

# Latitudinal variation of leaf morphological traits from species to communities along a forest transect in eastern China

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**Abstract:** Comprehensive information on geographic patterns of leaf morphological traits in Chinese forests is still scarce. To explore the spatial patterns of leaf traits, we investigated leaf area (LA), leaf thickness (LT), specific leaf area (SLA), and leaf dry matter content (LDMC) across 847 species from nine typical forests along the North-South Transect of Eastern China (NSTEC) between July and August 2013, and also calculated the community weighted means (CWM) of leaf traits by determining the relative dominance of each species. Our results showed that, for all species, the means ( $\pm$  SE) of LA, LT, SLA, and LDMC were  $2860.01 \pm 135.37 \text{ mm}^2$ ,  $0.17 \pm 0.003 \text{ mm}$ ,  $20.15 \pm 0.43 \text{ m}^2 \text{ kg}^{-1}$ , and  $316.73 \pm 3.81 \text{ mg g}^{-1}$ , respectively. Furthermore, latitudinal variation in leaf traits differed at the species and community levels. Generally, at the species level, SLA increased and LDMC decreased as latitude increased, whereas no clear latitudinal trends among LA or LT were found, which could be the result of shifts in plant functional types. When scaling up to the community level, more significant spatial patterns of leaf traits were observed ( $R^2 = 0.46\text{--}0.71$ ), driven by climate and soil N content. These results provided synthetic data compilation and analyses to better parameterize complex ecological models in the future, and emphasized the importance of scaling-up when studying the biogeographic patterns of plant traits.

**Keywords:** latitudinal pattern; leaf morphological trait; community weighted mean; forest ecosystem; North-South Transect of Eastern China

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## 1 Introduction

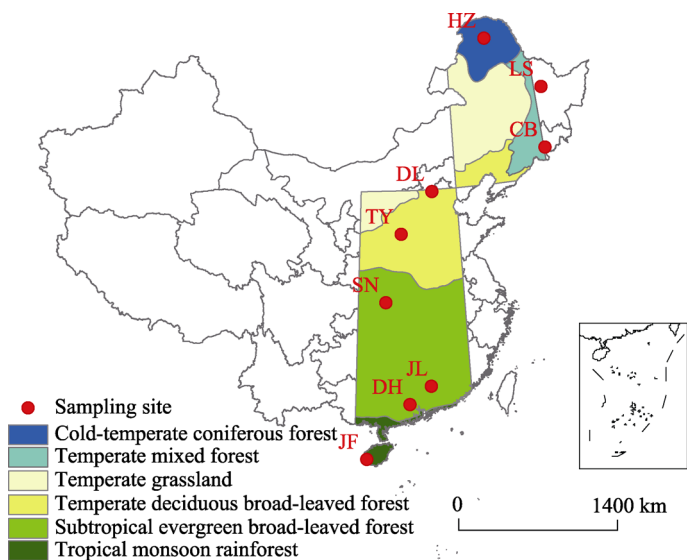
Leaves are the primary organs of photosynthesis in terrestrial ecosystems (Poorter *et al.* 2009). Leaf morphological traits, e.g., leaf area (LA), leaf thickness (LT), specific leaf area (SLA), and leaf dry matter content (LDMC), may reflect the leaf photosynthetic capacity and resource-use strategy of plant species experiencing changes in environmental conditions (Chapin *et al.*, 1993; Poorter *et al.*, 2009; Garnier and Navas, 2012). In addition, these traits are relatively easy and quick to measure when comparing the chemical and physiological traits of leaves (Cornelissen *et al.*, 2003), thus they have received special attention in the analysis of variation in leaf traits at the regional and global scales (Wright *et al.*, 2004; Reich *et al.*, 2007; Kazakou *et al.*, 2014).

In the past few decades, a number of scientists have investigated the spatial patterns of leaf functional traits along environmental gradients and demonstrated that their geographic patterns were shaped by environmental factors (climatic and edaphic gradients) and phylogenetic differences (Reich *et al.*, 2007; Poorter *et al.*, 2009; Ordonez *et al.*, 2010; Hodgson *et al.*, 2011; Moles *et al.*, 2014). For example, leaves in habitats characterized by high temperature and insolation or water limitation generally show high LT and LDMC (Niinemets, 2001) but low SLA (Poorter *et al.*, 2009). However, these studies on global leaf traits involve only a small number of forest ecosystems in China, and there is a lack of comprehensive information concerning geographic patterns of leaf morphological traits in Chinese forests. Here, we aimed to fill the gap by analyzing a dataset covering 847 forest species across a wide range of environments in China.

