Reconstructing paleoclimate and paleoecology using fossil leaves

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ABSTRACT

Plants are strongly influenced by their surrounding environment, which makes them reliable indicators of climate and ecology. The relationship between climate, ecology, plant traits and the geographic distribution of plants based on their climatic tolerances have been used to develop plant-based proxies for reconstructing paleoclimate and paleoecology. These proxies are some of the most accurate and precise methods for reconstructing the climate and ecology of ancient terrestrial ecosystems and have been applied from the Cretaceous to the Quaternary. Despite their utility, the relationships between plant traits and climate that underlie these methods are confounded by other factors such as leaf life-span and phylogenetic history. Work focused on better understanding these confounding factors, incorporating the influence of phylogeny and leaf economic spectrum traits into proxies, expanding modern leaf trait-climate and ecology calibration datasets to additional biogeographic areas and climate regimes, and developing automated computer algorithms for measuring leaf traits are important growing research areas that will help considerably improve plant-based paleoclimate and paleoecological proxies.

Key words: paleobotany, leaf physiognomy, leaf margin analysis, leaf area analysis, CLAMP, digital leaf physiognomy, nearest living relative, leaf economic spectrum, leaf vein density, leaf mass per area

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INTRODUCTION

Plants are stationary, primary producers whose productivity is based on their ability to photosynthesize and use water efficiently. Terrestrial plants use roots and rhizoids to take in water and minerals from the soil, which are essential for photosynthesis and for maintaining the water content of the plant. Leaves, a plant's primary photosynthetic organ, are used for gas and water exchange between the plant and the atmosphere, and generally have high surface to volume ratios. Plants must therefore balance water loss and uptake, light and carbon dioxide fixation, and heat gain and loss from their environment as these affect their water use efficiency and photosynthetic capacity. Thus for plants to be successful, they must have biochemical and physiological adaptations that are well matched to the conditions they experience in their environment. Given these relationships between plants and their surrounding environment, a plant's traits, such as the size and shape of its leaves, are intrinsically linked to the climate and environment in which it is growing.

A variety of methods have been developed over the last 100 years using the relationships between plant traits, climate, and ecology to develop paleoclimate and paleoecological proxies that can be applied to fossil leaves. In this review, we discuss univariate, multivariate, and taxonomic methods for reconstructing paleoclimate and paleoecology using fossil plants and their advantages and disadvantages. We also discuss new developments and future research directions for leaf-based methods of reconstructing paleoclimate and paleoecology.

LEAF TRAITS AND CLIMATE

The relationships between plant traits, and more specifically leaf traits, and the climate and environment have been noted for over 100 years (e.g., Billings, 1905; Bailey and Sinnott,

1915; Bailey and Sinnott, 1916). In particular, the sizes and shapes (physiognomy) of leaves correlate strongly with temperature and moisture, and these relationships have been used to develop proxies for reconstructing paleoclimate (e.g., Bailey and Sinnott, 1915; Bailey and Sinnott, 1916; Webb, 1959, 1968; Wolfe, 1971; Dilcher, 1973; Wolfe, 1978;1979; Dolph and Dilcher, 1980a, b; Greenwood, 1991; 1992; Wing and Greenwood, 1993; Wolfe, 1993, 1995; Wilf, 1997; Wilf et al., 1998; Jacobs, 1999; Gregory-Wodzicki, 2000; Jacobs, 2002; Kowalski and Dilcher, 2003; Greenwood et al., 2004; Traiser et al., 2005; Spicer, 2007; Adams et al., 2008; Peppe et al., 2011; Teodoridis et al., 2011; Yang et al., 2011; Yang et al., 2015; Spicer, 2016). Additionally, the climatic tolerances of plants very strongly influence their geographic distributions (e.g., Von Humbolt and Bonpland, 1807 Merriam, 1894; Kchler, 1964; Holdridge, 1967; Whittaker, 1975; Larcher and Winter, 1981;). Thus, a plant community, which is comprised of species with overlapping geographic ranges and environmental tolerances, should broadly reflect the climate in which it is growing, assuming the plant community is in equilibrium with climate (e.g., Svenning and Sandel, 2013). The assumption that a plant community is in equilibrium with climate is probably broadly true; however, there are notable situations when plant communities can be out of equilibrium with climate, often referred to as disequilibrium or community disequilibrium, particularly when climate is rapidly changing (e.g., Davis, 1986; Svenning and Sandel, 2013; Blonder et al., 2015) The relationship between plant geographic distributions and climate has been used to develop a variety of qualitative and quantitative “nearest living relative” approaches, in which fossil taxa are systematically assigned to a closely related modern plant taxon (i.e. their "nearest living relative") and then the fossil species assemblage is matched to the climatic conditions of its “nearest living relatives” (e.g., Heer, 1870, 1878b, a, 1882; Chaney, 1938; Axelrod, 1948, 1952; MacGinitie, 1953; Axelrod and Bailey, 1969; Hickey, 1977; Kershaw and Nix, 1988; Mosbrugger and Utescher, 1997).

