

Determining the paleoclimate and elevation of the late Eocene Florissant flora: support from the coexistence approach¹

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Abstract: Published estimates on the paleoclimate of the Florissant fossil beds site of Colorado (34.1 Ma) have led to extremely different estimates of paleoelevation. The purpose of this paper is to review the paleoclimate methods used and to add the coexistence approach (CA) method to estimate paleotemperature for the Florissant site. The basis of the CA method is the dependence on overlapping climatic requirements for different taxa in the flora and their nearest living relatives. These relationships tie the fossil identities to the actual plant habitats and climatic requirements of close relatives. Based on the CA method, we conclude that the mean annual temperature ranged between 14.3 and 18.2 °C. These results support the conclusions offered by several other studies that the Florissant was a warm temperate to subtropical flora, and they are consistent with recent conclusions by structural geologists as well as other studies, indicating that the Florissant site was deposited at a relatively low elevation, probably between 1 and 1.5 km.

Résumé : Les estimations publiées sur le paléoclimat du site à lits fossilifères de Florissant, au Colorado (34,1 Ma), ont mené à des estimations extrêmement variées de la paléoaltitude. L'objectif du présent article est d'examiner les méthodes paléoclimatiques utilisées et d'y ajouter la méthode de l'approche de coexistence (AC) pour estimer la paléotempérature au site de Florissant. La méthode AC repose sur le fait que différents taxons dans un assemblage de plantes et leurs parents vivants les plus proches dépendent d'exigences climatiques qui se chevauchent. Cette dépendance relie l'identité des fossiles aux habitats des plantes et aux exigences climatiques des parents proches. À la lumière de cette approche, nous concluons que la température annuelle moyenne était dans la fourchette de 14,3 à 18,2 °C. Ces résultats appuient les conclusions de plusieurs autres études à l'effet que le site de Florissant représente une flore de climat chaud-tempéré à subtropical, et ils concordent avec des conclusions récentes par des géologues structuraux, ainsi que d'autres études, qui indiquent que les roches du site de Florissant ont été déposées à une altitude relativement faible, probablement entre 1 et 1,5 km. [Traduit par la Rédaction]

Introduction

With its taxonomic richness and excellent floral and faunal preservation, the latest Eocene Florissant fossil flora (34.1 Ma) of Colorado is a key site for understanding the paleoclimatic conditions of the southern Rocky Mountains just prior to the Eocene–Oligocene transition. Well-dated sediments record the initial volcanic eruption series that continued well into the late Oligocene in Colorado. The Florissant flora is also important to the geologic history of the Colorado Plateau because it provides information on the elevation of the latest Eocene surface on which it lies. A number of published estimates of mean annual temperature (MAT) have provided wide-ranging results that depend on the method used (Table 1). The main purpose of this paper is to determine climate estimates for the Florissant flora using the coexistence approach (CA) method. Improved estimates reduce uncertainties regarding paleoelevation and climate of the Rocky Mountains at this time interval.

Background

Common methods for determining paleotemperature, including leaf margin analysis (LMA), nearest living relatives (NLR), and Climate Leaf Analysis Multivariate Program (CLAMP), use different parameters to provide climate estimates. At Florissant, MAT estimates have ranged between 10.8 °C (Gregory and McIntosh 1996) and 18.3 °C (MacGinitie 1953). Because of the connection

between temperature and elevation, some authors use modern terrestrial lapse rates, requiring assumptions about MATs at sea level to estimate at what elevation a paleotemperature occurred (Cather et al. 2012). These various methods have yielded wide-ranging and often conflicting paleotemperature estimates as a result (see Table 1).

One of the earliest botanical methods developed for determining paleotemperature is based on the percent of woody dicots in the flora having smooth (untoothed) leaf margins. Bailey and Sinnott (1915, 1916) described this feature in relation to MAT for living floras, leading to the development of the LMA method. Baker-Brosh and Peet (1997) and Royer and Wilf (2006) examined transpiration, photosynthesis, and sap flow to explain the relative relationship between leaf margins and climate. However, several factors appear to confound LMA. Toothed species are more common in wet environments, including lacustrine settings like Florissant, leading to underestimations of temperature by 2.5–5 °C (Royer 2012; Burnham et al. 2001). Seasonality (Royer and Wilf 2006), leaf thickness, leaf habit (whether a plant is deciduous or evergreen), and phylogeny (Royer 2012) may also impact the presence of teeth. Finally, because there are different regression equations used in LMA that pertain to different regions (e.g., East Asian, Australian), there is a question of which regression equation to use (Wilf 1997; Greenwood et al. 2004). Given the lacustrine

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Table 1. Inferred paleoelevation, mean annual temperature (MAT), and mean annual precipitation (MAP) for the Florissant flora of central Colorado.

