



# Influence of phylogenetic relatedness on paleoclimate estimation using fossil wood: Vessel and fiber-related traits

Hugo I. Martínez-Cabrera<sup>a,\*</sup>, Emilio Estrada-Ruiz<sup>b</sup>

<sup>a</sup> Museo de Múzquiz, A. C., Zaragoza 209, C.P. 26340 Melchor Múzquiz, Coahuila, Mexico

<sup>b</sup> Laboratorio de Ecología, Departamento de Zoología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, 11340 Ciudad de México, Mexico

## ARTICLE INFO

### Article history:

Received 19 September 2017

Received in revised form 4 January 2018

Accepted 24 January 2018

Available online xxxx

### Keywords:

Angiosperms

Biological uniformitarianism

Evolution

Fossil wood

Paleoclimate

Phylogenetic conservatism

## ABSTRACT

Wood anatomical traits have been historically used as a climate inference tool. During the last 20 years, the use of more formal statistical approaches has allowed the field to start moving from general qualitative paleoclimate inference to quantitative estimates. These estimates are derived from the correlation between wood anatomical traits and climate, however the role of shared evolutionary history in this relationship has not been assessed. Greater influence of phylogenetic relatedness on trait variation (phylogenetic conservatism) would entail a reduction of wood trait variation due to environmental convergence, the central premise of the paleoclimate inference approach using fossil wood. Here, we analyzed the role of phylogenetic relatedness in the relationship between wood anatomical traits and climate. We also assessed the strength of phylogenetic signal in wood traits and climate preferences, as well as their most likely mode of evolution. Although we found similar trends in the phylogenetically uninformed and informed regressions, the fit of the latter models was better for every trait. We also found moderate but significant non-random phylogenetic signal in all traits but potential hydraulic conductivity and vulnerability index. Our results suggest that despite adaptive evolution is driving the relationship between wood anatomy and climate, a significant role of phylogenetic signal indicates that paleoclimate estimates using fiber and vessel traits are subject to broader errors than initially anticipated.

© 2017 Elsevier B.V. All rights reserved.

## 1. Introduction

The close link between the expression of wood anatomical traits and environment was recognized in early comparative anatomy studies relating environmental gradients to wood trait variation (e.g. Starr, 1912; Baas, 1973; Carlquist, 1977). These relationships have been used by paleobotanists to develop analytical frameworks aiming at the prediction of paleoclimate using anatomical traits of fossil wood assemblages (Wiemann et al., 1998, 1999; Martínez-Cabrera and Cevallos-Ferriz, 2008). The utility of this approach lies on the extent to which environmental convergence is driving trait values. There is, however, some evidence that phylogenetic conservatism (i.e., the tendency of species to have similar traits and occupy similar niches because of common ancestry Felsenstein, 1985; Blomberg et al., 2003), might be driving, to some extent, the variation of wood anatomical traits (Zanne et al., 2010; Zheng and Martínez-Cabrera, 2013). Strong phylogenetic conservatism would lower the amount of trait variation explained by the environment because closely related species will tend to have similar trait values due to common ancestry. The effect of phylogenetic relatedness is clear in some traits, where clade affiliation has a large influence on variation

(e.g. tile cells in Malvaceae, storied structure in malvaceous and legume woods, vested pits in legumes, etc.). Some of these phylogenetically conserved traits have taxonomic value and are used in wood identification, as they often distinguish distinct taxonomic units. Even though storied structure and tile cells are strongly tied to phylogeny, they do not occur (storied structure), or their prevalence is fairly low (tile cells), outside of the tropics and thus could still provide climate information. Storied structure has actually been used in equations for prediction of mean annual temperature and coldest month mean temperature (Wiemann et al., 1998, 1999). In this case, however, the utility of the trait rather than arising from environmental trait convergence, climate information is indirectly provided by historical factors (e.g. historical biogeography). For some of these qualitative traits used in wood based paleoclimate inference (Wiemann et al., 1998, 1999; Martínez-Cabrera and Cevallos-Ferriz, 2008), there is no a clear mechanistic explanation or experimental evidence behind climate driven trait variation (i.e., similar adaptive responses in similar environments).