Univariate and multivariate leaf physiognomic methods and nearest living relative approaches have been applied hundreds, if not thousands, of times to Cretaceous and

Cenozoic angiosperm-dominated fossils floras to reconstruct paleoclimate (as an example, see supplement in Little et al. (2010) for a relatively complete list of papers from 1902 to 2010 that have utilized univariate and multivariate leaf physiognomic methods). These climate reconstructions are probably what fossil leaves are best known for among the broader geological and paleoanthropological communities and there are a number of other excellent detailed reviews on using angiosperm leaves to reconstruct climate (e.g., Chaloner and Creber, 1990; Greenwood, 2007; Wilf, 2008; Jordan, 2011; Royer, 2012a).

The basic observations underpinning leaf physiognomic paleoclimate methods are the relationships between leaf teeth and mean annual temperature (MAT) and leaf size and mean annual precipitation (MAP). In particular, the average leaf size of all species at a site positively correlate with MAP and the percentage of woody, dicotyledonous (dicot) angiosperm species at a site with toothed leaves and variables related to tooth count and size all negatively correlate with MAT (Fig. 1, 2; e.g., Bailey and Sinnott, 1916; Webb, 1968; Dilcher, 1973; Wolfe, 1979; Dolph and Dilcher, 1980a, b; Givnish, 1984; Greenwood, 1992; Wolfe, 1993; Wilf, 1997; Wilf et al., 1998; Jacobs, 1999; Jacobs, 2002; Huff et al., 2003; Greenwood et al., 2004; Royer et al., 2005; Peppe et al., 2011; Royer, 2012b; Yang et al., 2015). A number of studies have demonstrated that leaf shape in at least some species of angiosperms changes in response to climate both within the lifetime of a single plant (e.g., Royer et al., 2009b; Chitwood et al., 2016) and over evolutionary time scales (e.g., Schmerler et al., 2012). Further, it appears that distinct molecular pathways have evolved in plants to mediate changes in leaf shape in response to changes in photosynthesis, temperature, and light quality (e.g., Chitwood and Sinha, 2016), suggesting that plants have evolved mechanisms for changing leaf physiognomy in response to climate and environment.

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Leaf size typically scales with local water availability (Fig. 2B; e.g., Webb, 1968; Givnish, 1984; Wilf et al., 1998; Jacobs, 1999; Malhado et al., 2009). Larger leaves tend to be warmer because they have a thicker boundary layer (e.g., Vogel, 1970; Parkhurst and Loucks, 1972; Gates, 1980; Givnish, 1984; Vogel, 2009). Photosynthetic and transpiration rates both increase with increasing leaf temperature up to a maximum of ~35-40 °C, at which point plants begin to experience heat stress and photosynthetic and transpiration rates rapidly decrease (e.g., Mooney et al., 1978; Salvuci and Crafts-Bandner, 2004; Wahid et al., 2007; Michaletz et al., 2015). As a result, plants tend to have smaller leaves in drier climates to reduce evaporative cooling and larger leaves in wet climates where water loss related to increased transpiration is less important, as a means of balancing heat loss via evaporative cooling and water loss via transpiration (i.e., leaf energy balance) (e.g., Givnish, 1984; Montheith and Unsworth, 2007). Smaller leaves usually have higher densities of major veins, which makes them less vulnerable to embolisms caused by hydraulic disruptions that occur during drought conditions (Scoffoni et al., 2011), which may also help explain why plants in dry climates have smaller leaves than in wetter climates.