Inferred paleoelevation (km)	Inferred MAT or range of MAT (°C)	Inferred MAP (mm)	Source	Method
N/A	N/A	Likely summer moist sclerophyllous vegetation adapted to seasonal drought	Bouchal et al. 2014	Nearest living relative (NLR)
N/A	12.8±1.5; MAT range greater than today	720±310 annual, 570±160 growing season (mean monthly temperature >10 °C); Moist; Paleoclimate more favorable for <i>Sequoia</i> growth than today	Gregory-Wodziki 2001	Tree ring analysis of <i>Sequoioxylon</i> stumps
N/A	11–18	Summer moist	Leopold et al. 2008	NLR
0.455	15–16; little to no freezing	640	Axelrod 1998 (Haynes flora, pg. 31)	Lapse rate, NLR
<0.9	~18; few frosts	~520; summer moist	MacGinitie 1953	NLR
<1.0	15–18; few frosts	Summer moist	Leopold and Clay-Poole 2001	NLR
<1.0	14.3–18.2	<1562, pending	This report	CA
Low elevation	N/A	N/A	Barton and Fricke 2006, consistent with ~1 km	Clumped isotopes
1.4	N/A	N/A	Cather et al. 2012	Mapping
~1.6 to 2.8 (based on genus-derived MAT)	14.7±2.2 (generic); 15.6±2.5 (family)	Moist; seasonally wet	Boyle et al. 2008	Weighted average partial least-squares regression (WAPLS)
1.9±0.5 (68% confidence interval); 1.9±1.0 (95% confidence interval)	12.8	N/A	Gregory and McIntosh 1996 using Meyer 1986, 1992 method	Lapse rate 5.9 °C/km, CLAMP
2.4–2.7	10.7±1.5	N/A	Gregory and Chase 1992	Lapse rate
2.45	~14	Seasonal precipitation	Meyer 1986, 1992	Lapse rate 6.7 °C/km
~2.6	12.8, 13.9	570, 690 (growing season precipitation)	Gregory and McIntosh 1996	CLAMP
2.7–2.9	12	N/A	Wolfe 1992	Lapse rate
2.9±0.7 (95% confidence interval)	N/A	N/A	Gregory and McIntosh 1996 using Forest et al. 1995 method	Enthalpy
2.3, 4.1	10.8, 12.4	Moderate to low values with marked seasonal drought	Wolfe 1994	Lapse rate 5.5 and 3.0 °C/km, CLAMP
3.1±0.8 (68% confidence interval); 3.1±1.6 (95% confidence interval)	12.8	N/A	Gregory and McIntosh 1996 using Wolfe 1993 method	Lapse rate 3.0 °C/km, CLAMP
3.8±0.8	11.8	N/A	Wolfe et al. 1998	Moist static energy/enthalpy, CLAMP

Note: Confidence intervals are given where available. Modern values for elevation, MAT, and MAP today: 2.6 km, 4.1 °C, ~430 mm (USClimatedata.com.com 2015).

Table 2. Collections used in the Florissant study.

Slide No.	Location No./Collection	Locality information
D1083(1)	USNM loc. No. 9327, with leaf fossil	Florissant Fossil Beds National Monument, CO
D1323	E. Leopold, collected July 1958	Fish Beds, Florissant Fossil Beds National Monument, CO
D1496A–E	E. Leopold and C. Lind, collected July 1958; and EL-58-43 samples A,B,C,D,E	Fish Beds, Florissant Fossil Beds National Monument, CO; North of Twin Rocks Rd. Teller County, CO
D3495(1)	E. Leopold and C. Lind, collected September 1964	Sec. 25, T13S, R71W, Lake George Quadrangle, 500 ft. northwest of gate to Snare Ranch on north side of small hill
D3496(1)	E. Leopold and C. Lind, collected September 1964	Sec. 3, T13S, R71W, Lake George Quadrangle, 200 ft. north of house on Twin Creek Rd.; large excavation is south-facing side of small hill behind house
UW locality W-1	E. Leopold and C. Lind, collected September 1964; Measured section; See Leopold and Clay-Poole 2001	Sec. 1, T13S, R70W, W1/2 NW1/4 SW 1/4, Lake George Quadrangle; Florissant town site outcrop 1/4 mi. east of town on Highway 24, north-facing road cut

nature of the site and questions about the pertinent regression equation, LMA was not performed for this study.

CLAMP uses 31 leaf size and shape characteristics of woody dicots to estimate the paleotemperature of a fossil assemblage (Wolfe 1993; Yang et al. 2015). A recent refinement of CLAMP uses new data sets to improve on climate estimates (Teodoridis et al. 2011). Independent of taxonomic identifications and taxonomic loss (Spicer et al. 2011), CLAMP is also utilized to estimate atmospheric enthalpy, which in turn has been used to estimate paleoelevation (Forest et al. 1995).

A plant-based group of methods useful for determining paleotemperature relies on the identification of NLR of the fossil assemblage. The present range and climatic tolerances of each taxon in a flora are a basis for determining paleotemperature. The most reliable botanical determinations use megafossil evidence of both fruiting and leaf remains (Manchester 2001). Pollen data are also useful, especially when unique patterns of pollen morphology are present, and may support megafossil identifications. An early application of this general approach using megafossils was the work of MacGinitie (1953) on the Florissant flora.

Derived from NLR, CA provides a quantitative analysis of climatic requirements of a flora's taxa to infer temperature (Mosbrugger and Utescher 1997). CA applies modern limiting temperatures to a fossil plant assemblage and plots the values in MAT for each genus in an assemblage to identify the climatic ranges where the majority of taxa overlap (Utescher et al. 2014).

