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Large-scale dataset from China gives new insights into leaf margin–temperature relationships

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ABSTRACT

Leaf margin analysis (LMA) is an important method of estimating paleotemperatures from fossil leaf floras or modern floras. Although some calibration has been carried out based upon large-scale studies of modern forests, most of this research has been in North America and Europe, with relatively little calibration work in East Asia. In the present study, we used species range maps of 3116 native dicot trees of China to derive synthetic local floras for each county from the Chinese humid region, and compared the percentage of untoothed leaf margined species with several temperature and precipitation related parameters. The results confirm the generally strong relationship between the proportion of species with untoothed leaf margins and climatic parameters within China. Leaf habit (deciduous vs. evergreen) does not strongly affect this relationship. The transfer function obtained from China, while not identical, is similar to those obtained from other regions, and is affected by regional restrictions, such as complex topography and relic taxa. As such it clarifies the potential range of error inherent in the LMA method as applied to paleoclimate reconstruction. It is possible, however, that with the close similarity of the modern Chinese tree floras to Neogene floras in the Northern Hemisphere, the present estimate offers a better transfer function for reconstructing the Neogene paleoclimate in various regions without extremely cold conditions across the Northern Hemisphere.

1. Introduction

In most regions of the world, paleobotanists find that leaf physiognomy closely correlates with temperature and moisture, and these correlations have been widely used as proxies to reconstruct paleoclimate (Bailey and Sinnott, 1915, 1916; Dilcher, 1973; Wing and Greenwood, 1993; Wolfe, 1993; Wilf, 1997; Greenwood et al., 2004; Miller et al., 2006; Xia et al., 2009; Steart et al., 2010; Peppe et al., 2011; Royer et al., 2012). These proxies are critically important to our understanding of the evolutionary history of environments, and provide important information on climates (Parrish, 2001) and atmospheric composition (Ehleringer et al., 2005) in the past. For precise estimates of past temperature based on these leaf physiognomy–climate relationships, paleobotanists have long developed two popular techniques: Leaf Margin Analysis (LMA) and Climate–Leaf Analysis Multivariate Program (CLAMP).

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Leaf margin analysis is based upon the strong positive relationship between mean annual temperature (MAT) and the proportion of woody dicotyledons with untoothed leaves. This discovery was originally made by Bailey and Sinnott (1915), and has been refined by further research on modern floras around the world (Kowalski, 2002; Greenwood et al., 2004; Traiser et al., 2005; Adams et al., 2008; Steart et al., 2010; Su et al., 2010). The technique has been used widely in reconstructions of paleoclimate (Wing and Greenwood, 1993; Wolfe, 1993; Herman and Spicer, 1996; Wilf, 1997; Jacobs, 1999; Kowalski and Dilcher, 2003; Peppe et al., 2011). Climate–Leaf Analysis Multivariate Program (CLAMP), which includes 31 leaf categories, such as leaf-margin and leaf-size, is a multivariate statistical technique that reveals the relationship between physiognomic of woody dicotyledonous plants and climate across a range of foliar characteristics (Wolfe, 1993; Kovach and Spicer, 1996; Spicer et al., 2005; Spicer, 2007, 2009).

As a widely used method for paleoclimatic reconstructions, LMA models have been developed using two approaches: (1) sampling plant data in the field, and (2) compiling synthetic and chorological floras from publications. The first approach consists of collecting samples directly in the field and compiling climatic data from nearby weather stations (Wolfe, 1979, 1993). This approach more precisely reflects

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the microclimate of a local floral assemblage (Greenwood, 2005), although in some cases it is hard to find undisturbed vegetation near meteorological stations (Spicer, 2009). The other approach involving the compilation of synthetic and chorological floras from publications is on a much grander scale, whereby the spatial patterns of physiognomy with a high degree of resolution are established, and then the transfer functions for climatic parameters calculated (Traiser et al., 2005; Adams et al., 2008). Based on the distribution of 108 native woody dicotyledons in Europe and a large number of samples (1835 grids), Traiser et al. (2005) concluded close correlations between leaf physiognomy and environment in Europe, supporting results obtained from other continents, with samples directly collected from forests. Adams et al. (2008) presented the results of a systematic spatially-distributed analysis of the relation between leaf margins and temperature for North America, and demonstrated that there is indeed a strong relationship between leaf margin percentage and temperature on a regional scale in eastern North America. This approach represents a promising tool for analyzing relationships between leaf margin and climate using a much greater number of samples, although there has been debate about whether it is better to use more local floras for calibration as these usually include a higher proportion of swamp species, which have more toothed species in warmer climates, and may more closely resemble the assemblages that tend to show up in the fossil record (Greenwood et al., 2004).

Leaf habit (deciduous vs. evergreen) also can affect these leaf–climate relationships. The toothed margin tends to be associated with deciduous species, whereas the untoothed margin is primarily associated with evergreen species (Bailey and Sinnott, 1916; Givnish, 1979; Wolfe, 1993; Jacobs, 2002; Peppe et al., 2011; Royer et al., 2012). A deciduous canopy might obtain abundant irradiance during the early spring, and toothed leaves could benefit from it with higher capability of photosynthesis (Baker-Brosh and Peet, 1997).