Another challenge in leaf trait research is that majority of studies have conducted their analyses at the species level (across the species pool or average), and thus have shed little light on the adaptive mechanisms of plant communities along large-scale environmental gradients as a result of community assembly. Moreover, it is impossible, in theory, to build direct links between species-level leaf traits and ecosystem function on a large scale (Wang *et al.*, 2015). Recently, some ecologists have incorporated the community weighted mean (CWM) into leaf traits to assess community dynamics and ecosystem function. To do this, the leaf-level measurements are weighted by the relative abundance of each species in each plot (Garnier *et al.*, 2004; Vile *et al.*, 2006), and clear trends were found in community-level leaf traits along gradients of soil water availability (Cornwell and Ackerly, 2009), light (Dominguez *et al.*, 2012), the duration of abandonment (Garnier *et al.*, 2004; Vile *et al.*, 2006), and grazing disturbance (Klumpp and Soussana, 2009). However, most of these studies were conducted on a local scale, and little is known concerning the spatial variation in community-level leaf traits along these environmental gradients on a large scale (e.g., across different climate zones).

The North-South Transect of Eastern China (NSTEC) spans from a tropical rain forest in the south to a cold-temperate coniferous forest in the north, including almost all forest types in the Northern Hemisphere (Zhang and Yang, 1995) (Figure 1 and Table 1). This transect, therefore, provides an ideal set of experimental plots to explore the ecological and evolutionary responses of plants to environmental changes on a large scale. We comprehensively investigated LA, LT, SLA, and LDMC across 847 common plant species from nine typical forests along the NSTEC. Based on these measured data, we analyzed the biogeographic patterns of leaf morphological traits at the species and community levels, and specifically

investigated: 1) the latitudinal patterns of variation in leaf morphological traits, and whether they are similar at the species and community levels or not; 2) the primary factors controlling latitudinal variation.



**Figure 1** Geographic locations and vegetation types of sampling sites. JF, Jianfengling; DH, Dinghu Mountain; JL, Jiulian Mountain; SN, Shennongjia; TY, Taiyue Mountain; DL, Dongling Mountain; CB, Changbai Mountain; LS, Liangshui; HZ, Huzhong. Different colors highlighted in the North-South Transect of Eastern China (NSTEC) represent different vegetation types (Zhang and Yang, 1995).

**Table 1** Environmental characteristics and vegetation types of sampling sites

Site	Latitude (°N)	Longitude (°E)	MAT (°C)	MAP (mm)	SN (mg g <sup>-1</sup> )	Vegetation type	No. of species
JF	18.7	108.9	19.8	2449.0	1.95	Tropical monsoon rainforest	139
DH	23.2	112.5	20.9	1927.0	1.76	Subtropical evergreen broad-leaved forest	158
JL	24.6	114.4	16.7	1954.0	2.35	Subtropical evergreen broad-leaved forest	172
SN	31.3	110.5	10.6	1330.0	3.76	Subtropical mixed evergreen and deciduous broad-leaved forest	120
TY	36.7	112.1	6.2	662.0	2.56	Temperate deciduous broad-leaved forest	76
DL	40.0	115.4	4.8	539.1	3.12	Temperate deciduous broad-leaved forest	79
CB	42.4	128.1	2.6	691.0	6.37	Temperate mixed forest	109
LS	47.2	128.9	-0.3	676.0	4.59	Temperate mixed forest	104
HZ	51.8	123.0	-4.4	481.6	3.15	Cold-temperate coniferous forest	88

Note: MAT, mean annual temperature; MAP, mean annual precipitation; SN, soil N content.

## 2 Materials and methods

### 2.1 Study sites and field sampling

The NSTEC is the 15th standard transect of the International Geosphere-Biosphere Program

(IGBP), which extends from the Hainan Island to the northern border of China, ranging from 108°E–118°E to less than 40°N, and from 118°E–128°E to a minimum of 40°N, including 25 provinces and approximately 1/3 of China. Due to the influence of the eastern Asian monsoon, the climate in the NSTEC differs from that found in Europe and North America, and is characterized by clear latitudinal gradients of temperature and precipitation. Correspondingly, different types of zonal forest ecosystems are distributed along the NSTEC from north to south, including cold-temperate coniferous forests, temperate mixed forests, warm-temperate deciduous broad-leaved forests, subtropical evergreen broad-leaved forests, and tropical monsoon rainforests (Zhang and Yang, 1995; Yu *et al.*, 2006).