Included in NLR methods, Wolfe (1979) described the forest vegetation types of East Asia using the general climatic limits (in particular, MAT and mean annual range of temperature) for each extant vegetation type as defined by Wang (1961). If the genera of a fossil flora are comparable to one of these forest types, the climatic limits of the nomograms can be generally applied to the fossil assemblage.

The mutual climate range method (Sinka and Atkinson 1999) was developed for analyzing fossil insects in Quaternary deposits (Huppert and Solow 2004). Thompson et al. (2012) expanded this method to evaluate paleobotanic sites by comparing them to analogous modern forest assemblages. Because Thompson's method makes a comparison with modern equivalent floras on the species level, it is not useful for comparing with Eocene assemblages for which there is no living counterpart.

The climate reconstruction analysis using coexistence likelihood estimation (CRACLE) method (Harbert and Nixon 2015) is a new way of estimating climate from plant species coexistence data. It determines the likelihood of coexistence given the climatic tolerances of individual species using global data on species distribution. However, CRACLE uses extant species distributions in its calculations to evaluate fossil genera, which may limit its application with Eocene floras such as that at Florissant where the species are unknown or extinct.

Finally, Boyle et al. (2008) used weighted average partial least-squares regression (WAPLS) to compare genera with the fossil assemblage as an indication of similarity. Their review of global forest sites concluded that the Florissant flora was a warm temperate to subtropical association.

Methods

This study performed a literature review for paleoclimatic determinations based on the relevant botanical methods described above. Slides of pollen and spore samples collected at various sites in Florissant are listed in Table 2. The pollen and spore preparations used in this study with locality D numbers are deposited at the US Geological Survey Core Research Center at the Denver Federal Center. Slides from the locality designation of W-1 reside at the University of Washington Burke Museum.

The descriptions of Manchester (2001), supplemented by Wheeler (2001) and Wheeler and Meyer (2012), formed the baseline Florissant megafloora in this paper. Pollen and spore findings were reviewed using Leopold and Clay-Poole (2001), Bouchal (2013), Wingate and Nichols (2001), and identifications made in the Leopold Pollen and Seed Laboratory. These were added to the baseline megafossil list when such identifications were supported by megafossil evidence, were seen in quantity, or were well supported (Table A1).

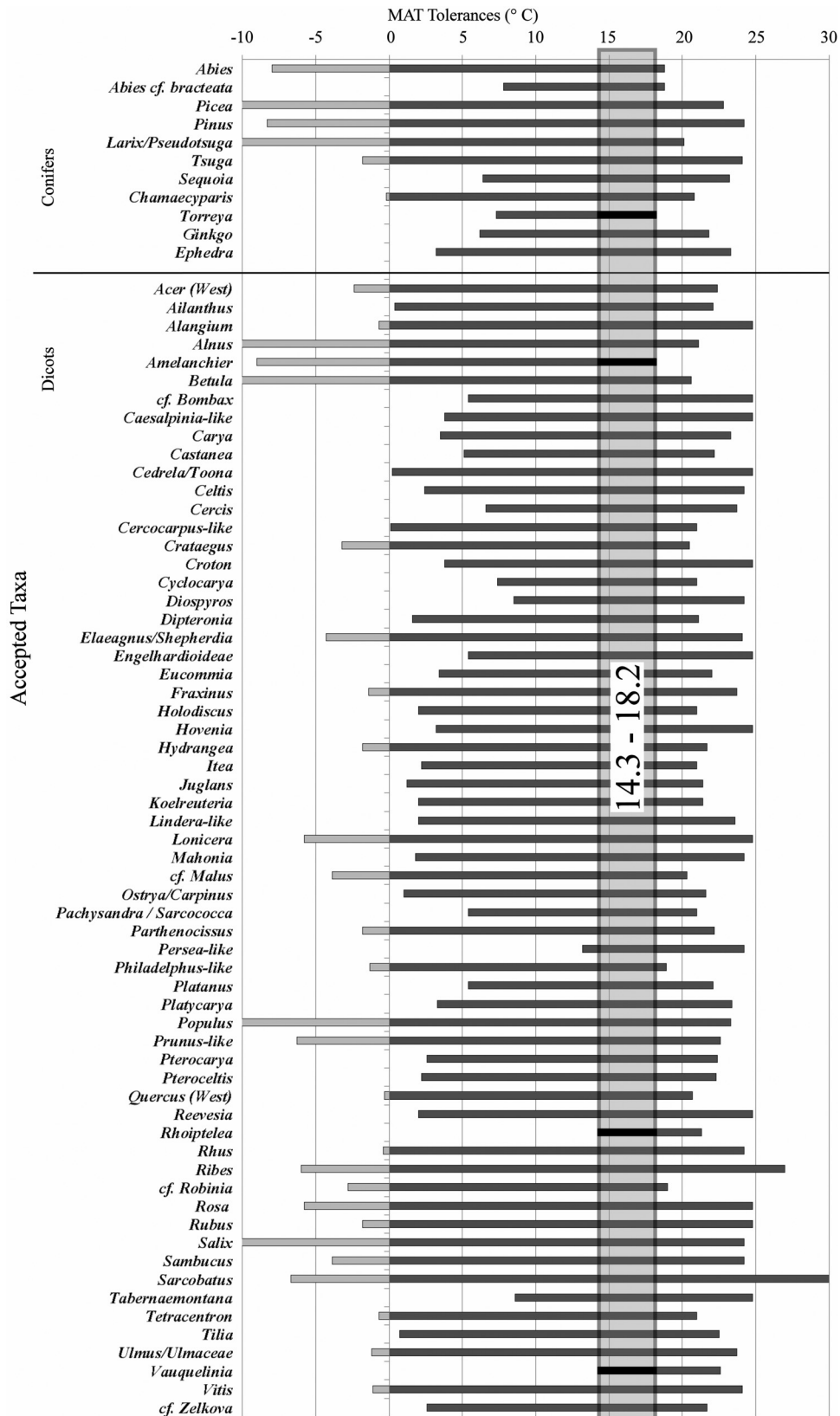
To avoid the use of questionable MAT data in the application of the CA method (see Grimm and Denk 2012), Fang et al. (2011), Thompson et al. (2015), and others were used as a source of the most current MAT values for living taxa. While all taxa accepted as found at Florissant are listed in Table A1, not all climatic ranges of MAT could be found for some taxa (Table B1). Environmental data for pollen or megafossils of uncertain identity (e.g., *Genus*-type) was excluded from the CA analysis.