In China, leaf margin analysis (LMA) was first carried out using the data set of Wolfe (1979), by Wing and Greenwood (1993), with 34 Chinese and Japanese sites. Recently, Su et al. (2010) proposed the untoothed percentage and MAT transfer function, based on 50 local samples from humid to mesic forests in China, chosen from natural forest with low levels of human activities and altitudes < 2400 m to avoid the disproportionate representation of untoothed leaves found in the alpine nest. Their study confirms that the untoothed percentage of species correlates most closely with MAT, which is consistent with previous studies. It is unclear whether the correlation in eastern Asia would be different if more large-scale data points were added.

No large-scale study of leaf physiognomy has so far been carried out in China, despite its large land area (nearly 9.6 million km^2), and wide range of climates. China is one of the countries marked by the greatest plant diversity in the world. It has 31,142 recorded species of vascular plants, belonging to 4508 genera in 301 families (Wu, 2004). Most importantly, the modern flora in China most closely resembles Neogene floras of Europe and North America (Wu, 1980; Manchester et al., 2009). Presently, China has a high level of endemism, with 243 known endemic genera (Ying and Zhang, 1994). There appear to be a number of underlying reasons for the floristic and endemic richness of China. Firstly, there is fact that China extends into the tropics, unlike Europe or the USA. Thus families of plants with predominantly tropical distributions contribute to the total floristic diversity of China. Secondly, 40% of the landmass of China consists of mountains, including many isolated mountain ranges which provide opportunities for both survivals of lineages (paleoendemites) and evolution of novel plants (neoendemites) (Ferguson et al., 1997). Thirdly, from the mid Miocene onwards, after which the climate of the Northern Hemisphere is considered to have become less favorable for plants and more particularly during the Pleistocene ice ages, China's land connections to the south provided refugia for many kinds of plants (Ferguson, 1994; Blackmore et al., 2013). Fourthly, the collision of the Indian subcontinent with the mainland of Asia, commencing about 50 million years ago, enabled different floristic elements to immigrate into China (Wu, 1996).

Botanists have already compiled important botanical reference works on the entire Chinese flora, notably the *Flora of China* in both Chinese (Wu, 2004) and English versions (http://flora.huh.harvard.edu/china/mss/alphabetical_families.htm). They have also established many databases, such as the *Seed Plants of China* and the Digital Herbarium (http://www.cvh.org.cn/). The database of *Seed Plants of China*, which includes 27,709 species, belonging to 2939 genera and 277 families, was established based on field data, literature, and herbarium records (Wu and Ding, 1999). The Digital Herbarium database was established based on the herbarium records of the Kunming Institute of Botany, and includes 790,000 vascular plants of specimen records. As a result, the information in these databases has led to a better understanding of the Chinese vegetation and floras, enabling a more extensive analysis of the relationships between leaf shape and climate on a broad scale. Based on these published sources, the present study uses a large amount of the latest floristic data, with many extra records and large numbers of sample species, across a great range of environments.

In the present study we use the compiled dataset on humid regions of China. Our primary aim is to test the applicability of existing linear regression models for temperature estimation via leaf margin analysis, and to use Geographic Information Systems (GIS) to check the relationship between temperature and leaf margin percentage based on spatial analysis on a large scale. Utilizing this data set, we analyze the correlations between spatial distribution patterns of the untoothed species percentages in present-day woody angiosperm vegetation, and variation in climatic parameters on a large scale. Then we develop transfer functions to test the applicability of linear models for temperature estimation via leaf margin analysis which include more species, and greater climatic and geographic diversity than any previous data set. Additionally, we tested for the potential role of leaf habit (evergreen vs. deciduous) in these correlations.

2. Materials and methods

2.1. Regional setting

This study focuses on the humid regions of China, where the mean annual precipitation is higher than 400 mm (Fig. 1). This humid region comprises 2082 counties, representing 88% of the total 2380 counties in China.

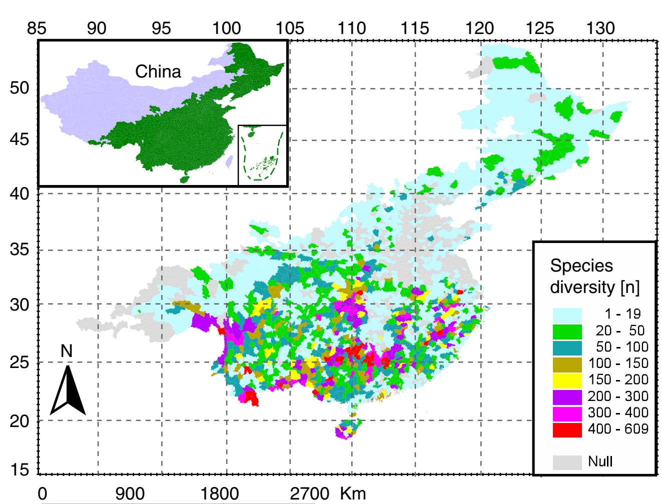

Fig. 1. Distribution pattern of tree species richness in humid regions of China (at county level), where the mean annual precipitation (MAP) is higher than 400 mm. Only counties with a minimum set of at least 20 species were scored in this study (n = 732).

