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Latitudinal and climate effects on key plant traits in Chinese forest ecosystems

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ABSTRACTS

A long-standing goal of ecology and forest management is to understand the environmental controls of resource utilization strategy of plants along geographical gradients. However, the mechanisms that guide this phenomenon, especially along latitude gradients, remain unclear. Using key leaf functional trait data of 1185 species within 120 sites in Eastern and Western China, we quantified the relationships between plant traits, namely leaf area (LA), specific leaf area (SLA), leaf nitrogen content, leaf phosphorus content, leaf dry matter content (LDMC) and leaf delta ^{13}C (d ^{13}C) content, and local climate along the latitude in Eastern and Western China. Our results revealed that: (1) Plant traits showed a wide variation across the study locations in China. The variation in plant traits was strongly correlated with latitude. (2) In Eastern China, latitude alone explained 54% and 53% of the variation in N:P and leaf phosphorus content (Pmass (g/kg)), respectively. In Western China, latitude alone explained 75% of the variation in leaf area. In Eastern China, most plant traits are significantly correlated with each other. However, this phenomenon is not obvious in Western China. (3) Immediate climate factors (mean climate in the month when the leaf traits were sampled) contributes most to explaining functional traits related to leaf nutrients, such as leaf nitrogen content (Nmass (g/kg), Narea (g/cm^2)), leaf phosphorus content (Pmass (g/kg), Parea (g/cm^2)), and annual mean climate contributes more to explaining functional traits related to leaf survival strategies. (4) In Eastern China, immediate climate and annual mean climate variables can explain the variance of 39.2% and 41.3% of plant traits variation, respectively. In Western China, the effect size of corresponding factors are 23.4% and 25.2%, respectively.

1. Introduction

Rapid climate warming is driving changes in the structure and composition of forest ecosystems (Post et al., 2009). Plant species adapt to climate change by relocating to regions with more suitable environmental conditions (Moritz and Agudo. 2014), and this involves change in resource acquisition and ecological strategies (Westoby et al., 2002; Mcgill et al., 2006; Cornelissen et al., 2010; Yang et al., 2014; Wright et al., 2017). Plant traits related to the resource economics spectrum, such as specific leaf area (SLA), leaf nutrient content, affect forest primary productivity and nutrient cycling (Lavorel and Garnier,

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2002; Cornelissen et al., 2010). While size-related traits, such as leaf area, mainly influence aboveground carbon storage (Westoby, 2004). Quantifying the relationships between the climate and plant functional traits is therefore important to understand the consequences of climate change (Wright et al., 2017).

Precipitation, temperature and solar radiation are primary climate variables constraining ecosystem productivity at global scales, such that each or a combination of these climate variables limits plant growth defined by species with special traits and life history strategies (Nemani et al., 2003). For example, Valladares et al. (2015) stated that plant trait variation is determined by climate in large-scale, meanwhile plant species exhibit similar functional traits under the same climatic conditions. With the change of climatic factors, the functional traits of plants show significant changes (Wright et al., 2005). Previous studies have shown that leaf functional properties exhibit an obvious change trend along temperature gradient, moisture gradient and light gradients (Domínguez et al., 2012; Wright et al., 2017; Yang et al., 2018). However, an important, unresolved question is how changes in climate variables will affect plant traits and what impact changes in traits and plant communities will have on patterns of forest function (Madani et al., 2018). Besides, studies intensively used the mean annual temperature, rainfall and other climatic factors, but rarely use the immediate climate factors to explore the relationship between climate and functional characteristics that also brings a lot of uncertainty.

With the change of latitudes, the climatic factors also undergo complex changes (Gao and Liu., 2018). However, numerous studies have found that the change of plant functional traits along latitudinal gradient pattern is not obvious (Domínguez et al., 2012). The existence of local habitat heterogeneity makes climate change along the latitudinal gradient not obvious. Forest ecosystems in China span several climatic zones, including tropical, subtropical, warm temperate and cold temperate climatic zones. Therefore, it provides an ideal opportunity to study the variations of leaf function attributes along latitudinal gradients. The climate heterogeneity in Eastern and Western China is quite different. Therefore, they have different functions in shaping functional traits of species. In order to better understand the latitude gradient pattern of plant traits in China, it is essential to divide China into two parts (Eastern and Western China).