Results

The Florissant flora was diverse (MacGinitie 1953; Manchester 2001; Wingate and Nichols 2001; Leopold and Clay-Poole 2001; Bouchal 2013), being comprised of 68 angiosperms, 15 gymnosperms, 7 monocots, and 3 lower plants (mainly genera and subfamily identifications; Table A1). Megafossil and pollen samples are extremely rich in woody dicot genera (63). The pollen samples in particular have abundant Pinaceae and Cupressaceae (probably *Sequoia*-type) pollen, with minor amounts of non-tree pollen (NAP).

CA results indicate that Florissant had a MAT of between 14.3 and 18.2 °C (Table 1; Fig. 1). The megafossil *Vauquelimia* and *Rhoiptelea* pollen (Leopold et al. 2008; Friis et al. 2011; Skarby et al. 2009; Takhtajan 2009) fixed the lower constraints for MAT, while *Torreya* and *Amelanchier* megafossils provided the upper limit for MAT. These results overlap with the estimates of Boyle et al. (2008), as well as with those of MacGinitie (1953) and Leopold and Clay-Poole (2001).

Fig. 1. Coexistence approach data: mean annual temperature. Note that the range lies between 14.3 °C, based on *Vauquelinia* (megafossil) and *Rhoiptelea* (pollen), and 18.2 °C, based on *Torreya* and *Amelanchier* (megafossils). No outliers. See [Table B1](#) for genera used.



Discussion

The late Eocene Florissant flora is known for its rich mixture of dry subtropical and warm temperate plant taxa characterizing a rich valley forest with streamside taxa (Table B1). However, the highlands were probably drier, based on the occurrence of arid-loving shrubs such as *Sarcobatus*, *Elaeagnus/Shepherdia*, *Vauquelinia*, *Cercocarpus*, and *Ephedra*, as well as the scarcity of ferns in the palynomorph record. Several authors characterize Florissant as having summer-moist (Cs) and winter-dry (Cw) climate and sclerophyllous taxa suggesting seasonal drought (Bouchal et al. 2014; MacGinitie 1953; Walter and Lieth 1967). Gregory-Wodziki (2001) estimated the growing-season precipitation at 570 ± 160 mm and MAP at 720 ± 310 mm (Table 1). Humid elements included *Cyclocarya*, *Rhoiptelea*, *Eucommia*, *Engelhardia*, *Alangium*, *Ostrya/Carpinus*, *Carya*, and *Croton*, which are common in the mixed mesophytic forest of eastern Asia (Bouchal et al. 2014; Wang 1961). The pollen flora included *Alangium*, *Itea*, *Cedrela*, *Croton*, and *Tetracentron* (insect-pollinated types which are unlikely to represent long-distance transport). The existence of certain gypsum-rich sediment layers and occasional pollen of dry-tolerant shrubs at Florissant exposures suggest that arid conditions at higher altitude areas occurred (MacGinitie 1953; Leopold and Clay-Poole 2001).

The hardwood dicots of Florissant were broad leaved, generally notophyllous with an unusual number of microphylls (MacGinitie 1953; H. Meyer, pers. comm., 2015), and with 60.9% toothed and 39.1% smooth-margined leaves (Table A1). Bouchal et al. (2014) emphasized the role of a few “truly humid-loving hardwoods” that occurred at Florissant, including taxa which grow primarily in the mixed mesophytic forest of southeast China (Wang 1961): *Eucommia*, *Engelhardia*, *Pterocarya*, *Cyclocarya*, *Ostrya/Carpinus*, and *Quercus*.

Method limitations

Nearest living relatives

The NLR method can be used on a wide range of plant fossil organs (T. Fletcher, pers. comm., 2015). However, it is dependent on correct identifications (Uhl et al. 2003), usually on the generic level. Extinct genera, which are not uncommon at Florissant, can make climate analysis difficult due to the lack of a NLR (H. Meyer, pers. comm., 2015). In addition, there is concern that the advanced age of the Florissant flora, being considerably pre-Neogene, may confound NLR results because the taxa may represent lineages that are not closely related to the modern taxa from which the environmental data are selected (Grimm and Denk 2012).