A field survey was carried out between July and August in 2013 across nine natural forests along the NSTEC. These sampling sites, from south to north, were Jianfengling (JF), Dinghu Mountain (DH), Jiulian Mountain (JL), Shennongjia (SN), Taiyue Mountain (TY), Dongling Mountain (DL), Changbai Mountain (CB), Liangshui (LS), and Huzhong (HZ) (Figure 1). The specific characteristics of the nine sampling sites are described in Table 1.

A detailed description of the floristic and environmental survey methods used here is presented in Wang *et al.* (2015). Briefly, we first established four sampling plots (30 × 40 m) in each forest ecosystem. Then, the geographic information (latitude, longitude, and altitude) as well as community structure was assessed for each plot. We recorded all plant individuals within each plot, and measured height and diameter-at-breast-height (DBH) for each woody individual with DBH ≥ 2 cm. For herbs, aboveground biomass was harvested and oven-dried. Meanwhile, 20 healthy mature leaves were collected from four individuals of each plant species and were measured as soon as possible after collection (within 4–8 h). A total of 1047 species-at-site observations were completed in 32 plots across nine forest ecosystems, representing 847 plant species in 427 genera and 159 families (some plant species were found in several forest types), including angiosperms, gymnosperms, and pteridophytes.

## 2.2 Leaf functional trait measurements

Following the standardized procedures of Cornelissen *et al.* (2003), LA (mm<sup>2</sup>, leaf projected surface area), LT (mm), SLA (m<sup>2</sup>·kg<sup>-1</sup>, the one-sided area of a fresh leaf divided by its oven-dried mass), and LDMC (mg·g<sup>-1</sup>, the oven-dried mass of a leaf divided by its water-saturated fresh mass) were determined for ten fully expanded leaves per individual sampled. LA was measured with a scanner (CanoScan LiDE 110, Japan) and Photoshop CS (Adobe Systems, San Jose, USA), while LT was measured with an electronic digital caliper on five to ten points per leaf (blade), avoiding the mid-vein. Leaves were then oven-dried at 70°C for 48 h and weighed to calculate SLA and LDMC.

## 2.3 Community-level leaf traits

To measure leaf traits at the community level, we calculated the CWMs of leaf traits as the community-level integrative indices (Garnier *et al.*, 2004), as follows:

$$CWM = \sum P_i \times trait_i \quad (1)$$

where  $P_i$  is the relative dominance of species  $i$  within a community based on the aboveground biomass. For woody plants, aboveground biomass, including stems, branches, and leaves, was calculated using species-specific allometric regressions with DBH and height, which were obtained from the Chinese Ecosystem Research Net (CERN) database (<http://>

159.226.111.42/pingtai/cernc/index.jsp), published studies, and our previous field measurements. When the allometric equations of a species were not available, we substituted the equations from the same genera, and used similar plant functional type (PFT), or mixed-species equations of a specific forest. A total of 246 allometric biomass equations ( $R^2 = 0.52\text{--}1.00$ ) were implemented in this study. All of the allometric regressions are available in Wang *et al.* (2015). For herbs, the aboveground live biomass was sorted according to species and weighted after drying.

## 2.4 Environmental data

Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) for each study site were derived from the meteorological database (1961–2007) produced by CERN (He *et al.*, 2014).

At each plot, soil samples were taken at depths of 0–10 cm using a 6 cm diameter auger and were sieved to remove roots and visible organic debris. Samples were mixed thoroughly and air-dried prior to chemical analyses. Soil total carbon (SC,  $\text{mg}\cdot\text{g}^{-1}$ ) and nitrogen (SN,  $\text{mg}\cdot\text{g}^{-1}$ ) were determined by an elemental analyzer (Vario MAX CN; Elementar, Germany).

## 2.5 Data analysis

Data of leaf traits were  $\log_{10}$  transformed when it was necessary to obtain approximate normality and homogeneity of residuals. Species-by-site data were averaged for each species, and the average for each species was then classified into different groups: growth form (herbs, shrubs, and trees), leaf type (coniferous and broad-leaved trees), and leaf habit (evergreen and deciduous broad-leaved trees). A one-way analysis of variance (ANOVA) with least significant difference (LSD) *post-hoc* testing was used to compare leaf traits among various PFTs.

To investigate the latitudinal patterns of leaf traits, we first related leaf traits to latitude using a polynomial regression at the species and community levels. Next, to decompose the variance of species-level leaf traits into among-site and within-site components, these data were further analyzed through nested ANOVAs with species nested within sites.