The main purpose of our study was to elucidate the relationships between bioclimatic variables and plant traits to identify the critical factors affecting the covariation of plant functional traits along latitudinal gradients in Eastern and Western China. Specifically, we analyzed relationships between bioclimatic factors (immediate climate and mean climate) related to precipitation, temperature and solar radiation, and selected key dominant community plant traits. Here, we aim to answer 1) Whether the functional traits of plants show significant difference with latitude changes in Eastern and Western China ? 2) Are functional traits of plants relating to latitude correlated with climatic variables? and 3) Is there any difference in the latitude pattern of plant functional traits between Eastern and Western China? And whether the leading environmental factors causing these differences are the same?

2. Materials and methods

The data are collected from the China Plant Trait Database (Wang et al., 2017), which includes plant leaf functional traits of more than 1215 plant species from 120 sites. Leaf area (LA), specific leaf area (SLA), leaf nitrogen content (Nmass (g/kg), Narea (g/cm^2)), leaf phosphorus content (Pmass (g/kg), Parea (g/cm^2)), Nmass/Pmass, leaf dry matter content (LDMC) and leaf d ^{13}C content were selected as key plant traits. Detailed methods of trait measurement and the studied sites, climate variables can be found in Wang et al. (2017) and Yang et al. (2018).

To explore the effects of bioclimatic factors on functional traits are immediate or long-term, we divided climate factors of the last 50 years into two groups. One group includes Sun.collected (Sunlight intensity during the month of collection traits, %), Tem.collected (Temperature during the month of collection traits, $^\circ$), Pre.collected (Precipitation during the month of collection traits, mm). Another group includes PAR0 (photosynthetically active radiation during the thermal growing season, mol photon m^{-2}), MAT (mean annual temperature, $^\circ$), MAP (mean annual precipitation, mm), MMP (mean precipitation in wettest months, mm), Sun annual (mean annual sunlight intensity, %), MTC0 (mean temperature coldest month, $^\circ$).

We logarithmically transformed all the data of functional traits (except N/P and d^{13}C) and climatic factors to make them more normally distributed. Linear regression models were used to examine the relationships between plant traits, climate variables and latitude. R^2 was used to evaluate the explanatory power of the regression models. We adopted pairwise correlation analysis to test the relationships between climate variables and plant traits.

To estimate the relative importance of climate factors in each functional traits, we used boosted regression trees (BRTs), which is a machine learning based regression approach. The advantage of BRTs is the independence of presumptions regarding the relationship between predicted (plant traits) and predictor variables (climate variables) and can deal with nonlinear relationships and multiple co-linearity between predictors. The relative influence is scaled to add up to 100% for each model.

Principal components analysis (PCA) and redundancy analysis (RDA) are powerful multivariate analysis techniques in ecology (Maire et al., 2015; Yang et al., 2018). We assessed ecological strategy variation by assessing multivariate shifts of all leaf traits and climate variables using PCA and used RDA to analyze the relationships of trait variation to climate variables. After homogenization of data, we first performed detrended correspondence analysis (DCA) for the choice of RDA and CCA. As the size of the first axis of lengths of gradient of DCA less than 3.0, we selected RDA to investigate the traits-climate relationship. Then, we used variance inflation factor analysis to analyze all environmental factors by collinearity. In turn, we deleted collinear environmental factors until all variables are less than 10. Finally, we used the step model to select the lowest AIC value model as the best model. These analyses were performed using the vegan package in R.