2.2. Calibration of data set

As a source of information on woody dicotyledonous species, our dataset relies on the use of *Seed Plants of China* (Wu and Ding, 1999), specimen records in the Herbarium of the Kunming Institute of Botany (KUN), and the published *Flora of China* (Wu, 1979, 1980, 1982, 1984, 1988, 1995, 1996, 1998). We used species digital distribution maps of native Chinese dicotyledonous trees and large shrubs (defined as woody plants >3 m in height). Our dataset includes 3166 native woody species, belonging to 536 genera and 111 families (see Supplementary Data 1). Maps of the present-day distribution of 3166 species were compiled and digitized for application in a Geographical Information System (GIS). All species were plotted on the map at county level.

In our study, the spatial resolution is defined at the county level with an average grid cell size of approximately 60 km West–East and 60 km North–South in the humid region of China. This county level scale was chosen to obtain several hundred independent grids at fine climate resolution, and to minimize the effects of variable topography where a range of temperature zones would complicate the analysis. We restricted our data set to those counties where at least 20 native species are available so that the species richness is sufficient to achieve reliable statistical analyses. As a result of these restrictions, the calibration dataset used for the analysis consists of 732 data units at the county level (Fig. 1).

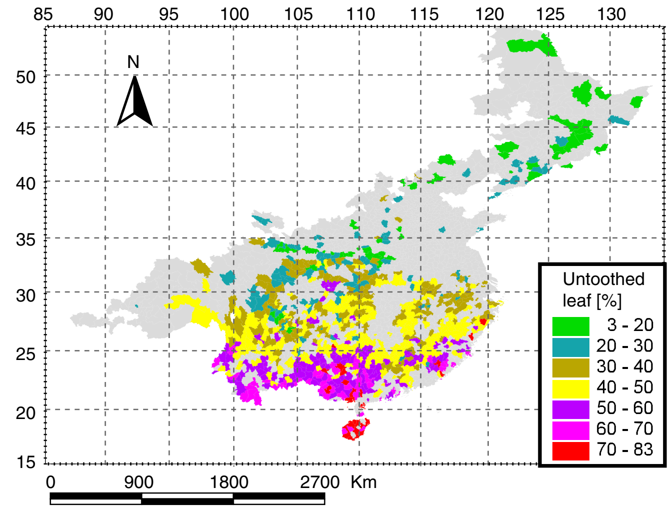

Fig. 2. Spatial distribution pattern of the percentage of untoothed leaves species among Chinese native trees, color is coded by the percentage of untoothed leaf margin; grid cells with fewer than 20 species are in gray.

2.3. Climatic parameters

Climate data with 30-year record in average (1951–1980) were obtained from weather stations in each individual county by referring to Yunnan Provincial Meteorological Bureau (YPMB) and China Meteorological Data Sharing Service System (available online: http://cdc.cma.gov.cn/). Four climatic parameters are included in this study (see Supplementary Data 2): mean annual temperature (MAT), mean temperature of the warmest month (WMMT), mean temperature of the coldest month (CMMT) and mean annual precipitation (MAP). These parameters were selected because they enable a direct comparison with the results of previous studies.

2.4. Data analysis

In this study, definition tooth is a projection with vasculature along leaf margin, and its length is within one quarter of the length from midvein to the projection (Ellis et al., 2009). We exclude marginal spines, because spines might play a function as defense against herbivores. Leaf margin type for each species was determined visually using the specimens in KUN. Toothed species were given a score of 0; both toothed and untoothed margins occur within one species were given a score of 0.5, and untoothed species were given a score of 1 (Wolfe, 1993). The percentage of untoothed leaf species in each county was the sum of scores of all species divided by the number of all species.

Data for leaf habit (deciduous vs. evergreen) are from the database of *Seed Plants of China* (Wu, 2004), specimens at KUN, and published floras of China (Wu and Ding, 1999) (0 = deciduous; 1 = evergreen; 0.5 = species with both leaf forms).

To analyze statistically the relationship between the spatial patterns of the percentage of species with untoothed leaf margins and climatic parameters across the study area, single linear regression (SLR) was applied (SPSS17; SPSS Science).

3. Results

3.1. Spatial distribution of untoothed leaf margin species, and its relationship to climatic parameters

The percentage of entire margins shows a clear latitudinal trend in China, ranging from 83% to 3% (Fig. 2). This percentage reaches its highest value in southern China, on Hainan Island and in Guangdong, Guangxi, and Yunnan. The floras with the lowest proportions of entire leaves (colored green in Fig. 2) are in the northeast of China, and some areas of central China (Fig. 2: orange), e.g. Shanxi, Gansu, and Qinghai.

The spatial patterns of change in MAT, WMMT, CMMT, and MAP across the study area are shown in Fig. 3. Both MAT and CMMT (Fig. 3, a, c) are clearly related to latitude, but with no clear longitudinal trend, and some anomalous areas of low temperature where elevation is generally high, e.g. northwest Yunnan, a part of the Qinghai–Tibetan Plateau. By contrast, the general trend of WMMT is longitudinal except for the region in northeastern China (Fig. 3, b). MAP shows an increasing trend from the northwest to the southeast (Fig. 3, d). Generally, the range of individual climatic parameters in this study is very broad, for example MAT of our study region ranges from −2.4 to 25.4 °C, WMMT from 8.7 to 31.0 °C, CMMT from −28.0 to 20.8 °C, and MAP from 418.1 to 2745.4 mm.