Coexistence approach

CA is less affected by taphonomic variables than CLAMP, but it is less sensitive to minor climate changes (Uhl et al. 2003). There are also difficulties posed by deciding which taxa may be considered outliers, which can be an issue when the limits of range are set by taxa represented by pollen only, such as the monotypic *Rhoiptelea*. Some authors elect to discard such pollen identifications altogether and set the limits of climatic range based on confidently identified megafossils only (Boyle et al. 2008) out of concern that the palynomorphs may be long-distance wind-transported. However, excluding pollen specimens may be unnecessarily restrictive, especially in the case of insect-pollinated taxa such as *Croton* (which are more likely to be growing locally or transported over short distances), or when uniquely configured grains are documented in multiple samples or are otherwise abundant, as is the case with *Rhoiptelea* (Leopold et al. 2008). Boyle et al. (2008) indicated that the inclusion of pollen taxa in their study had minimal impact on estimations of temperature at Florissant.

An important review of the CA method by Grimm and Denk (2012) raised concerns about the availability of accurate MAT data for individual genera, especially those found in localities in East Asia. One problem is due to the areas of mixed mesophytic forest growing on the steep flanks of the Yangtze River in China. Use of

appropriate maps and ways to correct such MAT values is desirable. Grimm and Denk (2012) also made it clear that differences in MAT of Chinese or Japanese values provided by the older Fang data (Fang et al. 2009) are probably significant and on the order of ~3–4 (or more) degrees. In an attempt to avoid these and other concerns, the most recent data from Fang et al. (2011), Thompson et al. (2015), and others were used (Table A1).

CLAMP and paleoenthalpy

Although CLAMP and paleoenthalpy have been widely used (Wolfe et al. 1998; Gregory and McIntosh 1996; Forest et al. 1995; and others), CLAMP is sensitive to the calibration set used (Uhl et al. 2003), and not all regions have been sampled (Boyle et al. 2008). Teodoridis et al. (2011) added more data sets in an attempt to address these limitations. In addition, recent studies have shown that this method can underestimate leaf area measurements when compared to digitally obtained measurements (Peppe et al. 2010). This “leaf area bias” can result in temperature estimates two or more degrees cooler than other methods and can even double the standard error; this has produced erroneous results severe enough to call for the abandonment of the technique for calculating paleoelevation (Peppe et al. 2010). Finally, as with LMA, CLAMP-derived temperatures can be underestimated by between 2.5 and 5 °C due to the effect of wet soils, such as those found in lakeside deposits (Burnham et al. 2001; Kowalski and Dilcher 2003). If a 2.5 °C correction were made to the CLAMP estimates found in Table 1, the resulting MAT estimates would be within the lower constraint of our CA results.

Paleoelevation

As Table 1 demonstrates, there is wide disagreement about estimates of paleoelevation. In particular, there is no consensus about which lapse rate to use. Terrestrial lapse rates vary spatially and over time. If present day lapse rates of an area differ from the modern global average because of local physical features such as topography, then using those present day lapse rates to predict past elevations with unknown topography may not yield realistic results. In addition, estimates of elevation are impacted by local climate variability at coastal coeval floral sites, which can contribute to over- and underestimation of paleoelevation at inland sites (Feng and Poulsen 2016). Given that scientists are not in agreement as to the topography of the southern Rocky Mountain region in the late Eocene, and that the modern lapse rate is a reflection of the modern topography, then this method seems to have an uncertain basis for estimating past elevations.

The data in Table 1 generally demonstrate that the inferred paleoelevation is broadly linked with the inferred MAT. MAT estimates of between 14.3 and 18.2 °C predict paleoelevations ~1.5 km or less, while cooler MAT estimates of 10–14 °C predict higher paleoelevations from ~2 to 4 km (Table 1). Elevation estimates using CLAMP and lapse rate methods require a robust MAT from a coeval sea level site, which presents another limitation of the lapse rate method. Certain MAT values combined with various lapse rates result in paleoelevations that seem excessive, including 3.8 and 4 km (Wolfe et al. 1998; Wolfe 1994); these do not leave much room for the 0.5–1.0 km uplift that has occurred there since the late Miocene (Cather et al. 2012; Karlstrom et al. 2012). A reasonable paleotemperature determined from estimates of vegetation type is therefore an important parameter because of its impact on paleoelevation. Of 241 comparative forest plots in the New World, the three most like the Florissant flora taxonomically (Florida, Tamulipas, Mexico, and northern Argentina) each lie at elevations below 1000 m (Boyle et al. 2008). The MATs at these stations were 20.5, 21.6, and 18 °C, respectively.

Interpretations

The CA results demonstrate that the plant-tolerance range of MAT of the Florissant Fossil beds flora was between 14.3 and 18.2 °C

based on the environmental tolerances provided by *Vauquelinia*, *Rhoiptelea*, *Torreya*, and *Amelanchier* (Fig. 1). Fifty-five percent of the modern taxa used for this analysis are warm loving and require MAT ranges above 0 °C, and three of these taxa (*Rhoiptelea*, *Vauquelinia*, and *Persea*) require MAT ranges of 10 °C or more (Table B1). Furthermore, clumped isotope Δ_{47} thermography based on original lacustrine carbonates suggests an MAT for Florissant of ~18 °C (Hyland and Huntington 2015), with an error of ± 2 °C (E. Hyland, pers. comm., 2015). Original lacustrine carbonates are more reliable than paleosol carbonates because they are not impacted by the time of year of deposition and therefore not biased to the warm season (E. Hyland, pers. comm., 2015). These data are consistent with findings of other studies which indicate that the Florissant site was deposited at a low elevation, e.g., ~1–1.5 km (Table 1).