Besides the obvious examples mentioned above of traits where variation is clearly phylogenetically driven, the importance of phylogenetic component in the variation of traits that have been historically regarded as climate driven (in particular vessel and fiber related traits and the presence/absence of growth rings) has not been clearly addressed. Indeed, phylogenetic signal has been detected for some wood

\* Corresponding author.

E-mail address: [hugomartinez2w@gmail.com](mailto:hugomartinez2w@gmail.com) (H.I. Martínez-Cabrera).

anatomical traits (Zanne et al., 2010; Zheng and Martínez-Cabrera, 2013), and new research suggest that there are temporal shifts in phylogenetic signal across time (Martínez-Cabrera et al., 2017). These findings have two main implications in the context of paleoclimate estimation using fossil wood. The main one is that the basic assumption of environmental trait convergence may not hold if trait variation is not phylogenetically random. Second, the trait-environment relationship may have not been constant due to the varying influence of phylogeny in trait variation through time (Martínez-Cabrera et al., 2017). Consequently, even if environmental trait convergence is present today, predictive models may be less accurate (or do not work at all) when we try to use them in older floras. Here, in order to assess the validity of current approaches using wood anatomy in paleoclimate estimation, we set out to quantify the extent to which phylogenetic history shapes the relationship between vessel and fiber traits with climate.

## 2. Materials and methods

### 2.1. Datasets

We compiled a dataset consisting of 8 wood anatomical traits from 272 species across 14 communities (Martínez-Cabrera and Cevallos-Ferriz, 2008; Schenk et al., 2008; Martínez-Cabrera et al., 2009, 2011). These plant communities represent a wide range of environmental conditions: they range from tropical rainforest (from Mexico, Brazil and Suriname) and dry deciduous forest (Mexico), to drier communities such as mesquite and desert vegetation (southern USA and Argentina) and temperate forest (USA) (Table 1). The compiled traits are related to water conduction characteristics (vessel density, diameter and grouping, potential hydraulic conductivity [ $K_s$ ] and vulnerability index [VI]) and investment in mechanical support (fiber diameter, fiber wall-thickness and fiber wall to lumen ratio).

For details on the methods used to measure the anatomical traits used here consult (Martínez-Cabrera and Cevallos-Ferriz, 2008; Schenk et al., 2008; Martínez-Cabrera et al., 2009, 2011). Fiber wall-thickness and fiber and vessel lumen diameter were based on an average of at least 25 random measurements in the tropical communities described in Martínez-Cabrera and Cevallos-Ferriz, 2008 and Martínez-Cabrera et al., 2011. While in the communities described in Schenk et al. (2008) and Martínez-Cabrera et al. (2009, 2011), which are mostly from dry or temperate areas, these traits were measured on 100 to 200 cells. We calculated potential hydraulic conductivity per stem cross sectional area ( $K_s$ ) following Zanne et al. (2010):  $K_s \propto F^{1.5}S^{0.5}$  where  $F$  is the vessel fraction and  $S$  is a vessel size contribution metric. Vessel fraction  $F$  is mean vessel area  $\bar{A}$  times vessel density ( $N$ ) ( $F = \bar{A} \cdot N$ ;  $\text{mm}^2 \cdot \text{mm}^{-2}$ ), and  $S$

is the ratio of the same anatomical traits ( $S = \bar{A}/N$ ;  $\text{mm}^4$ ).  $\bar{A}$  is the mean individual vessel cross sectional area and  $N$  is the vessel number per unit of sapwood area (Zanne et al., 2010).  $\bar{A}$  was calculated using mean vessel diameter. Vulnerability index (Carlquist, 1977) was calculated as  $VI = \text{vessel diameter}/\text{vessel density}$ .