3.2. Relationships of species with untoothed leaf margins and climatic parameters

Relationships between the percentage of species with untoothed leaf margins in the Chinese arboreal flora and climatic parameters were analyzed statistically using Single Linear Regression (SLR), based on the 732 calibration grids. We find a strong correlation between MAT and the untoothed leaf-margin percentage in the more humid regions of China (Function 10 in Table 1; Fig. 4). Untoothed leaf margins show a higher correlation with CMMT ($r^2 = 0.60$) (Fig. 4, c) than to MAT ($r^2 = 0.53$) (Fig. 4, a). Much lower correlations are found between leaves with an entire margin and MAP ($r^2 = 0.34$) (Fig. 4, d). In particular, the percentage of species with untoothed leaf margins shows very weak correlations with WMMT ($r^2 = 0.10$) (Fig. 4, b).

Our linear transfer function based on the Chinese dataset for untoothed leaf margins is defined as:

$$\mathrm{MAT} = 6.68 + 0.223 \times \mathrm{P}$$

(Fig. 5).

With $r^2 = 0.53$, $F = 827$, $p < 10^{-119}$, $SE = 3.09$ and P = the percentage of untoothed leaves of woody dicotyledonous species.

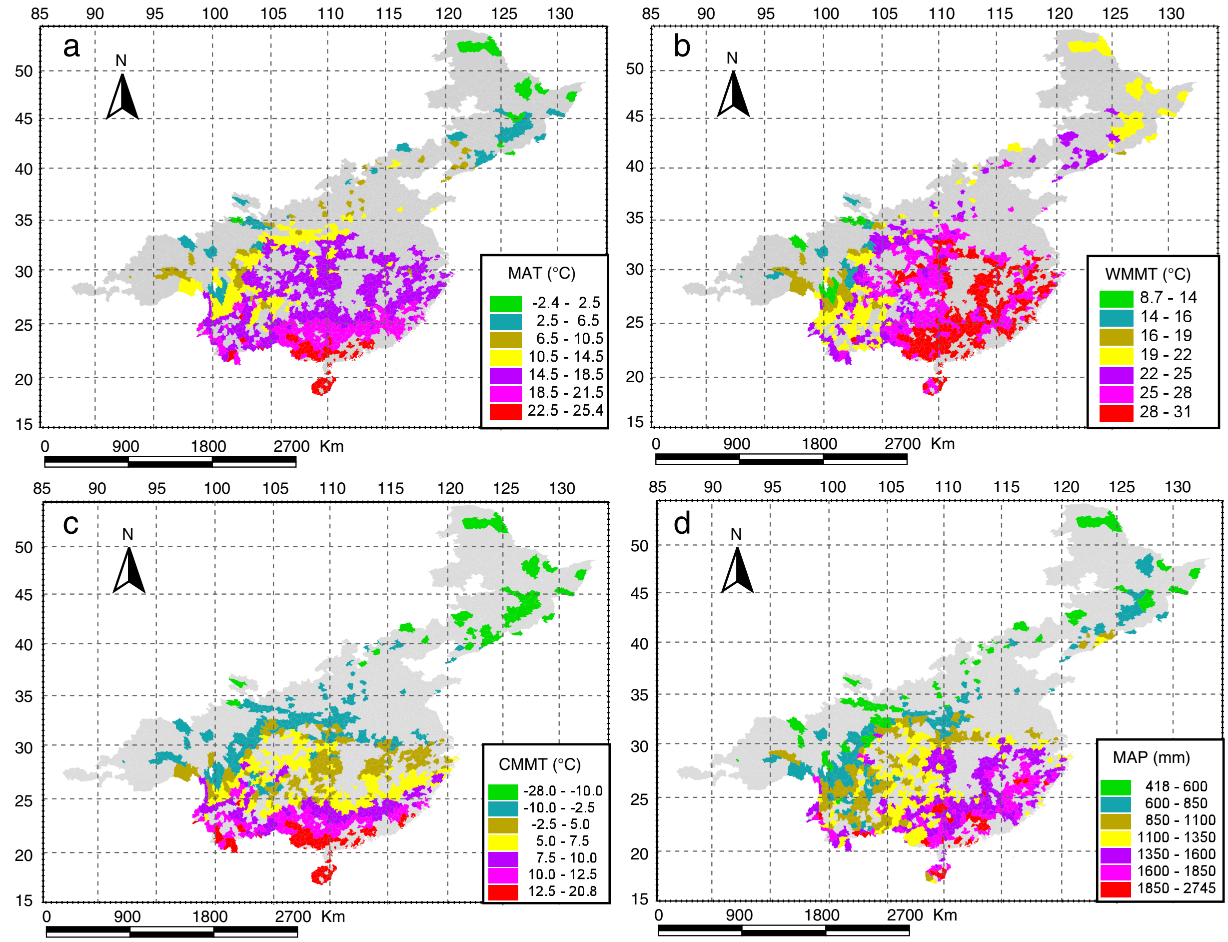

Fig. 3. Distribution pattern of the change of mean annual temperature (MAT), mean temperature of the warmest month (WMMT), mean temperature of the coldest month (CMMT), and mean annual precipitation (MAP) in the humid region of China; grid cells with fewer than 20 species falling within that cell are in gray.