Conclusion

The published lines of evidence for the paleoclimate and paleoelevation history of the Rocky Mountains of Colorado are in conflict due to different parameters and assumptions in the various methods used to calculate MAT. Because of the connection between temperature and elevation, MAT is a key parameter influencing conclusions regarding paleoelevation. Differences in MAT estimates alone are enough to yield differing and conflicting paleoelevation results. Here we reviewed various methods that have been used for the latest Eocene Florissant fossil beds of Colorado to estimate MAT. We utilized the CA method to better estimate the climate of the Florissant flora just prior to the Eocene–Oligocene transition.

From this study of megafossil and pollen records of Colorado, we concur with previous studies that identify the Florissant valley vegetation as a broad-leaved hardwood forest flora with conifer representatives. CA yielded temperature results indicating the climate was warm, with a MAT between 14.3 and 18.2 °C. Fifty-five percent of the taxa require MATs above freezing, while three of the taxa require MATs of 10 °C or higher. These warm temperature ranges are consistent with a paleoelevation of around 1–1.5 km. Certain CLAMP values have error bars that fall within the temperature range established here. These results are further supported by clumped isotope data on original lacustrine carbonates (Hyland and Huntington 2015), which indicate a MAT of $\sim 18 \pm 2$ °C. We conclude that the MAT of the Florissant flora lies between 14.3 and 18.2 °C in accord with the subtropical to warm temperate nature of the flora. The MAT data from this study support recent conclusions by structural geologists as well as other studies indicating that the Florissant site was deposited at a relatively low elevation, probably between 1 and 1.5 km.

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Appendix A

Table A1. Accepted taxa for Florissant flora (34.1 Ma) with sources.

Taxon name	Material	Source	Tooth status (score)
Conifers			
<i>Abies</i>	M, P	2; 4; 6; 9; 12	—
<i>Abies cf. bracteata</i>	P	2; 4	—
<i>Cathaya</i> -type (uncertain identity)	P	12	—
<i>Cedrus</i> -type (uncertain identity)	P	2	—
<i>Picea</i>	M, P	2; 4; 6; 9; 12	—
<i>Pinus</i>	M, P	2; 4; 6; 12	—
<i>Larix/Pseudotsuga</i>	P	2; 12	—
<i>Tsuga</i>	P	2; 9; 12	—
<i>Sequoia</i>	M, P	2; 6; 7; 9	—
TCT	P	2; 4; 9; 12	—
<i>Chamaecyparis</i>	M	6	—
<i>Torreya</i>	M	6	—
<i>Ginkgo</i>	M, P	1; 11; 12	—
<i>Podocarpus</i> -type (uncertain identity)	P	4; 9	—
<i>Ephedra</i>	P	2; 4; 9; 12	—
Monocots			
<i>Dioscorea</i>	M	6	—
Palmae	M	6	—
<i>Potamogeton</i>	M, P	6	—
<i>Smilax</i> or similar Liliales	M, P	2; 6; 9	—
Poaceae	M, P	2; 6; 9; 10; 12	—
<i>Sparganium</i>	P	2; 9; 12	—
<i>Typha</i>	M, P	2; 6; 12	—
Dicots			
<i>Acer</i> (West)	M, P	2; 4; 5; 6; 9; 12	T (0)
<i>Ailanthus</i>	M, P	5; 6	E (1)
<i>Alangium</i>	P	9; 10	E (1)
<i>Alnus</i>	P	9; 10; 12	T (0)
<i>Amelanchier</i>	M	5; 6	T (0)
<i>Betula</i>	P	1; 2; 10; 12	T (0)

Table A1 (continued).

