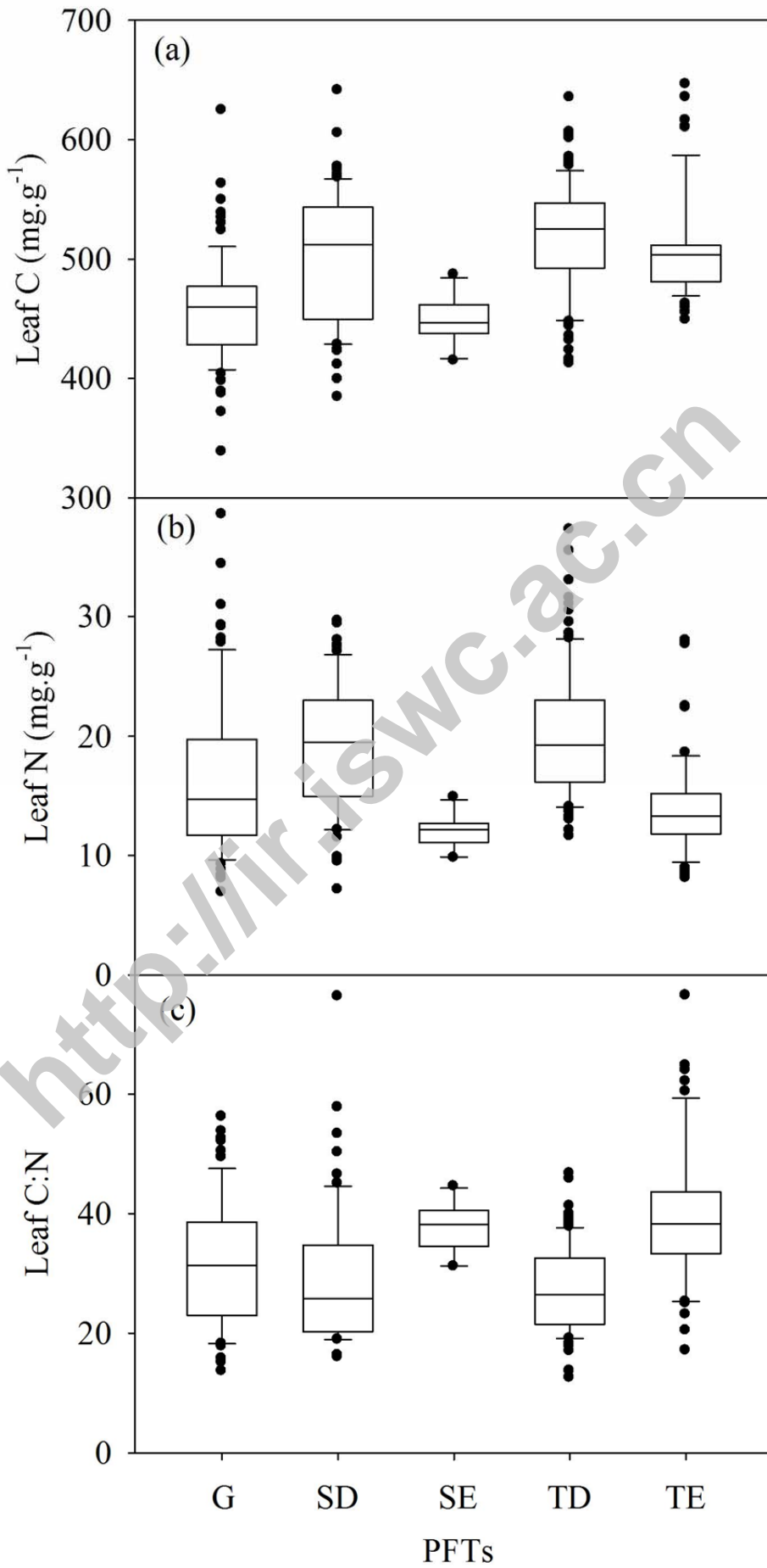
**Table S1.** Bivariate and multivariate linear regressions of leaf traits on climatic factors and soil nutrient proxies. MAP, mean annual precipitation; MAT, mean annual temperature; Soil N, Soil total N; Soil C:N, Soil total C: N ratio. Leaf traits were log<sub>10</sub>-transformed before analyses.