The application of the transfer function back onto the Chinese data set in a bootstrap analysis results in a spatial correlation between predicted MAT (Fig. 6, b) and actual MAT (Fig. 6, a). The residual (predicted MAT minus actual MAT values) plot (Fig. 6, c) reveals a spatial pattern representing regions with systematic underestimations and overestimations. MAT is slightly overestimated (by 3.0–7.0 °C) in northern China and the Hengduan Mountains (Yunnan), whereas larger overestimates (7.0–11.3 °C) occur in northeastern China, Qinghai province, and Tibet. In contrast, a slight underestimation of MAT (3.0–7.0 °C) can be observed in parts of the provinces Guangdong, Shanxi, and Sichuan. Mabian county, Sichuan province and Pingyuan county, Guangdong province show much stronger underestimations of 9.7 °C and 8.4 °C, respectively.

3.3. Effect of evergreen vs. deciduous leaf habit

We selected sites from our calibration (grid cells with ≥20 species) that each contained >15% evergreen and >15% deciduous species (n = 586 sites) (Peppe et al., 2011). We gained the linear correlations between MAT and the proportion of untoothed deciduous/evergreen species, and the slope of its correlations is almost the same, but there

Table 1
Linear equations of leaf margin analysis published by different authors; P = the percentage of untoothed leaves of woody dicotyledonous species; N = number of samples; SE = standard error.

	Transfer function	N	region	R^2	SE	P-value	Author
1	MAT = 1.141 + 0.306 × P	34	East Asia	0.98	0.8	<0.001	Wing and Greenwood (1993)
2	MAT = 2.240 + 0.286 × P	9	N, M, S America	0.94	2.0	<0.0005	Wilf (1997)
3	MAT = −0.266 + 0.291 × P	106	N, M America, East Asia	0.76	3.4	<0.0005	Wilf (1997)
4	MAT = −0.059 + 0.316 × P	14	S America	0.89	1.6	–	Gregory-Wodzicki (2000)
5	MAT = −2.120 + 0.270 × P	74	Australia	0.63	–	<0.0001	Greenwood et al. (2004)
6	MAT = 0.512 + 0.314 × P	1835	Europe	0.60	1.7	<0.00001	Traiser et al. (2005)
7	MAT = 1.320 + 0.314 × P	84	N, M America	0.91	–	–	Miller et al. (2006)
8	MAT = 1.038 + 0.276 × P	50	China	0.79	1.9	$<10^{-17}$	Su et al. (2010)
9	MAT = 4.60 + 0.204 × P	92	N, M, S America, Europe, Asia, Australia	0.58	4.8	$<10^{-18}$	Peppe et al. (2011)
10	MAT = 6.68 + 0.223 × P	732	China	0.53	3.1	$<10^{-119}$	This study