There are many hypotheses about the functional relationship between leaf teeth in angiosperms and climate. Leaf teeth are sites of increased transpiration (Canny, 1990). Thus in cold climates, teeth could be an adaptation for increased carbon uptake via enhanced sap flow early in the growing season, which would allow rapid early season growth ("early season gas-exchange hypothesis"; e.g., Billings, 1905; Bailey and Sinnott, 1916; Baker-Brosh and Peet, 1997; Wing et al., 2000; Royer and Wilf, 2006). Leaf teeth also commonly have hydathodes, which are fixed pores in teeth that probably allow for water loss via guttation (Feild et al., 2005). The hydathodes likely also help the plant enhance sap flow, which allows it to release excess root pressure, preventing flooding of intercellular spaces in the leaf and, in colder climates, freeze-thaw embolisms ("root-pressure hypothesis"; Feild et al., 2005). Leaf shape, and in particular dissections of a leaf, are also probably related to bud packing ("bud-packing

hypothesis"; Kodayashi et al., 1998; Couturier et al., 2011; 2012; Edwards et al. 2016). Additionally, at least some plants exhibit seasonal heteroblasty, in which there are systematic differences in leaf form associated with position along a branch ("seasonal heteroblasty hypothesis"). More specifically, studies have shown that "preformed" leaves, which are leaves that undergo a period of arrested development within a bud, differ in shape from "neoformed" leaves, which are leaves that develop continuously within a bud (Critchfield 1960; 1971; Edwards et al., 2016).

The early season gas-exchange hypothesis provides a functional explanation for the relationship between leaf teeth and MAT because, based on this hypothesis, species with teeth are able to grow and photosynthesize more rapidly early in the growing season than untoothed species, which is a considerable advantage in colder climates with short growing seasons. The root-pressure hypothesis (e.g., Feild et al., 2005) is not as clearly related to MAT because it is related to water movement and freeze-thaw cycles through the plants, which has at best a weak link to climate. However, this hypothesis might help provide a mechanism to explain how plants maintain enhanced sap flow during rapid leaf expansion early in the growing season. The relationship between leaf teeth, enhanced sap flow and increased water loss also helps explain why toothed species are often more abundant in locally wet environments where the potential negative implications of water loss through leaf teeth are mitigated (e.g., Wolfe, 1993; Burnham et al., 2001; Kowalski and Dilcher, 2003; Greenwood, 2005; Royer et al., 2009a; Peppe et al., 2011). The seasonal heteroblasty hypothesis is also not directly linked to MAT. However, it provides a functional explanation for how temperature may influence leaf development and may help at least partially explain why leaf trait variability appears to be more strongly related to annual climate instead of growing season climate. For example, in *Viburnum*, preformed leaves tend to be rounder, more lobed and toothier than neoformed leaves, which were more elliptical with greatly reduced teeth (Edwards et al., 2016). This seasonal variation in leaf shape could be due to two co-occurring forces: first, the different scenarios of early development (e.g., winter

dormancy vs. continual development from bud primordia to leaf flush) and second, the plastic response to different light and temperature regimes experienced in the early versus late season (Edwards et al., 2016). The bud-packing hypothesis is based on the premise that there are constraints on leaf shape that are driven by how the fold and boundaries of leaf primordia are arranged in a bud, which is unlikely to be driven by climate. However, the bud-packing and seasonal heteroblasty hypothesis are very similar in that both argue that climate influences leaf development within the bud, which in turn influences leaf shape, suggesting that climate plays an important role in influencing leaf shape from the beginning of bud development. Although each of these hypotheses help explain some aspects of the relationship between leaf physiognomy and climate, we still lack a physiological or evolutionary mechanism that fully explains how and why the empirical relationships that have been observed between leaf physiognomy and climate in modern floras exist. Work to better understand the mechanism linking climate and leaf physiognomy is ongoing (see for example review in Chitwood and Sinha, 2016) and help offer insights that will likely significantly improve leaf physiognomy-climate models in the future.

The occurrence of leaf teeth are likely also influenced by a variety of factors not directly related to climate, such as phylogeny, leaf life-span, and leaf thickness. Phylogenetic history influences the occurrence of leaf teeth (e.g., Little et al., 2010; Burnham and Tonkovich, 2011; Hinojosa et al., 2011). This suggests that the leaf teeth-climate relationship observed in modern floras may reflect a combination of plants' responses on both short term (i.e., seasonal) and long term (i.e., evolutionary) time scales and processes of plant community assembly (Schmerler et al., 2012). Plant leaf life-span and leaf thickness also influence the occurrence of leaf teeth as both deciduous species and species with thinner leaves more commonly have teeth than evergreen species and species with thicker leaves (Royer et al., 2012). However, neither plant life-span (i.e., deciduous vs. evergreen) nor leaf thickness correlate strongly with MAT (e.g., Reich et al., 1999; Wright et al., 2004; Wright et al., 2005; Royer et al., 2012), indicating that non-climatic factors also play a role in the occurrence of leaf teeth. The influence

of phylogeny, leaf life-span, leaf thickness and other non-climatic factors on leaf physiognomic methods for reconstructing climate is unclear, but may inherently bias paleoclimate estimates (see Royer, 2012a for more details). Leaf physiognomic methods that incorporate phylogenetic and leaf ecological information are in development and aim to address the potential influence of phylogeny and other non-climatic drivers of leaf teeth on paleoclimate estimates.