Then, we qualified the effects of environmental variables and PFT on each of the leaf traits using mixed-effect models and the lmer function in the package lme4 (R version 2.15). For species-level traits, we treated PFT and environmental variables as fixed effects and sites as a random effect in order to account for the non-independence of species occurring at the same site. Given that the environmental variables were strongly coupled with each other, only one of the climate and soil variables was included in each main effect model to avoid instance of multiple collinearity. The environmental factors with significant effects ( $P < 0.05$ ) on leaf traits and interaction terms between PFT and the environmental variables were included in the final models. For community-level traits, the explanatory variables were climatic and soil variables. If more than one environmental variable was significant, models with lower Akaike's Information Criterion (AIC) values were selected as the final best-fit models (Aho *et al.*, 2014).

All analyses were conducted using SPSS 13.0 statistical software (SPSS Inc., Chicago, IL, USA, 2004) and R software (version 2.15.2, R Development Core Team 2012). The significance levels were set at  $P < 0.05$ .

### 3 Results

#### 3.1 Overall statistics of leaf traits

For all 847 species, the means ( $\pm$  standard error, SE) of LA, LT, SLA, and LDMC were  $2860.01 \pm 135.37 \text{ mm}^2$ ,  $0.17 \pm 0.003 \text{ mm}$ ,  $20.15 \pm 0.43 \text{ m}^2 \cdot \text{kg}^{-1}$ , and  $316.73 \pm 3.81 \text{ mg} \cdot \text{g}^{-1}$ , with ranges of 4.09–56085.43  $\text{mm}^2$ , 0.01–0.78 mm, 1.89–94.99  $\text{m}^2 \cdot \text{kg}^{-1}$ , and 44.46–775.68  $\text{mg} \cdot \text{g}^{-1}$  (Table 2), respectively. Among these four traits, the LA had the greatest variation (coefficient of variation, CV=1.51), and that of the LDMC was the least (CV=0.39).

At the community level, the means ( $\pm$  SE) of  $\text{LA}_{\text{CWM}}$ ,  $\text{LT}_{\text{CWM}}$ ,  $\text{SLA}_{\text{CWM}}$ , and  $\text{LDMC}_{\text{CWM}}$  were  $1443.80 \pm 169.35 \text{ mm}^2$ ,  $0.34 \pm 0.03 \text{ mm}$ ,  $9.83 \pm 0.71 \text{ m}^2 \cdot \text{kg}^{-1}$ , and  $421.78 \pm 8.76 \text{ mg} \cdot \text{g}^{-1}$ , respectively (Table 2). Similar to what was found among species, the variation was greatest for LA and the least for LDMC.

**Table 2** Statistics for leaf traits at the species and community levels

Level	Traits	<i>n</i>	Mean	Minimum	Maximum	SE	CV	Skewness
Species	LA ( $\text{mm}^2$ )	847	2860.01	4.09	56085.4	135.37	1.51	5.54
	LT (mm)	847	0.17	0.01	0.78	0.003	0.56	2.71
	SLA ( $\text{m}^2 \cdot \text{kg}^{-1}$ )	847	20.15	1.89	94.99	0.43	0.68	1.29
	LDMC ( $\text{mg} \cdot \text{g}^{-1}$ )	847	316.73	44.46	775.68	3.81	0.39	0.27
Community	$\text{LA}_{\text{CWM}}$ ( $\text{mm}^2$ )	32	1443.8	22.98	3547.5	169.35	0.66	0.49
	$\text{LT}_{\text{CWM}}$ (mm)	32	0.34	0.18	0.69	0.03	0.46	1.00
	$\text{SLA}_{\text{CWM}}$ ( $\text{m}^2 \cdot \text{kg}^{-1}$ )	32	9.83	5.08	18.34	0.71	0.41	0.68
	$\text{LDMC}_{\text{CWM}}$ ( $\text{mg} \cdot \text{g}^{-1}$ )	32	421.78	364.16	544.01	8.76	0.12	0.72

Note: *n*, number of species or plots; SE, standard error; CV, coefficient of variation.