Taxon name	Material	Source	Tooth status (score)
cf. <i>Bombax</i> (subfamily Bombacoideae)	P	9; 10; 12	E (1)
<i>Caesalpinia</i> -type	M, P	5; 6; 9; 12	E (1)
<i>Cardiospermum</i>	P	2; 5	N/A (herb)
<i>Carya</i>	M, P	2; 4; 5; 6; 12	T (0)
<i>Castanea</i>	P	1; 12	T (0)
<i>Cedrela/Toona</i>	M, P	5; 6	T, E (0, 1)
<i>Celtis</i>	P	2; 12	T (0)
<i>Cercis</i>	M	5; 6	E (1)
<i>Cercocarpus</i> -like	M	5; 6; 12	T (0)
<i>Crataegus</i>	M	5; 6; 12	T (0)
<i>Croton</i>	P	2	E (1)
<i>Cyclocarya</i>	P	2	T (0)
<i>Diospyros</i>	P	1; 12	E (1)
<i>Dipteronia</i>	M	5; 6	T (0)
<i>Elaeagnus/Shepherdia</i>	P	2; 9; 12	E (1)
<i>Engelhardioideae</i>	P	2; 4	E (1)
<i>Eucommia</i>	M, P	2; 4; 6; 12	T (0)
<i>Fraxinus</i>	P	9; 12	B (0.5)
<i>Holodiscus</i>	M	6	T (0)
<i>Hovenia</i>	M	8	E (1)
<i>Humulus</i>	M	6	N/A (herb)
<i>Hydrangea</i>	M	5; 6	T (0)
<i>Itea</i>	P	4; 9	E (1)
<i>Juglans</i>	P	2; 4; 9; 12	B (0.5)
<i>Koeleruteria</i>	M	5; 6; 7	T (0)
<i>Lindera</i> -like	M	5; 6	E (1)
<i>Lonicera</i> (subfamily Caprifolioidae)	P	9	E (1)
<i>Mahonia</i>	M	5; 6	T (0)
cf. <i>Malus</i>	M, P	2; 5; 6	T (0)
<i>Nuphar</i>	P	9; 10	N/A (aquatic)
<i>Ostrya/Carpinus</i>	P	2; 4	T (0)
<i>Pachyandra/Sarcococca</i>	P	3; 9; 10	B (1)
<i>Parthenocissus</i>	P	2	T (0)
<i>Persea</i> -like	M	5; 6	E (1)
<i>Philadelphus</i> -like	M	5; 6	E (1)
<i>Platanus</i>	M	5; 6; 12	T (0)
<i>Platycarya</i>	P	2	T (0)
<i>Populus</i>	M	6	T (0)
<i>Prunus</i> -like	M	5; 6	T (0)
<i>Pterocarya</i>	P	2; 4	E (1)
<i>Pteroceltis</i>	P	2; 9	T (0)
<i>Quercus</i> (West)	M, P	2; 4; 5; 6; 9; 12	T, E (0, 1)
<i>Reevesia</i>	P	9; 10	E (1)
<i>Rhoiptelea</i>	P	2	T (0)
<i>Rhus</i>	M	5; 6	T, E (0, 1)
<i>Ribes</i>	M, P	4; 5; 6	T (0)
cf. <i>Robinia</i>	M	5; 7	E (1)
<i>Rosa</i>	M	5; 6	T (0)
<i>Rubus</i>	M	5; 6	T (0)
<i>Salix</i>	M, P	2; 5; 6; 9; 10	T, E (0, 1)
<i>Sambucus</i>	M	5; 6	T (0)
<i>Sarcobatus</i>	P	2; 4; 12	E (1)
<i>Semeiandra</i> -type	P	2	N/A (herb)
<i>Tabernaemontana</i>	P	2; 12	E (1)
<i>Tetradactylon</i>	P	1; 12	T (0)
<i>Tilia</i>	M, P	2; 5; 10	T (0)
<i>Ulmus/Ulmoideae</i>	M, P	2; 4; 5; 6; 9; 12	T (0)
<i>Vauquelinia</i>	M	5; 6	T (0)

Table A1 (concluded).

Taxon name	Material	Source	Tooth status (score)
<i>Viburnum</i> -type	P	1; 2	B (0.5)
<i>Vitis</i>	M, P	5; 6	T (0)
<i>Xylonagra</i> -type (woody)	P	2	E (1)
cf. <i>Zelkova</i> -type	M, P	2; 5; 7	T (0)
Lower plants			
<i>Azolla</i>	S	9	—
<i>Lygodium</i>	S	2	—
<i>Selaginella</i> cf. <i>densa</i>	S	2; 4	—

Note: M, megafossil; P, pollen; S, spore. Dicot tooth status: T, toothed form (score=0); E, entire form (score=1); B, both toothed and entire (pollen only; score=0.5). When a genus presents with both toothed and entire forms in separate megafossil specimens, each form is counted separately.

KEY of Sources:

1 Bouchal 2013.

2 Leopold and Clay-Poole 2001.

3 Leopold et al. 2008.

4 Leopold and Zaborac-Reed 2014.

5 MacGinitie 1953.

6 Manchester 2001.

7 Wheeler 2001.

8 Wheeler and Meyer 2012.

9 Wingate and Nichols 2001.

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12 Bouchal et al. 2016.

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Appendix B

Table B1. Climate ranges for nearest living relatives of the Florissant flora (34.1 Ma) with sources.