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Methods of paleoclimate reconstruction

Methods that reconstruct paleoclimate using fossil leaves can be broadly divided into two main types: leaf physiognomic methods and nearest living relative (NLR) methods. Leaf physiognomic methods use the relationship between leaf traits and climate, while NLR approaches use the climatic, and less commonly, the ecological requirements of the taxon that is the nearest living relative to the fossil taxon being studied.

Leaf physiognomic methods – univariate approaches: The relationship between leaf physiognomy and climate was first noted a century ago by Bailey and Sinnott (1915; 1916) and this relationship has become the cornerstone of leaf physiognomic paleoclimate methods (e.g., Wolfe, 1971, 1979; Dilcher, 1973; Wing and Greenwood, 1993; Wolfe, 1993; Wilf, 1997; Wilf et al., 1998; Jacobs, 1999; Gregory-Wodzicki, 2000; Greenwood et al., 2004; Spicer, 2007; Peppe et al., 2011; Spicer, 2016). In particular, Bailey and Sinnott (1915; 1916) noted that the proportion of a flora with entire-margined leaves and with large leaves increased with decreasing latitude and suggested that these relationships could be used to estimate ancient climate. Following this pioneering work, paleobotanists used similarities between the relative abundance of species with entire margins and the different size classes of leaves in modern vegetation, as well as Paleogene and Neogene floras to qualitatively infer paleoclimate (e.g.,

MacGinitie, 1953; Wolfe and Hopkins, 1967; Hickey, 1977; Christophel and Blackburn, 1978). Despite the acknowledgement of the relationship between leaf physiognomy and climate and its application to fossil floras and ancient climates, it took more than a half a century before the qualitative relationships noted by Bailey and Sinnott (1915; 1916) were demonstrated quantitatively.

Using floral lists from East Asia, Wolfe (1979) demonstrated a remarkably strong relationship between the percentage of woody dicot species at a site with entire margins, defined as species lacking either marginal teeth or lobes, and MAT. However, although Wolfe (1979) presented a linear regression in his figure that showed the relationship between the percent of species with entire margins and MAT, the statistics and the equation for the regression were not presented. This relationship was then quantified by Wing and Greenwood (1993) using linear regression to develop a predictive equation to estimate MAT based on the percentage of woody dicot species at a site with entire margined species:

$$\text{(Eq. 1) } \text{LMAT} = 30.6P + 1.14$$

where LMAT is mean annual temperature estimated using leaf margin analysis and P is defined as:

$$\text{(Eq. 2) } P = \frac{r}{n}$$

where n is the total number of species sampled, r is the number of species at a site with entire margins, and $(n - r)$ is the number of species with toothed margins. In cases where a species has both entire and non-entire margins, the r score for the species is 0.5.

Since Wing and Greenwood's (1993) recalculation of Wolfe's (1979) East Asian leaf margin analysis (LMA) regression, the relationship between leaf margin and MAT has been tested on floras from most major geographic locations and climate biomes on earth and many global, regional, and site specific LMA regressions have been developed (Fig. 1; Table 1). Significantly, since Wilf (1997), leaf margin type has been classified as toothed or entire (i.e.,

non-toothed). Although many factors confound the relationship between margin percentage and MAT, as discussed above and reviewed by others (e.g., Greenwood, 2007; Jordan, 2011; Peppe et al., 2011; Royer, 2012a; Royer et al., 2012), the relationship between leaf margin and MAT is typically statistically significant and similar across geographic regions (Fig. 2a). Based on these LMA regressions, LMA has been applied to numerous of Cretaceous and Cenozoic fossil floras to estimate MAT using fossil leaves (see for example studies cited in supplementary materials in Little et al., 2010).