3. Results

We observed wide variation in plant traits across the study locations in China (Fig. 1a and b), $d^{13}C$, LDMC, Narea, Nmass, Parea and N/P in Eastern China is higher than that in Western China. However, LA and SLA in Eastern China is lower than that in western China. The functional traits showed significant trends along latitudes (Fig. 2). In Eastern China, latitude alone explained 54% and 53% of the variation in N:P and log Pmass, higher than logLDMC (41%), logParea (33%), $d^{13}C$ (33%) and logLA (22%). In China west, latitude alone explained 75% of the variation in logLA, highest among all the traits. In Eastern China, most plant traits are significantly correlated with each other (Fig. 4a). In Eastern China, N/P and logLA is strongly correlated with other plant traits. In China west, logSLA is significantly corrected with logLDMC, logNmass, logNarea and logParea.

Immediate climate contributes most to explaining functional traits related to leaf nutrients, such as logNarea, logNmass, logParea and logPmass, and annual mean climate contributes more to explaining functional traits related to leaf survival strategies, such as $d^{13}C$, logLA, logSLA and N/P (Fig. 5a and b). In Eastern China, temperature related climatic factors are relatively good explanations for plant traits. However, in China west, solar radiation related climatic factors are relatively good explanations for plant traits.

We calculated the plant traits for the first (PC1) and second (PC2) principal component in Eastern and Western China (Fig. 6). logSLA and logLA captured most of the variation across PC1 (45%) and PC2 (32%) of the variance for plant traits in Eastern and Western China. We calculated the interpretation degree of environment factors (immediate climate and annual mean climate) on plant traits (Table 1). We found that:in Eastern China, climate variables can explain the variance of 39.2% (immediate climate) and 41.3% (annual mean climate) of plant traits variation. In Western China, the degree of variation of plant traits explained by climate factors is lower (23.4% and 25.2%) than that in Eastern China.

4. Discussion

Overall, plant traits are significantly correlated with latitude across China. LA is significantly lower with increasing latitude in Eastern and Western China. Leaf area is mainly affected by temperature (Wright et al., 2017). As the latitude increases, the temperature decreases correspondingly (Fig. 3). LDMC is significantly higher with increasing latitude. LDMC represents the ability of plants to acquire resources (Yang et al., 2018).