#### 3.2 Differences in leaf traits among functional types

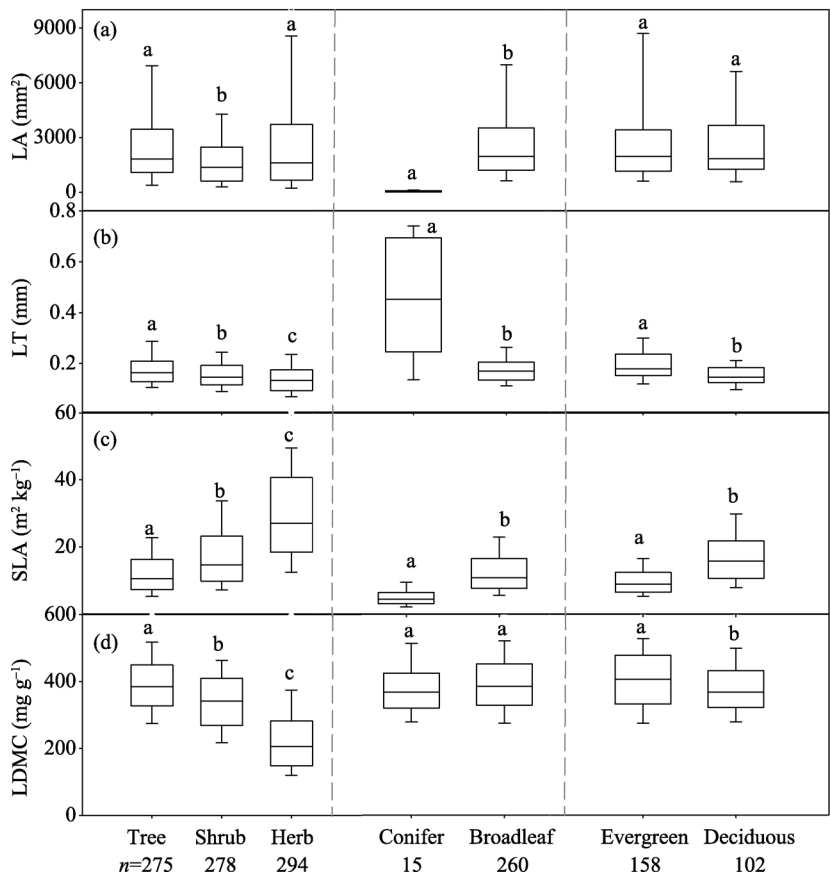
Results of the ANOVA analyses showed that leaf traits varied largely among different PFTs (Figure 2). Compared with the values obtained for shrubs and trees, the leaves of herbs had higher LA and SLA (LA:  $F = 6.90$ ,  $P = 0.001$ ; SLA:  $F = 201.13$ ,  $P < 0.001$ ) but lower LT and LDMC (LT:  $F = 18.39$ ,  $P < 0.001$ ; LDMC:  $F = 231.02$ ,  $P < 0.001$ ). The broad-leaved trees had larger LA and SLA (LA:  $F = 6.90$ ,  $P = 0.001$ ; SLA:  $F = 201.13$ ,  $P < 0.001$ ) and thinner leaves (LT:  $F = 213.61$ ,  $P < 0.001$ ) than those of the coniferous trees. Evergreen broadleaves had higher LT and LDMC (LT:  $F = 37.34$ ,  $P < 0.001$ ; LDMC:  $F = 5.06$ ,  $P = 0.025$ ) and lower SLA ( $F = 83.13$ ,  $P < 0.001$ ) than those of their deciduous counterparts.

#### 3.3 Latitudinal patterns of leaf traits at the species and community levels

Latitudinal variation in leaf traits differed remarkably between the species level and community level (Figure 3). At the species level, similar trends occurred when analyzing the latitudinal variation in leaf traits of trees, shrubs, and herbs. In general, SLA increased and LDMC decreased with increasing latitude ( $P < 0.05$ ), whereas the latitudinal trends of LA and LT were weak ( $R^2 = 0.02\text{--}0.06$ ,  $P < 0.05$ , Figure 3a).

At the community level, as latitude increased,  $\text{LA}_{\text{CWM}}$  and  $\text{SLA}_{\text{CWM}}$  initially increased and

then decreased, while  $LT_{CWM}$  increased and  $LDMC_{CWM}$  decreased linearly (all  $P < 0.05$ , Figure 3b).