Taxon name	MAT (°C)			MAP (mm)		
	Low	High	Source	Low	High	Source
Conifers						
<i>Abies</i>	-8.0	18.2	3	169	4366	3
<i>Abies cf. bracteata</i>	7.8	18.2	2; 3	500	1780	3; 9
<i>Picea</i>	-12.4	22.8	1	321	1736	1
<i>Pinus</i>	-8.3	24.2	3	49	4930	3
<i>Larix/Pseudotsuga</i>	-10.1	20.1	3	174	3479	3
<i>Tsuga</i>	-1.8	24.1	1	311	2992	1
<i>Sequoia</i>	6.4	23.2	2; 3; 13	610	3100	3; 12
<i>Chamaecyparis</i>	-0.2	20.8	3	418	4930	3
<i>Torreya</i>	7.3	18.2	1	644	1997	1
<i>Ginkgo</i>	6.2	21.8	1	428	1997	1
<i>Ephedra</i>	3.2	23.3	3	34	725	3
Dicots						
<i>Acer (West)</i>	-2.4	22.4	3	42	4366	3
<i>Ailanthus</i>	0.4	22.1	1	203	2859	1
<i>Alangium</i>	-0.7	24.8	1	370	2992	1
<i>Alnus</i>	-10.8	21.1	3	140	4390	3
<i>Amelanchier</i>	-9.0	18.2	3	131	4366	3
<i>Betula</i>	-16.9	20.6	3	113	4366	3
<i>cf. Bombax</i>	5.4	24.8	1	741	3495	1
<i>Caesalpinia-type</i>	3.8	24.8	1	596	2992	1
<i>Carya</i>	3.5	23.3	3	425	1939	3
<i>Castanea</i>	5.1	22.2	3	795	1939	3
<i>Cedrela/Toona</i>	0.2	24.8	1	386	2435	1
<i>Celtis</i>	2.4	24.2	3	146	1899	3
<i>Cercis</i>	6.6	23.7	3	145	1939	3
<i>Cercocarpus-like</i>	0.1	21.0	3	96	1571	3
<i>Crataegus</i>	-3.2	20.5	3	185	4366	3
<i>Croton</i>	3.8	24.8	1	868	3495	1
<i>Cyclocarya</i>	7.4	21.0	1	517	1997	1
<i>Diospyros</i>	8.5	24.2	3	272	1939	3
<i>Dipteronia</i>	1.6	21.1	1	373	1562	1
<i>Elaeagnus/Shepherdia</i>	-4.3	24.1	1	63	2850	1
<i>Engelhardioideae</i>	5.4	24.8	1	741	3495	1
<i>Eucommia</i>	3.4	22.0	1	548	1922	1
<i>Fraxinus</i>	-1.4	23.7	3	80	2230	3
<i>Holodiscus</i>	2.0	21.0	4; 8	500	1630	10
<i>Hovenia</i>	3.2	24.8	1	367	2435	1
<i>Hydrangea</i>	-1.8	21.7	1	320	3495	1
<i>Itea</i>	2.2	21.0	1	797	2435	1
<i>Juglans</i>	1.2	21.4	3	293	1939	3
<i>Koelreuteria</i>	2.0	21.4	1	349	1997	1
<i>Lindera-like</i>	2.0	23.6	1	512	2993	1
<i>Lonicera</i>	-5.8	24.8	1	34	3495	1
<i>Mahonia</i>	1.8	24.2	1	527	1828	1
<i>cf. Malus</i>	-3.9	20.3	3	646	4930	3
<i>Ostrya/Carpinus</i>	1.0	21.6	3	154	1939	3
<i>Pachysandra/Sarcococca</i>	5.4	21.0	1	741	2445	1
<i>Persea-like</i>	13.2	24.2	3	661	1619	3
<i>Philadelphus-like</i>	-1.3	18.9	1	341	1997	1
<i>Platanus</i>	5.4	22.1	3	186	1939	3
<i>Platycarya</i>	3.3	23.4	1	367	2680	1
<i>Populus</i>	-15.0	23.3	3	73	4366	3
<i>Prunus-like</i>	-6.3	22.6	3	57	3257	3
<i>Pterocarya</i>	2.6	22.4	1	367	2580	1
<i>Pteroceltis</i>	2.2	22.3	1	377	1997	1
<i>Quercus (West)</i>	-0.3	20.7	3	115	2220	3
<i>Reevesia</i>	2.0	24.8	1	741	2435	1
<i>Rhoiptelea</i>	14.3	21.3	1	1007	1776	1
<i>Rhus</i>	-0.4	24.2	3	194	1939	3
<i>Ribes</i>	-6.0	27.0	6	300	5800	11
<i>cf. Robinia</i>	-2.8	19.0	1	244	1939	3
<i>Rosa</i>	-5.8	24.8	1	32	3495	1

Table B1 (concluded).

Taxon name	MAT (°C)			MAP (mm)		
	Low	High	Source	Low	High	Source
<i>Rubus</i>	-1.8	24.8	1	144	3495	1
<i>Salix</i>	-16.2	24.2	3	34	4366	3
<i>Sambucus</i>	-3.9	24.2	3	96	4930	3
<i>Sarcobatus</i>	-6.7	37.0	5; 7	76	508	5; 7
<i>Tabernaemontana</i>	8.6	24.8	1	868	2993	1
<i>Tetracentron</i>	-0.7	21.0	1	370	1751	1
<i>Tilia</i>	0.7	22.5	3	429	1939	3
<i>Ulmus/Ulmoideae</i>	-1.2	23.7	3	317	1939	3
<i>Vauquelinia</i>	14.3	22.6	3	214	520	3
<i>Vitis</i>	-1.1	24.1	1	321	2993	1
<i>cf. Zeltkova</i>	2.6	21.7	1	373	2713	1

Note: These data were used in the coexistence approach analysis. MAT, mean annual temperature; MAP, mean annual precipitation. MAP results using coexistence approach are unclear; further analysis and interpretation is pending.

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2 Griffin and Critchfield 1976.

3 Thompson et al. 2015.

4 Pond 2003.

5 Natural Resources Conservation Service 2015.

6 Marshall 1995.

7 Anderson 2004.

8 U.S. Department of Agriculture 2011.

9 Las Pilitas Nursery 2012.

10 Las Pilitas Nursery 2014a.

11 Las Pilitas Nursery 2014b.

12 Olson et al. 2015.

13 USClimateData.com 2015.

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