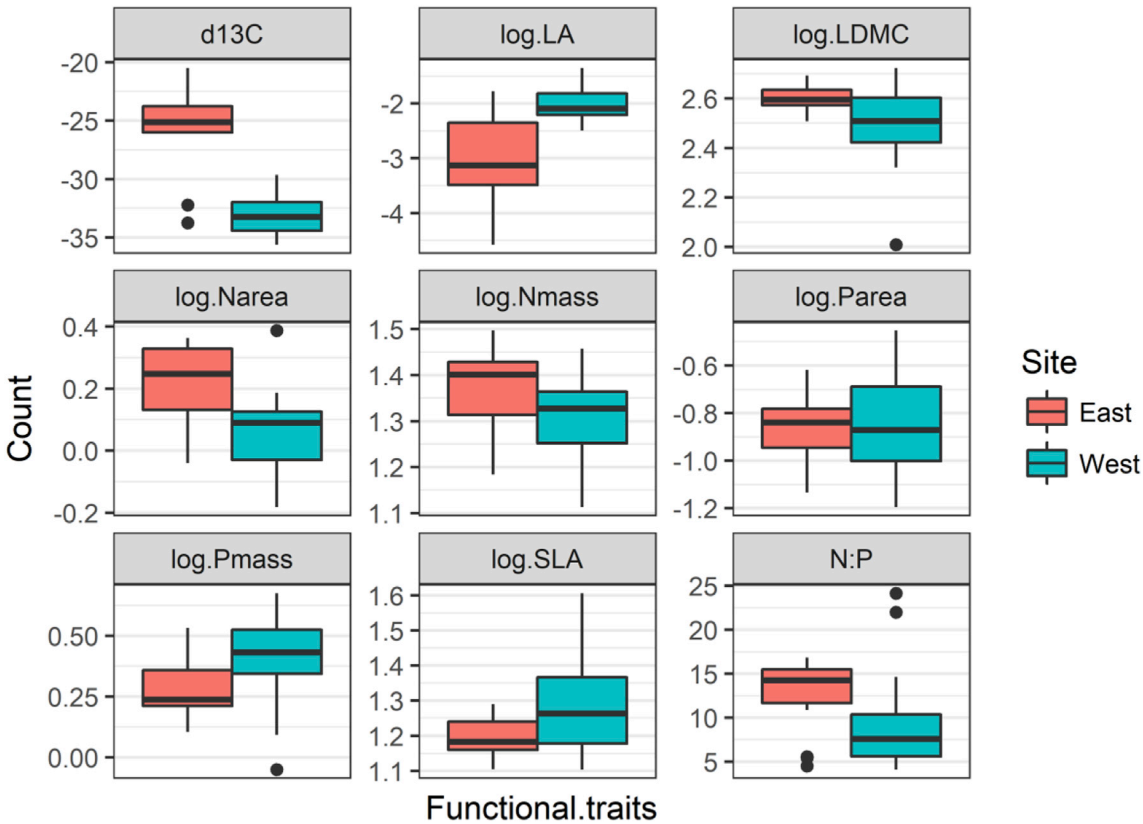

Fig. 1. Characteristics of plant functional traits in Eastern and Western China.