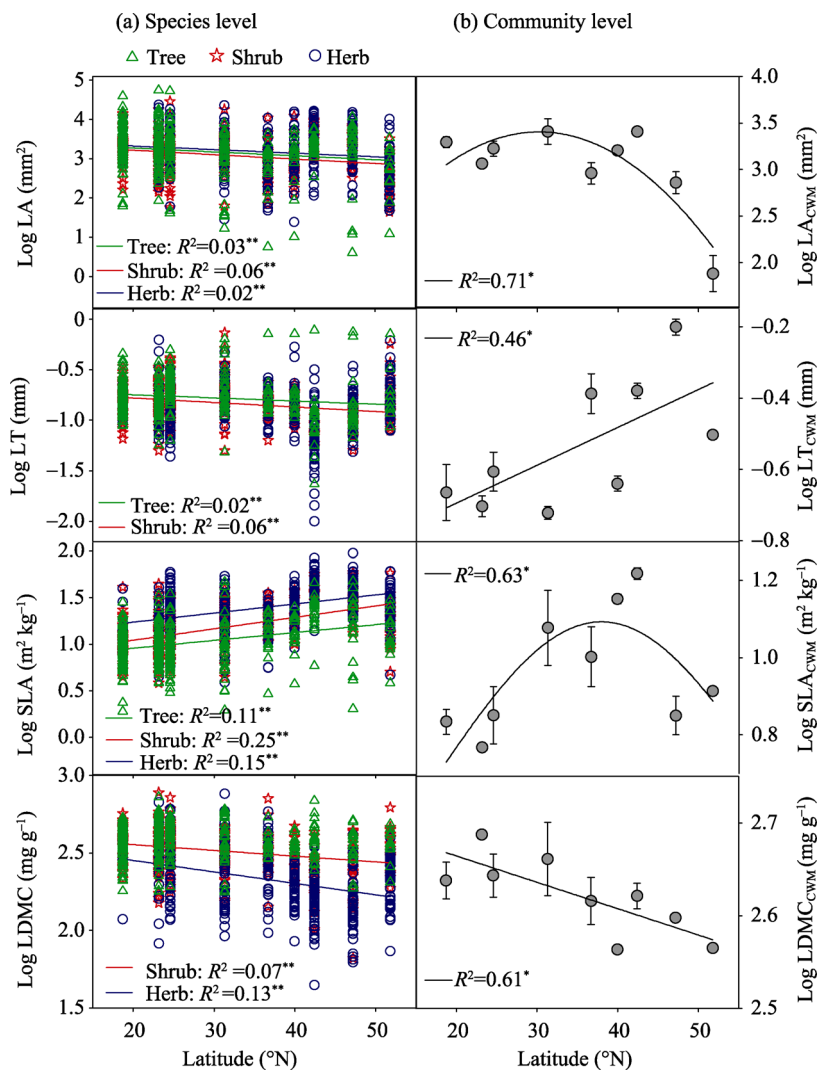


**Figure 2** Differences in leaf traits among plant functional types. The black lines across the boxes are median values.  $n$ , species number. Statistical differences are denoted using different letters ( $P < 0.05$ ).

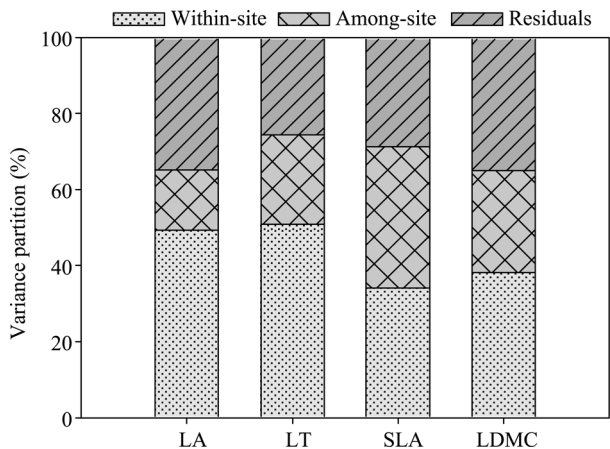
The results of nested ANOVA analyses revealed that 38.15%–50.87% of the variance in species-level leaf traits occurred within sites, and 15.96%–37.20% of the variance occurred across sites (Figure 4). In addition, compared with SLA and LDMC, a higher proportion of the variance ( $> 49\%$ ) in LA and LT was attributed to differences among species within a site.

### 3.4 Factors influencing latitudinal variation in leaf traits

From the results of mixed-effect models, the PFT could explain the largest proportion of the variation in LA, LT, SLA, and LDMC (19.43%–41.57%, Table 3) at the species level, while the effects of climate and soil nutrition were trivial (1.65%–9.13%, Table 3). However, the variation of community-level leaf traits was mainly driven by climate and soil N content. Specifically, MAT was the most important factor influencing variation in  $LA_{CWM}$  and  $LDMC_{CWM}$ , and accounted for 25.08% and 48.04% of the total variation, respectively. In addition, 32.75% of the variation in  $LT_{CWM}$  was explained by MAP, and 36.41% of that in  $SLA_{CWM}$  depended on soil N (Table 4).