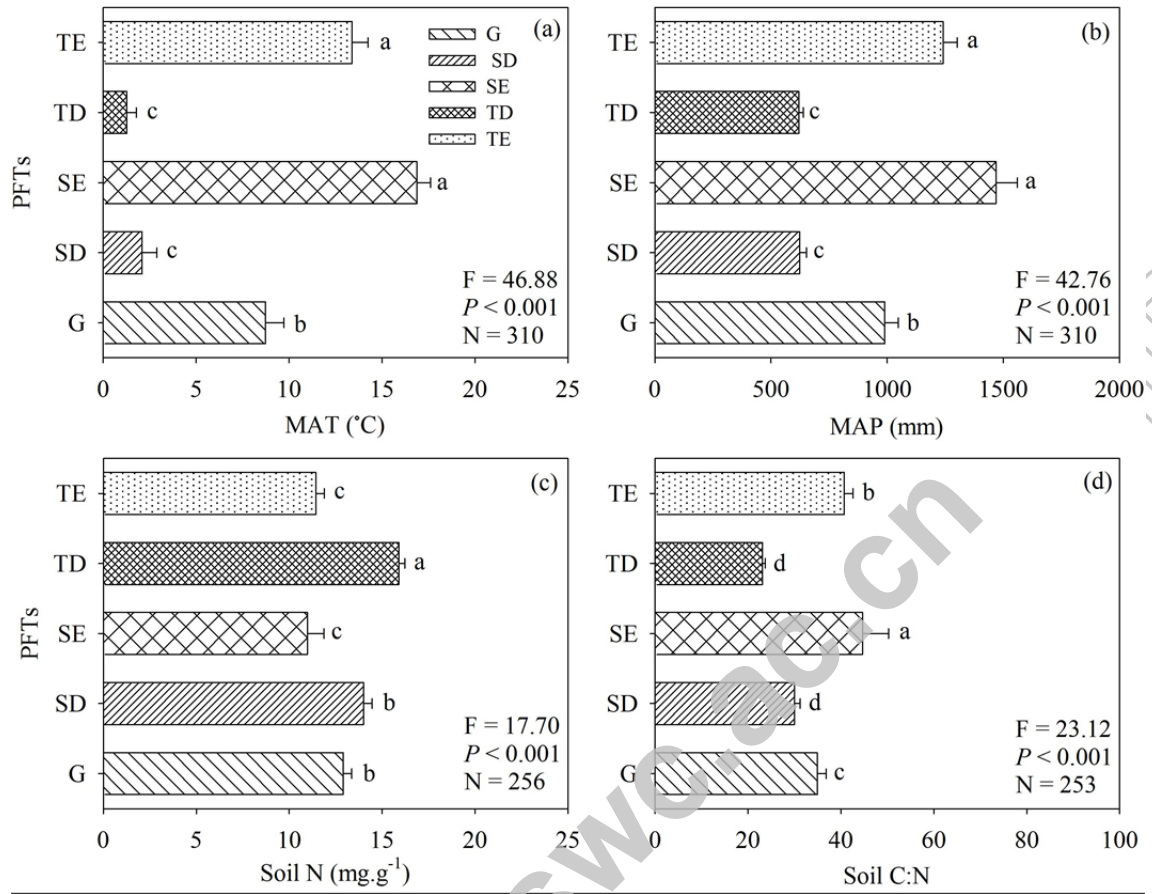
Variables in the model	N	lg leaf N			lg leaf C:N		
		R <sup>2</sup>	F	P	R <sup>2</sup>	F	P
1 MAT	310	0.077	25.81	<0.001	0.071	6.72	0.010
2 MAP	310	0.140	50.31	<0.001	0.086	29.06	<0.001
3 MAT+MAP	310	0.152	27.47	<0.001	0.141	25.18	<0.001
4 Soil N	256	0.176	54.61	<0.001	0.102	28.96	<0.001
5 Soil C:N	253	0.165	49.68	<0.001	0.102	28.65	<0.001
6 Soil N + Soil C:N	253	0.177	26.98	<0.001	0.106	14.78	<0.001
7 MAT + MAP + Soil N + Soil C:N	253	0.239	19.47	<0.001	0.180	13.56	<0.001