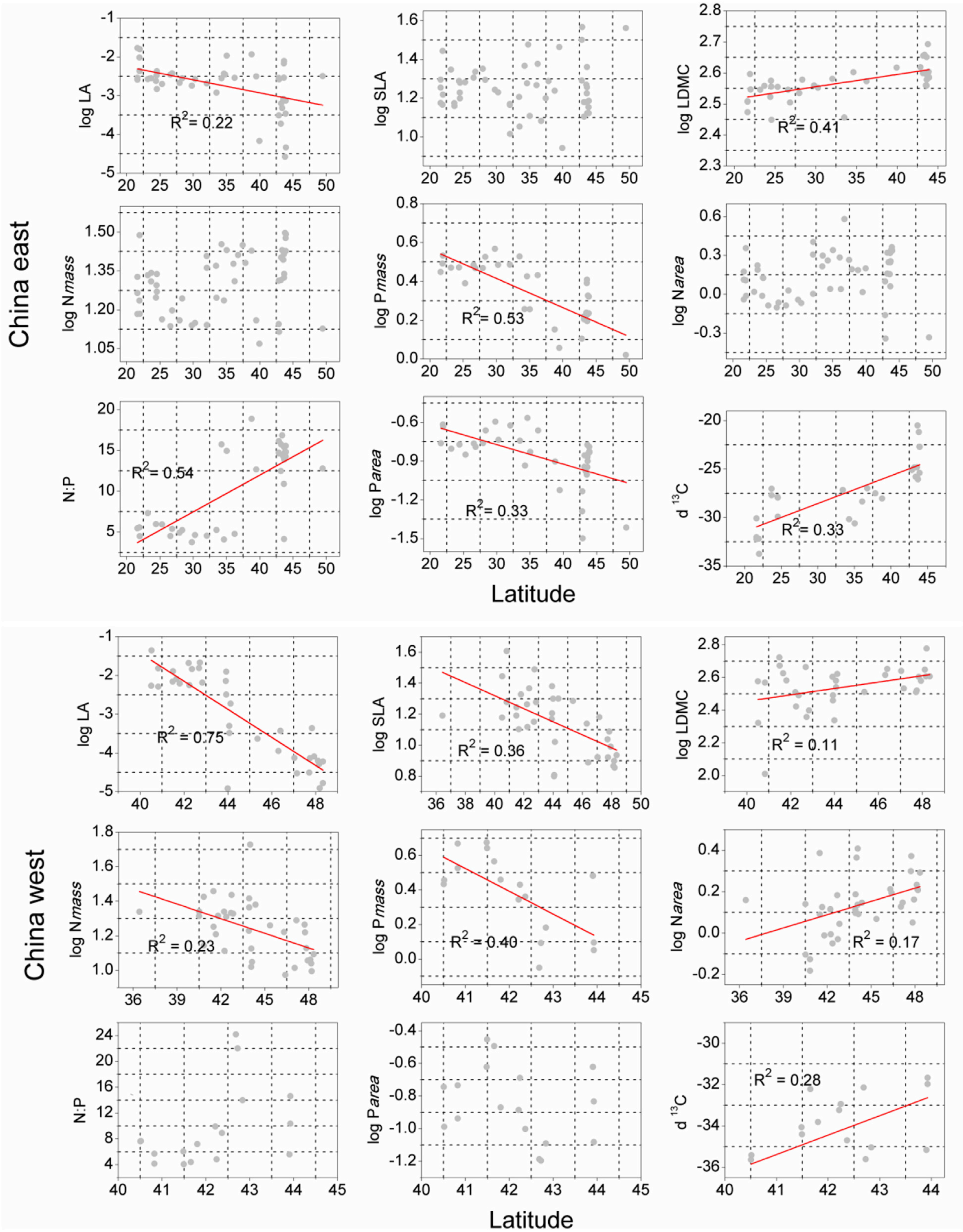

Fig. 2. Latitude gradient pattern of key plant functional traits in Eastern and Western China. R^2 is used to test the interpretation degree of latitude to functional traits, confidence interval is 95%.