Climate information (mean annual temperature and precipitation, aridity index and potential evaporation) was obtained from weather stations in close proximity to the studied localities (Martínez-Cabrera and Cevallos-Ferriz, 2008). Aridity index is calculated as  $AI = MAP / PET$  (United Nations Environment Programme, 1992).

For the Mexican montane and tropical rainforest communities the information was extracted from the ERIC (Extractor Rápido de Información Climatológica) database (INTA, 2000); climate information from the Mexican tropical deciduous forest was obtained from the historical records of the weather station at the Biological Station of Chamela (UNAM). The climate variables from the Brazilian tropical rainforests communities (Manaus and Porto Velho) were obtained from historical information of a 30-year period (Instituto Nacional do Meteorologia, Brazil). For each of the drier sites, long-term 30-year climate data was obtained for the nearest weather station (Schenk et al., 2008; Martínez-Cabrera et al., 2009).

### 2.2. Phylogeny

We reconstructed the phylogenetic relationships among species using PHYLOMATIC (Webb and Donoghue, 2005). Some of the polytomies of the resulting tree were resolved using information from published phylogenies (Olmstead and Palmer, 1992; Alverson et al., 1999; Robinson and Harris, 2000; Urbatsch et al., 2000, 2003; Lia et al., 2001; Floyd, 2002; Goertzen et al., 2003; Baum et al., 2004; Wojciechowski et al., 2004; Martins and Barkmani, 2005). When the same species was present in more than one site (only three cases) these were analyzed as separate taxa (i.e., sister species in the phylogenetic tree). We calculated the branch lengths of the resulting using the branch length-adjusting algorithm (bladj) implemented in the program PHYLACOM (Webb et al., 2007). We used the angiosperm node ages according to Wikstrom et al. (2001) to calibrate the phylogenetic tree. The resulting tree was used for the pglS and phylogenetic signal analysis. The existing polytomies of the base backbone tree were randomly resolved using the program APE (Paradis et al., 2004).

### 2.3. Phylogenetic regression, models of evolution and phylogenetic signal

We related wood anatomical traits and climate variables using generalized least squares (GLS) and phylogenetic generalized least-squares (pGLS). Phylogenetic generalized least-squares regression includes the

**Table 1**  
Plant communities used in the analyses.

Site	Location	Vegetation type	No. of species	MAP (mm)	AI	PET (mm)	Temperature (°C)
Chamela	Jalisco, Mexico	Dry deciduous forest	57	798	0.47	1688	24.6
Copper Breaks	Texas, USA	Mesquite savanna	7	663	0.46	1450	17.2
Coweeta	North Carolina, USA	Hardwood forest	4	1850	2.06	900	12.7
Cruz de Piedra	San Luis, Argentina	Mesquite savanna	11	680	0.59	1149	17.2
Desert Center	California, USA	Desert scrub	5	100	0.06	1585	20.8
El Palmar	Entre Rios, Argentina	Palm forest	9	1190	1.21	981	18.4
Ocuilan	Estado de Mexico, Mexico	Mountain forest	26	1312	0.94	1400	15.7
La Tranca	San Luis, Argentina	Desert scrub	12	250	0.22	1141	19.8
Porto Velho	Porto Velho, Brazil	Tropical rain forest	25	2170	2.74	793	25
Manaus	Manaus, Brazil	Tropical rain forest	25	2286	2.82	812	26.7
Tafelberg	Tafelberg, Suriname	Tropical rain forest	25	2500	3.32	754	27
Tucker	California, USA	Sage scrub	8	325	0.28	1143	17.3
Los Tuxtlas	Veracruz, Mexico	Tropical rain forest	55	4556	4.45	1024	22.8
Whitehall	Georgia, USA	Hardwood forest	6	1250	1.23	1018	16.7

MAP = mean annual precipitation; AI = aridity index; PET = potential evaporation.

Download English Version:

<https://daneshyari.com/en/article/8916638>

Download Persian Version:

<https://daneshyari.com/article/8916638>

[Daneshyari.com](https://daneshyari.com)