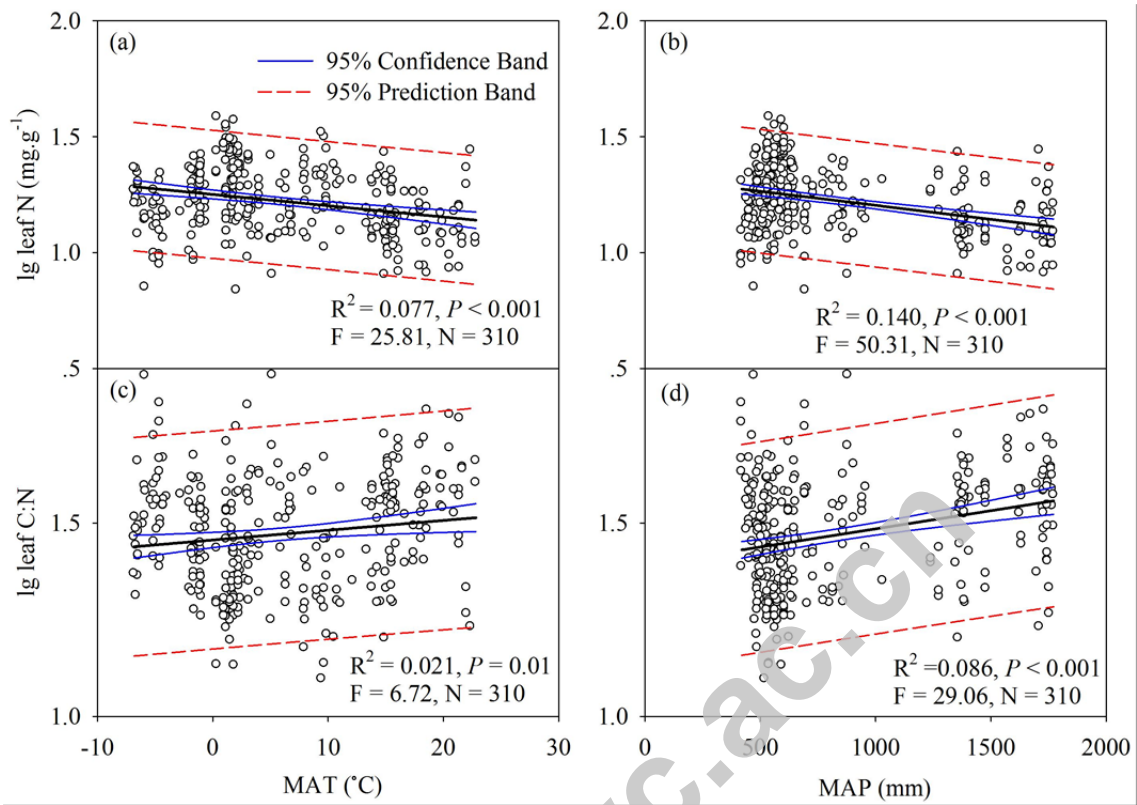
**Figure S1.** Latitudinal trends in leaf traits of deciduous trees (TD) vs. evergreen trees (TE). (a) leaf N; and (b) leaf C:N ratio. The latitudes were divided into seven bands: 20~25, 25~30, 30~35, 35~40, 40~45, 45~50 and >50 (°N). Mean and standard error bars were shown for deciduous trees and evergreen trees in each latitude band, respectively. The circle denoted the deciduous percentage in trees in each band.