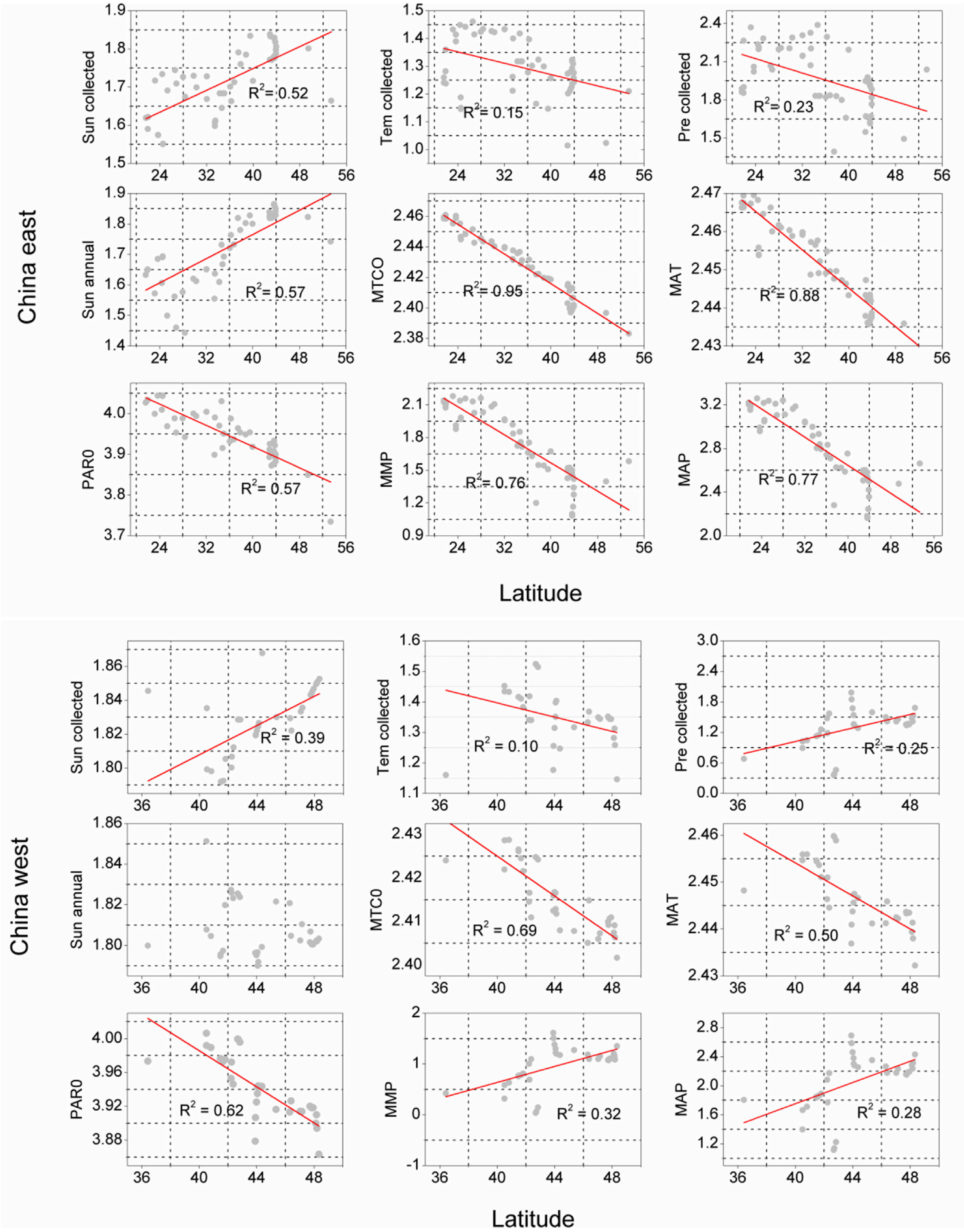

Fig. 3. Latitude gradient pattern of climate variables in Eastern and Western China. R^2 is used to test the correlation degree of latitude to climate variables, confidence interval is 95%.

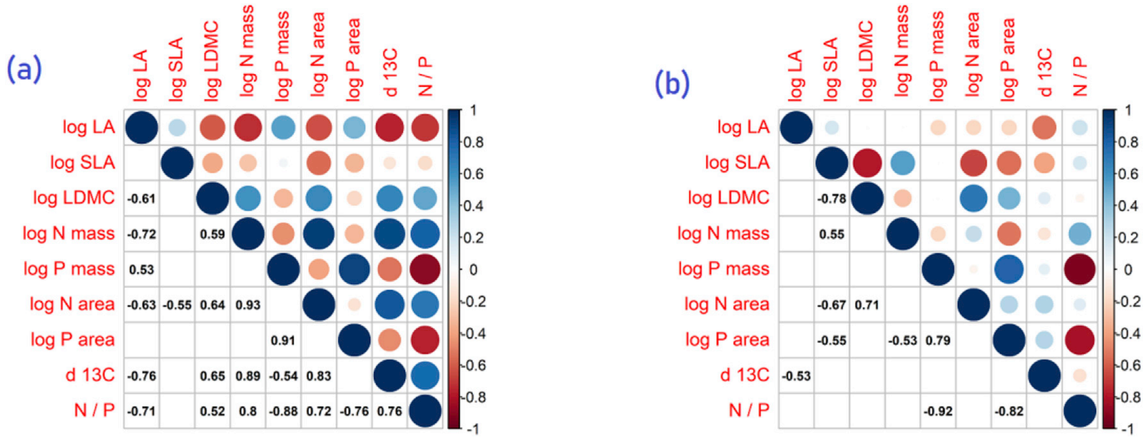

Fig. 4. Interactions between functional traits in Eastern (a) and Western (b) China. R^2 with significant differences ($p < 0.05$) is drawn in the picture.

We have also found that SLA is smaller in Eastern than in Western. In China, rainfall is much larger in Eastern than in the Western. Plants with higher average temperature, higher radiation intensity or growth in arid regions have smaller SLA (Ordoñez et al., 2010; Poorter et al., 2010). The content of d ^{13}C represents the degree of water stress in plants (Leffler and Enquist, 2002; Cernusak et al., 2013), so it presents a significant latitude gradient pattern. In Eastern China, N/P is significantly higher with increasing latitude. This indicates that the N is limited by the low latitude area, and is mainly restricted by P in the high latitudes (Wright et al., 2005).

The larger LA and SLA, the larger the light capture area of the leaves, the more favorable the assimilation of C (Wilson et al., 2010), showing significant negatively correction with other traits in Eastern and Western China, which related with plant nutrients. we also found that d^{13}C is closely related to leaf nutrient (N, P and K). SLA and LA captured most of the variation across PC1 and PC2 of the variance for plant traits in China. Leaves with smaller SLA have more cells or larger biomass of individual cells, and plants with smaller SLA have stronger ability to support and resist environmental stress, especially in resource-deficient environments, which further proves that plants adapt to the environment by adjusting the size of SLA (Castro-Diez et al., 2000).

