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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).

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.

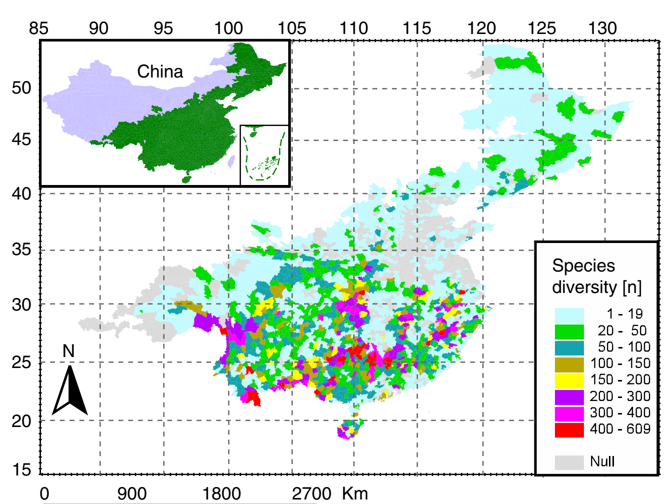

Fig. 1. Distribution pattern of tree species richness in humid regions of China (at county level), where the mean annual precipitation (MAP) is higher than 400 mm. Only counties with a minimum set of at least 20 species were scored in this study (n = 732).