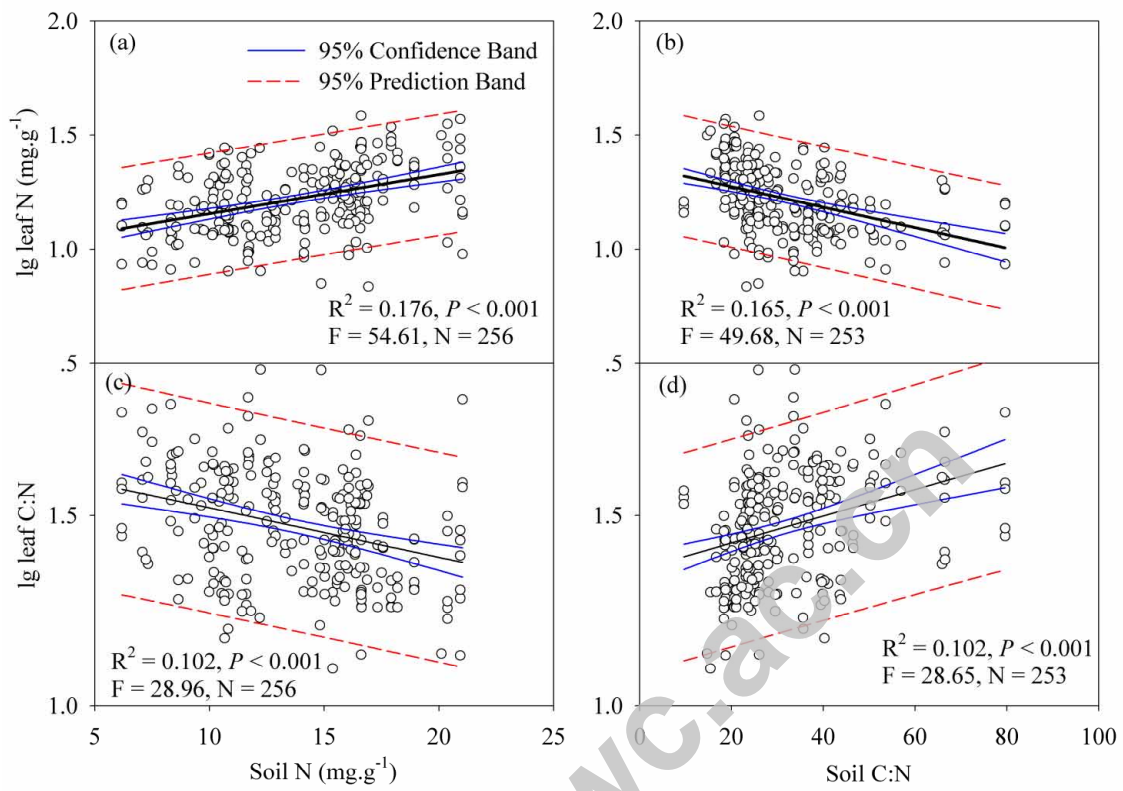








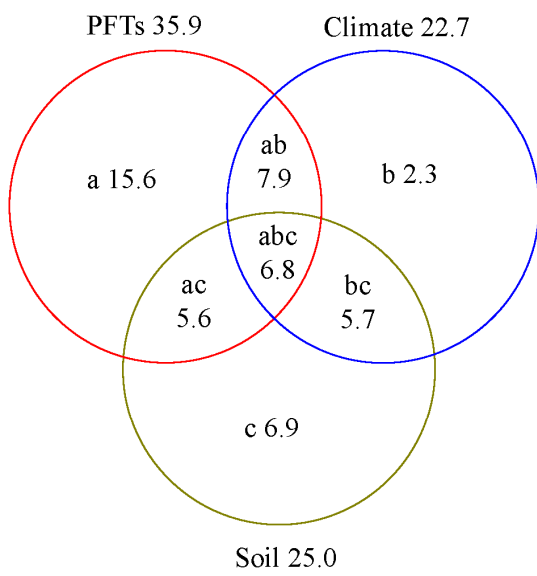




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(a) Full model for leaf N: 50.8 (%)



(b) Full model for leaf C:N: 42.6 (%)