The results of BRTs showed that the nutrient traits of plants will change significantly with immediate climate. However, plant traits such as leaf area are the results of long-term climate adaptation (Wright et al., 2005). In Eastern China, with the increase of latitude, the temperature decreases significantly, so it becomes the dominant factor affecting most plant traits. In western China, with the latitude rising, the illumination factors will drastically change, affecting the ability to obtain plant resources, thus becoming a key factor affecting plant traits.

Climate factors can give a considerable amount explanation to most of the variation of single functional traits. The plant traits described reveal the extent to which climate variables shape forest communities in China forest ecosystems. Strong temperature- and moisture-related spatial gradients in traits related to competitive ability (for example, LA and LDMC) and resource capture and retention (for example, leaf nutrition and SLA) reflect trade-offs in plant ecological strategy from benign (wram,wet) to extreme (cold, dry) conditions (Reich et al., 2007 & Reich, 2014). Community-level trait syndromes, as reflected in ordination axes, are also strongly related to both temperature, precipitation, and sunlight suggesting that climate drivers structure not only individual plant traits but also trait combinations. Long-term climate variables did not significantly alter d^{13}C and N levels of the plants. Short-term rainfall variability, however, significantly increased foliar d^{13}C of the plants, indicating higher water use efficiency during a more severe drought (Farquhar et al., 1982; Zhao et al., 2013). The results indicate that short-term climate variables significantly affects the plant functions. The nutrient elements of plant leaves will change with the season. Therefore, short-term climatic factors contribute more to the nutrient content of leaves. (Zhao et al., 2013).

Climate, as the main environmental filter, changes the species composition and community structure in the community, and then determines the difference of the weighted average value of leaf function attributes under different environmental conditions (Domínguez et al., 2012). According to the theory of community construction, the difference of adaptability of species to the external environment is the main reason that species composition changes along the environmental gradient in the community (Andersen and Dalling, 2012). The spatial variability of leaf morphology, nutrients and physiological attributes was explained more by plant functional type (PFT) than by climate factors (Reich et al., 2007). Differences in leaf functional attributes among different plant functional types are the common result of plant genetic factors and their adaptation to habitats (Poorter et al., 2010; Kikuzawa et al., 2013). Although climate factors cannot fully explain the latitude pattern of leaf attributes at community level, they have some direct and indirect effects on the spatial distribution of leaf attributes. On the one hand, climate factors can directly affect plant leaf morphology and carbon distribution related to metabolic activities

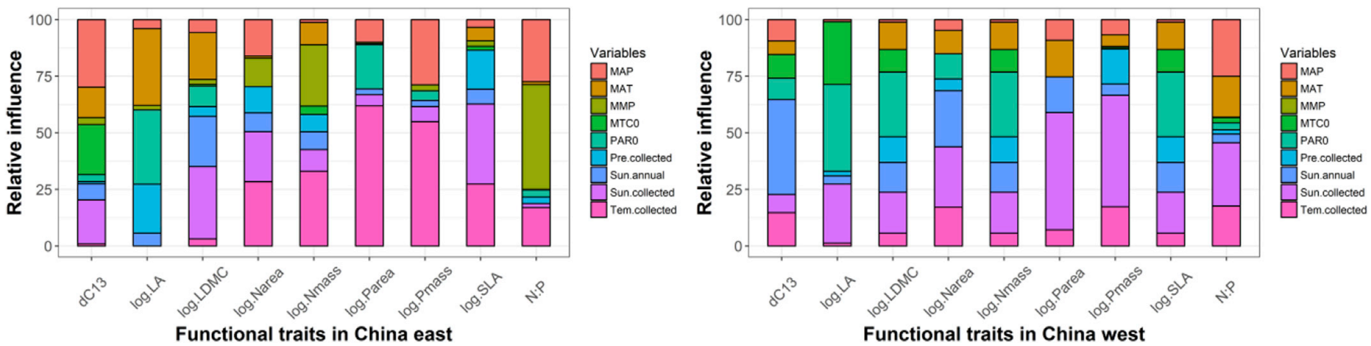

Fig. 5. Effects of climate factors on each functional trait by BRTs analysis in Eastern (a) and Western (b) China.