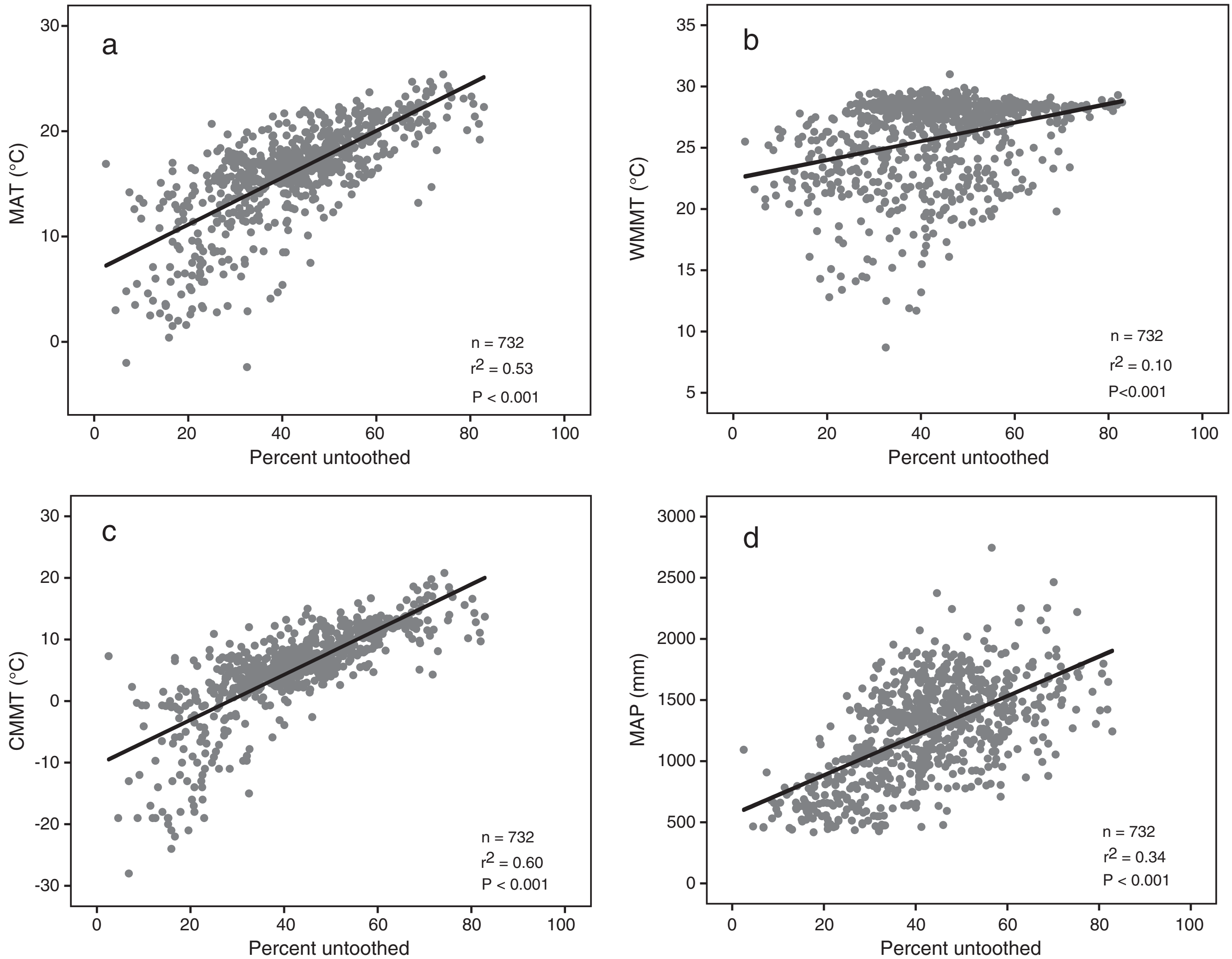

Fig. 4. Bivariate plots of mean annual temperature (MAT), mean temperature of the warmest month (WMMT), mean temperature of the coldest month (CMMT), and mean annual precipitation (MAP) versus the proportion of woody dicotyledonous species with untoothed leaf margins.

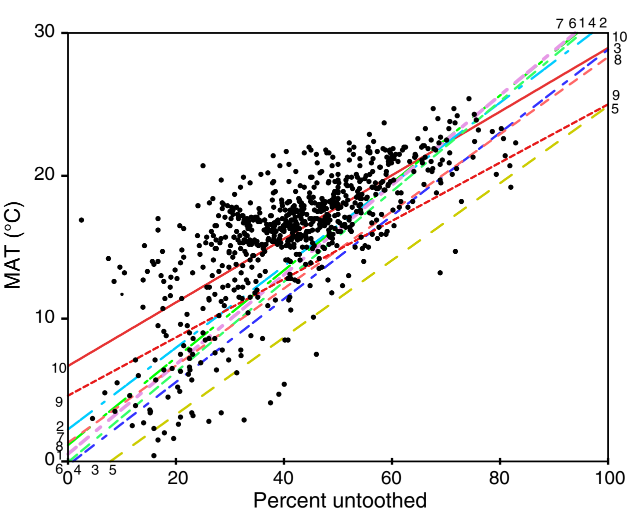

Fig. 5. Single linear regression transfer functions for mean annual temperature (MAT) based on different calibration data sets from different regions of the world. Numbers of the transfer functions correspond to Table 1.

is a marked difference in intercept between deciduous and evergreen regressions (Fig. 7).

4. Discussion

4.1. Correlation between untoothed leaf margins and climate

This study demonstrates the existence of strong relationships between untoothed leaf margins and climatic parameters on a continental scale within East Asia (Fig. 4). However, in contrast to other studies where the proportion of woody dicotyledons with untoothed leaves correlates most strongly with MAT (Bailey and Sinnott, 1915, 1916; Wolfe, 1979, 1993; Wing and Greenwood, 1993; Wilf, 1997; Wiemann et al., 1998; Su et al., 2010), our study reveals a weaker coefficient of determination for this parameter ($r^2 = 0.53$) (Table 1). In our dataset, the strongest correlation with untoothed percentage is observed for CMMT ($r^2 = 0.60$), this result is consistent with certain other studies (Jordan, 1996; Wing and Greenwood, 1996). Species richness is primarily determined by winter coldness because most clades of plants evolved in a quasi tropical climate and hence could only with difficulty disperse into cold, temperate regions owing to their niche conservatism (Latham and Ricklefs, 1993; Kerr and Packer, 1997; Wiens and Donoghue, 2004). The richness of woody species in China is primarily determined by winter cold, and suggests that this distributional pattern mainly results from the increasing intensity of frost filtering for tropical