**Figure 3** Latitudinal patterns of leaf traits at the species (a) and community levels (b). Error bars in panels (b) represent  $\pm 1$  standard error. Only significant regressions are given ( $P < 0.05$ ).



**Figure 4** Variance partitioning of species-level leaf traits into within-site, among-site, and residual components



**Table 3** Influences of the plant functional type and environmental factors on species-level leaf traits

Factor	Log LA			Log LT			Log SLA			Log LDMC		
	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%
PFT	4	56.79**	19.43	4	1.26**	41.57	4	163.24**	36.83	4	129.50**	34.18
MAT	1	98.16**	6.72							1	41.41**	2.19
MAP				1	25.22**	1.65	1	127.55**	5.76			
SN	1	30.49**	2.09	1	139.73**	9.13	1	197.69**	8.92	1	77.47**	4.09
PFT×MAT										4	9.90**	2.09
PFT×MAP				4	4.45**	1.16	4	6.73**	1.21			
PFT×SN				4	3.90**	1.02	4	2.67*	0.48	4	4.30**	0.91
MAT×SN										1	10.18**	0.54
MAP×SN				1	80.67**	5.27	1	12.48**	0.56			
Site	8	6.31**	3.46	8	5.14**	2.68	8	3.86**	1.39	8	4.51**	1.90
Residuals	997		68.31	1001		65.51	992		44.85	1022		54.11

Note: PFT, plant functional type; MAT, mean annual temperature; MAP, mean annual precipitation; SN, soil N concentration; *df*, degrees of freedom; SS%, percentage of sum of squares explained. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

**Table 4** Influences of environmental factors on community-level leaf traits

Factor	Log LA <sub>CWM</sub>			Log LT <sub>CWM</sub>			Log SLA <sub>CWM</sub>			Log LDMC <sub>CWM</sub>		
	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%	<i>df</i>	<i>F</i>	SS%
MAT	1	3.34*	25.08				1	7.77*	16.51	1	22.56**	48.04
MAP				1	5.30**	32.75						
SN							1	7.75**	36.41			
MAT×SN							1	0.003	1.79			
Site	8	14.09**	58.43	8	14.99**	54.87	8	5.86*	15.42	8	1.471	3.01
Residuals	22		16.49	22		12.38	20		29.87	22		48.95

Note: MAT, mean annual temperature; MAP, mean annual precipitation; SN, soil N concentration; *df*, degrees of freedom; SS%, percentage of sum of squares explained. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

## 4 Discussion

This study comprehensively documented the biogeographic patterns of leaf morphological traits among forest ecosystems in eastern China. The ranges of LA, LT, SLA, and LDMC were comparable to those reported in other regions (Cornelissen *et al.*, 2003; Hodgson *et al.*, 2011), although they varied largely across 847 species.

### 4.1 Latitudinal variation in species-level leaf traits and the controlling factors

Clear latitudinal trends were observed for SLA and LDMC, whereas the trends for LA and LT were weak (Figure 3a). Compared with SLA and LDMC, higher variation in LA and LT among co-existing species within a site ( $> 49\%$ , Figure 4) may result in relatively weak spatial variation. Similarly, in an analysis of global leaf traits, Moles *et al.* (2014) found that the majority of variation occurred at the local scale or within communities, e.g., 34% for plant height and 43% for LA. The larger variance occurring within sites may be the result of micro-site variability, phylogenetic or historical effects, or biotic interactions and competition

(Ordóñez *et al.*, 2010). This indicates that taking inter-specific differences and site scale (or community-level scale) into consideration is essential for the study of biogeography and the assessment of plant trait variability (Liu *et al.*, 2010; Freschet *et al.*, 2011).

The spatial variation of leaf morphological traits at the species level was mainly controlled by shifts in the PFT, while climate and soil nutrient availability had only marginal effects (Table 3). This is in line with the idea that the PFT may account for more global variation in leaf economic traits compared to climatic metrics (Reich *et al.*, 2007). Variation in leaf morphological traits among PFTs is considered to be a result of genetic and adaptive differences to the external environment (Ordóñez *et al.*, 2010).

In spite of the weak relationships between environmental variables and leaf traits, climate and soil variables may exert both direct and indirect effects on the patterns of leaf traits. Through regulating the metabolic activity and carbon allocation of plants (Moles *et al.*, 2014), climate directly influences the morphology of leaves. In addition, climate may influence the geographic distribution of leaf traits indirectly by shaping the biogeography of the vegetation as well as soil nutrient availability (Chapin *et al.*, 2002; Ordóñez *et al.*, 2009).