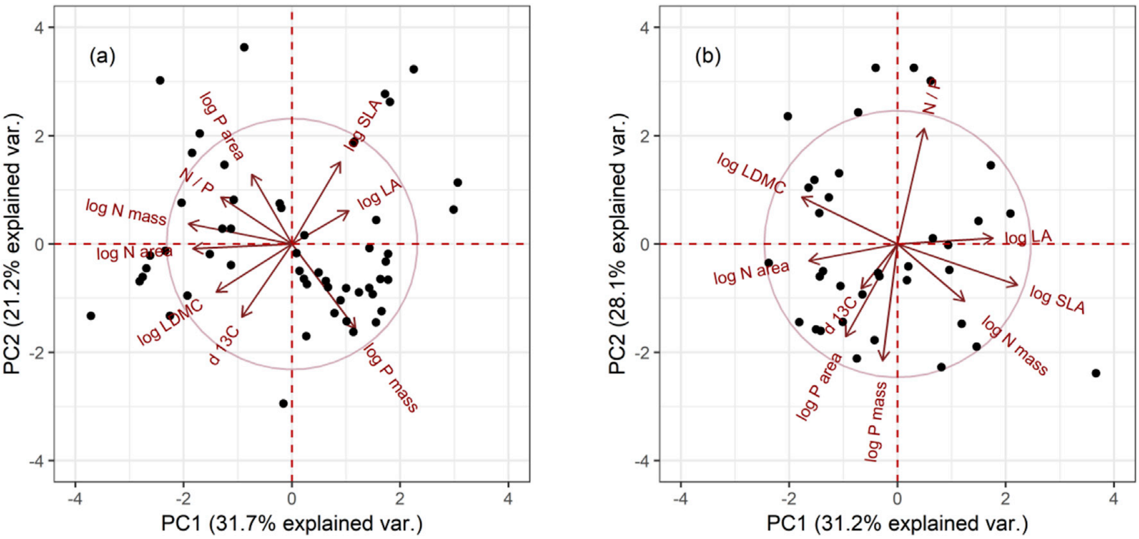

Fig. 6. Principal component analysis (PCA) of key plant traits in Eastern (a) and Western (b) China.

Table 1
Redundancy Analyses (RDA) of leaf traits in Eastern and Western China.

	Analysis	immediate climate variables	Average climate variables
Eastern China	RDA	Sun.collected, Tem.collected, Pre.collected	PAR0, MMP
	RD1	28.2	30.1
	RD2	10.1	9.8
	Total amount explained	39.2	41.3
	p	0.03	0.01
Western China	RDA	Sun.collected, Pre.collected	PARO, MMP
	RD1	14	16.2
	RD2	8.1	7.9
	Total amount explained	23.4	25.2
	p	0.04	0.003

(Moles et al., 2014). On the other hand, climate conditions shape the large-scale geographical pattern of vegetation types under natural conditions, and also regulate the availability of soil resources (Garnier et al., 2010; Han et al., 2011).

Forest ecosystem models are increasingly moving to incorporate relationships between plant traits and the climate, as this can improve estimates of ecosystem change (Butler et al., 2017). Our results inform these projections of future China forest ecosystem functional change by explicitly quantifying the link between climate variables and key plant traits across the biome. In particular, our study highlights the importance of accounting for future changes in temperature, water availability, as this will probably influence both the magnitude and direction of change for many plant traits.

Author contributions

Xing Zhang, Jie Gao, Xin He and L Wang designed the study, Xing Zhang performed analyses and led the writing; J Gao and Xing Zhang contributed substantially to revisions.

Conflict of interest

None declared.

Data accessibility statement

Data from: Wang, H., Harrison, S. P., Colin, P. I., Yang, Y., Bai, F., & Togashi, H. F., et al. (2017). The china plant trait database: towards a comprehensive regional compilation of functional traits for land plants. *Ecology, 99*.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00527.

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