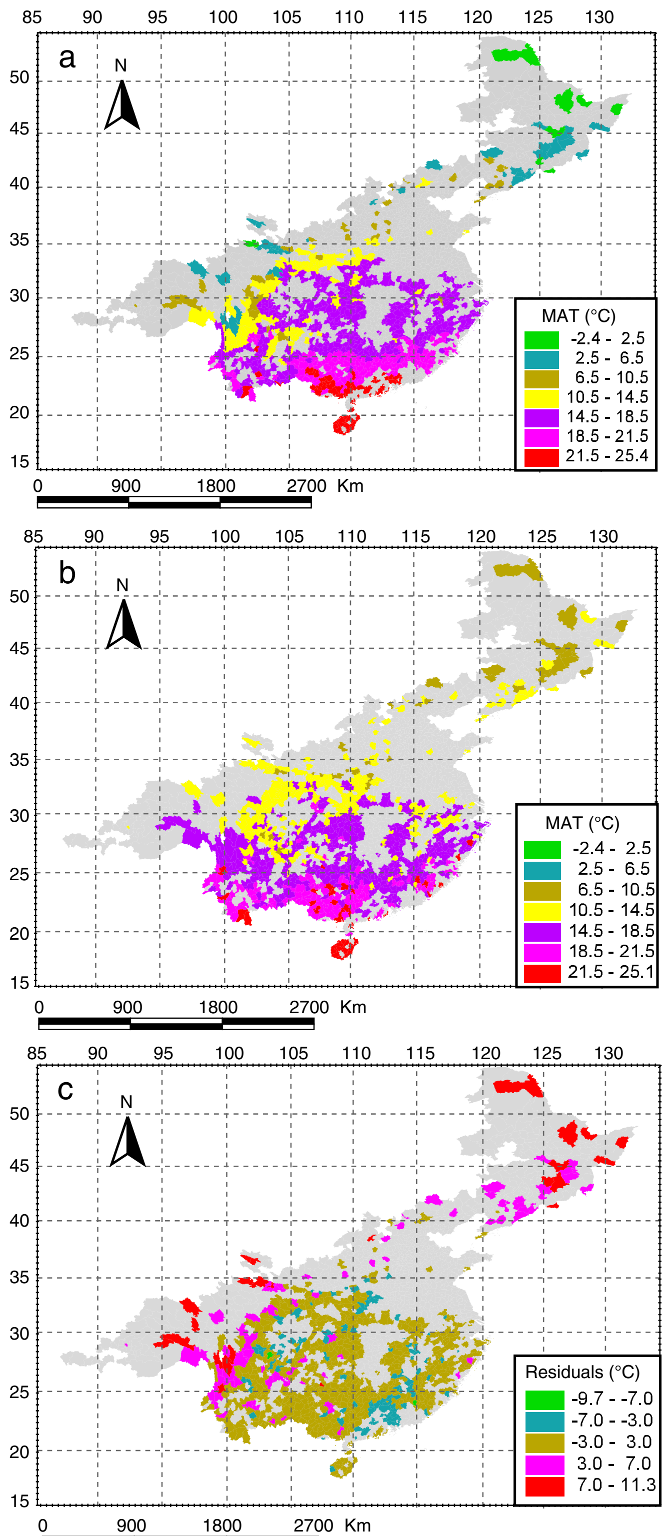

Fig. 6. Distribution pattern of mean annual temperature (MAT). (a) Actual MAT; (b) predicted MAT from the transfer function; (c) residuals of predicted and actual MAT.

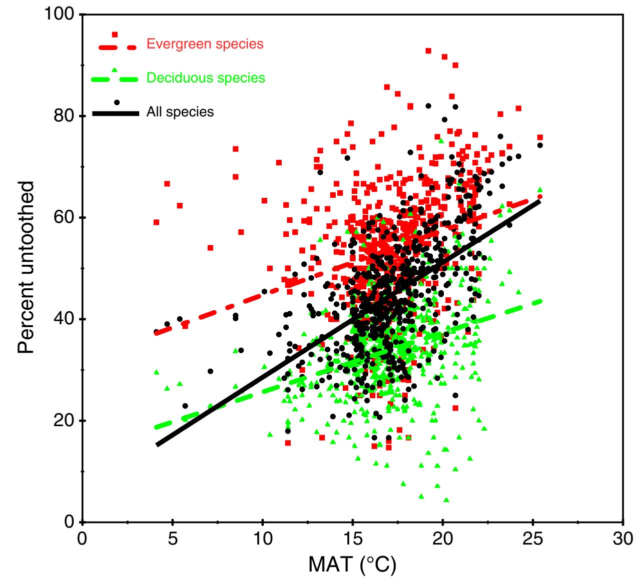

Fig. 7. Relationships between the percentage of untoothed leaf margins of deciduous species, evergreen species, and all species in a flora and mean annual temperature (MAT). For each grid cell, the number of species is no less than 20, and the percentage of evergreen/deciduous species is more than 15%.

species from the equator towards the poles (Wang et al., 2011). This implies that the distribution of untoothed percentage is mainly controlled by the CMMT in China.

Moreover, the overall correlation patterns in our study are consistent with other research based on large-scale datasets (Traiser et al., 2005, $r^2 = 0.60$; Peppe et al., 2011, $r^2 = 0.58$; Adams et al., 2008, $r^2 = 0.29$). However, our coefficients of correlation are lower than previous studies from eastern Asia, due to our dataset being based on a large amount of sampling and covering more extensive areas.

The broad spatial scale of sampling (732 samples) and the larger number of species (3166) used here would be expected to yield a different representation because this method covers a much broader region than samples taken directly from the forests. Our study reveals a weaker coefficient of determination than those of more local studies. This may be partly because our dataset covers a large region; it includes complex topography and a wide range of climates. The ranges of individual climatic parameters are very broad (MAT, −2.4–25.4 °C; WMMT, 8.7–31.0 °C; CMMT, −28.0–20.8 °C; MAP, 418.1–2745.4 mm). Similarly, the range of the percentage of entire margins is higher (3% minimum and 83% maximum) than in more local studies. The wide variation in the proportion of untoothed leaves seen in our dataset may be partly due to the complex topography of China. In regions with complex terrain, the numerous microclimates can produce locally more extreme climates in some areas. The wide climatic range covered by our data points across China is reflected in the wide variation in percentage of untoothed leaves found within China (Fig. 2).

By contrast with the large dataset used here, the leaf margin analysis by Wing and Greenwood (1993), which was mainly based on samples from eastern Asia, only involved 34 sites. The correlation between the proportion of untoothed leaves and MAT is remarkably strong in Wolfe's (1979) dataset ($r^2 = 0.98$). These coefficients of correlation in eastern Asia may be that high because of factors associated with sample size and over-dispersion in the binary dataset which inflates these (Miller et al., 2006). Based on 50 samples ranging from humid to mesic forests in China, Su et al. (2010) obtained a relatively high correlation coefficient ($r^2 = 0.78$). This correlation has never been tested on a large scale in eastern Asia. In the present study, we used the collective results of an enormous amount of floristic sampling, and included a wide range of environments in a way that more fully represents the floristic and environmental diversity of China's forested areas. We also noticed that climate data could vary judging by the variation of country sizes. Additionally, vegetation disturbance might add “noise” to the leaf–climate correlation. Consequently, coefficients of correlation are lower than previous studies from eastern Asia.