#### 4.2 Latitudinal variation in community-level leaf traits and the driving factors

In comparison with species-level leaf traits, community-level leaf traits have stronger relationships with latitude (Figure 3b). Domínguez *et al.* (2012) and Vile *et al.* (2006) reported similar results on a local scale that, compared with species-level plant traits, more significant trends along the light gradient or according to forest age were found when species abundance was considered using CWM values. These results suggested that species-level traits (especially the mean values across different plant species) did not accurately reflect the real community-level traits unless the relative abundance of species was considered. This was because the processes and functioning of ecosystems are overwhelmingly determined by the functional traits of the dominant species within a specific community (the mass ratio hypothesis) (Garnier *et al.*, 2004). In other words, the substitution of species mean traits for community-level traits may undermine or cancel the influence of the dominant species and misconstrue results (Vile *et al.*, 2006). In contrast, the CWM values, which integrate the data from the community structure (Garnier *et al.*, 2004), can better explain the response of the real community to environmental factors on a large scale (Cornwell and Ackerly, 2009; Domínguez *et al.*, 2012).

Climate or soil N had a strong influence on community-level traits and their latitudinal patterns (Table 4), indicating that these were the main environmental parameters driving the latitudinal patterns of community-level leaf traits through the regulation of species composition. According to community assembly theory, species turnover within communities across abiotic gradients is primarily derived from the adaptive differences of each species to the external habitat (Cornwell and Ackerly, 2009; Andersen *et al.*, 2012). In this study, on one side of the environmental gradient from south to north, woody plant species with evergreen broadleaves (low SLA but high LDMC) dominated in the tropic regions characterized by hot, humid, and infertile habitats, accompanied by low  $SLA_{CWM}$  and high  $LDMC_{CWM}$ . On the other side, distinct seasons and fertile habitats in temperate forests favor deciduous trees with high SLA (thus high  $SLA_{CWM}$ ). Coniferous species dominate at high latitude with low LA and SLA but high LT allows them to increase leaf mechanical resistance (Onoda *et al.*,

2011) and minimize the incidence and severity of freezing stress (Poorter *et al.*, 2009), resulting in low  $LA_{CWM}$  and  $SLA_{CWM}$  and high  $LT_{CWM}$ .

## 5 Conclusions

This study is, to our knowledge, the first to comprehensively document the biogeographic patterns of leaf morphological traits in Chinese forests and quantify the potential influencing factors at both the species and community levels. The main results and conclusions are:

(1) Across 847 species from nine forest ecosystems in eastern China, the means ( $\pm$  SE) of LA, LT, SLA, and LDMC were  $2860.01 \pm 135.37 \text{ mm}^2$ ,  $0.17 \pm 0.003 \text{ mm}$ ,  $20.15 \pm 0.43 \text{ m}^2 \cdot \text{kg}^{-1}$ , and  $316.73 \pm 3.81 \text{ mg} \cdot \text{g}^{-1}$ , respectively.

(2) At the community level, the means ( $\pm$  SE) of  $LA_{CWM}$ ,  $LT_{CWM}$ ,  $SLA_{CWM}$ , and  $LDMC_{CWM}$  were  $1443.80 \pm 169.35 \text{ mm}^2$ ,  $0.34 \text{ mm} \pm 0.03$ ,  $9.83 \pm 0.71 \text{ m}^2 \cdot \text{kg}^{-1}$ , and  $421.78 \pm 8.76 \text{ mg} \cdot \text{g}^{-1}$ , respectively.

(3) Different latitudinal variations in leaf morphological traits were observed at the species and community levels. At the species level, SLA increased and LDMC decreased with increasing latitude, whereas no clear latitudinal trends in LA or LT were found. When scaling up to the community level, more significant spatial patterns in leaf traits were observed ( $R^2 = 0.46\text{--}0.71$ ,  $P < 0.05$ ).

(4) Different factors controlled these spatial patterns of leaf traits at the species and community levels. Specifically, changes in PFT were the main influencing factor regarding the latitudinal variation of species-level traits, while for community-level leaf traits, climate and soil N content acted as the main environmental parameters driving latitudinal patterns through the shifts of species composition within communities.

These findings suggest that the real community-level traits could not be simply represented by those of the species pool or among the most common species identified, and emphasize the importance of considering community structure in analyses when scaling-up from organisms to populations, communities, or ecosystems.

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