4.2. Effect of deciduous vs. evergreen leaf habit

Our study shows that the slope of the linear regression between the proportion of untoothed deciduous species and MAT is almost the same as that of evergreen species, but there is a marked difference in intercept between the deciduous and evergreen regressions (Fig. 7). Across all sites in this study combined, the percentages of untoothed evergreen species and deciduous species are different, with mean values of 53.9% and 34.1%, respectively. Therefore, there is a marked difference in intercept between deciduous and evergreen regressions. This implies that the woody dicots with untoothed leaves are more likely to be present in evergreen species than in deciduous species at mostly sites. This result supports the supposition that evergreen species are more likely to be untoothed than deciduous species (Bailey and Sinnott, 1916; Givnish, 1979; Wolfe, 1993; Jacobs, 2002; Peppe et al., 2011; Royer et al., 2012).

Peppe et al. (2011) compared linear correlations between MAT and the proportion of untoothed deciduous/evergreen species; they found the slope of the correlation is greater in deciduous species than evergreen species. Moreover, the difference in frequency of toothed forms between deciduous and evergreen species diminishes above 16 °C MAT (Peppe et al., 2011). However, our study results in a slope that is almost identical and this discrepancy does not diminish with MAT (Fig. 7). When the MAT is above 7.5 °C, both deciduous and evergreen species contribute to the leaf–climate relationship, with the proportion of untoothed leaves of all species being an average of evergreen species and deciduous species. In colder climates (below 7.5 °C MAT), the deciduous species have a stronger impact on the relationship of leaf margins to MAT than evergreen species, because forests in the northern China are dominated by deciduous species (Wu, 1980). This demonstrates that the relationship between mean annual temperature and the proportion of untoothed leaves is not strongly affected by leaf habit in China.

4.3. Implications for climatic estimates based on untoothed leaf margins

The results obtained in this study broadly confirm previous findings in leaf margin analysis, through using a more rigorous and thorough analysis. There are indeed strong general relationships between leaf margins and temperature, which may be useful in developing improved proxies for reconstructing the paleotemperature in China. By comparison to other regions in the North Hemisphere, such as Europe and western North America, the plant diversity and general vegetation types of China more closely resemble the pre-Quaternary state in all these regions. Therefore, vegetation in China represents the best analogy to Neogene floras in the Northern Hemisphere (Wu, 1980; Manchester et al., 2009). However, the leaf–margin analysis regression relationship in our calibration is considerably weaker than those obtained through previous continental-scale studies (standard error (SE) = ± 3.1 °C) (e.g., Wilf, 1997; Gregory-Wodzicki, 2000; Greenwood et al., 2004; Miller et al., 2006; Tables 1, Fig. 4). Moreover, because of the large scale, we observe only a relatively weak SE by comparison with the results of previous studies in China (Wolfe, 1993, SE = 0.8 °C; Su et al., 2010, SE = 1.9 °C). The intercepts of SLR transfer function is 6.68, which demonstrates that climatic zones where MAT is below 6.68 °C should not be used to reconstruct paleoclimate using LMA here. According to effect of deciduous vs. evergreen leaf habit, in cold regions (MAT below 7.5 °C), our function should be used with caution in this climatic zone, because cold regions in China are dominated by deciduous trees, leaf–climate relationship in these regions is more affected by deciduous habit than evergreen habit.

Our study reveals the limits in the accuracy of temperature estimates derived from the univariate leaf margin analysis, which when used to reconstruct climate results in substantially overestimated or underestimated MATs in some regions. The spatial distributions of the residual of predicted MAT (Fig. 6, b) and actual MAT (Fig. 6, a) highlight these regions (Fig. 6, c). Extreme overestimates (7.0–11.3 °C) occur in cold areas of northeast China, Qinghai province, and Tibet, with only deciduous broad-leaved forest types. In northern China and the Hengduan Mountains (Yunnan), where deciduous forests predominate, the MAT tends to be slightly overestimated by between 3.0 and 7.0 °C. The difficulty in obtaining good predictions for cold regions based on leaf physiognomy has been recognized before (Spicer et al., 2004). In contrast, for the evergreen broad-leaved forest types that dominate southern China, it is possible to predict the MAT to within ± 3.1 °C (standard error, SE) in many areas, with relatively slight underestimates (− 3.0 (− 7.0 °C)) in others. This underestimation of MAT can be observed in some parts of Shanxi (Taihang Mountains), Guangdong (Nanning Mountains), and Sichuan (Sichuan Basin). Generally, regions of complex topography yield less precise estimations.

Overall, our findings demonstrate that leaf margin analysis based on a large-scale dataset remains an effective and convenient method to estimate paleotemperature in China. In future this method may be improved considerably by allowing for regional complexities (i.e., complex topography and extremely cold temperature). The inherent uncertainties in the estimates of paleoclimate that are obtained highlight the need to combine this method of analysis with other proxies whenever possible.

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