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The accuracy and precision of MAT estimates using LMA has been shown to improve when more species are sampled. In his original LMA work, Wolfe (1971) suggested ≥ 30 species were necessary to calculate a reliable MAT estimate, though he suggested that the minimum bar was ≥ 20 species, which has been the practice of most paleobotanists. While the total number of species sampled is important, the proportional recovery of the total flora is more significant. For example, Burnham et al. (2001; 2005) found that in very diverse, extant floras with 55 to >400 species, ≥ 25 of the most common species had to be sampled to make an accurate MAT estimate using LMA. This suggests that LMA should only be applied to well-sampled floras and that MAT estimates made using poorly sampled floras and/or floras with low species richness are unlikely to be accurate.

Sample size also affects the uncertainty of LMA estimates. Based on their reanalysis of the Wolfe (1979) East Asian LMA, Wing and Greenwood (1993) calculated the standard error of LMA estimates of MAT to be ± 0.8 °C. However, the standard errors of the East Asian LMA regression alone considerably underestimate the uncertainty of leaf margin analysis mean annual temperature (LMAT) estimates. To account for additional uncertainty in LMAT estimates, Wilf (1997) proposed using the binomial sampling error for LMA estimates, which

accounts for the standard error of the LMA regression and uncertainty related to sampling the species richness of a fossil flora:

$$(Eq. 3) \sigma[LMAT] = c\sqrt{\frac{P(1-P)}{n}}$$

where c is the slope of the MAT vs. leaf-margin regression in the dataset used, P is the proportion of species with entire margins, and n is the number of species sampled.

Wilf (1997) suggested the minimum uncertainty of a LMAT estimate was at least ± 2.0 °C and that the larger of the two errors given by the binomial sampling error and the standard error of the regression if it were > 2.0 °C was the appropriate uncertainty for LMAT estimates. In Wilf's (1997) study, he noted that the binomial sampling error only accounted for part of the total uncertainty in LMAT estimates. Miller et al. (2006) incorporated the uncertainties associated with the estimation of the proportion of species at a site with teeth (P) into the estimation of uncertainty of LMAT estimates:

$$(Eq. 4) \sigma[LMAT] = c\sqrt{[(1 + \phi(n - 1)(P(1 - P)))\frac{P(1-P)}{n}]}$$

where c is the slope of the MAT vs. leaf-margin regression in the dataset used, P is the proportion of species with entire margins, n is the number of species sampled and ϕ is the overdispersion factor for P , which was calculated by Miller et al. (2006) to be 0.052.

The Miller et al. (2006) estimation of uncertainty provides the best measurement of the precision of LMAT; however, they noted that there may be additional systematic uncertainties in LMAT based on sampling differing forested environments. Greenwood et al. (2004) documented this effect in a series of sites from Australia that showed a significant correlation between margin percentage and MAT ($r^2 = 0.57$, $P < 0.001$), but a larger uncertainty than datasets from East Asia and North and Central America ($\sigma = \pm 3$ °C). Based on a large global compilation of sites, Peppe et al. (2011) showed that the uncertainty associated with LMAT estimates using a globally derived LMA is at least ± 4 °C. Conservatively, given uncertainties associated with sampling (accounted for in equation 4) and all of the potential confounding

factors that affect the relationship between climate and the proportion of species with teeth uncertainties, which are currently not accounted for in any uncertainty calculation, a minimum uncertainties for LMAT estimates is probably ± 5 °C (see also Jordan, 1997, 2011; Royer, 2012a). Despite these uncertainties, LMAT estimates are typically in agreement with other proxies and are generally accurate, and reasonably precise, making the LMA method a useful tool for estimating MAT in the past.

Building on another of Bailey and Sinnott's (1915; 1916) observations that large leaves were more common in warm, mesic environments, several researchers have noted a strong positive relationship between leaf size and mean annual precipitation (MAP) (Webb, 1968; Dilcher, 1973; Dolph and Dilcher, 1980a, b; Hall and Swaine, 1981; Givnish, 1984). The correlation between leaf size and MAP was first quantified by Givnish (1984) for floras from South America, Central American and Australia. Wilf et al. (1998) expanded on Givnish's (1984) work and used the correlation between the mean of the natural log of species' leaf area (MlnA) and the natural log of MAP (lnMAP) at 50 sites from North America, Central America, South America, and Africa to develop a predictive equation for MAP:

$$\text{(Eq. 5) } \ln(\text{MAP}) = 0.548\text{MlnA} + 0.768$$

MlnA was calculated for the entire flora by first determining the Raunkier-Webb (Webb, 1959) size category for each species and then determining the proportion of species in each of the seven size categories:

$$\text{(Eq. 6) } \text{MlnA} = \sum a_i p_i$$

Where a_i is the seven means of the natural log areas of the size categories and p_i is the proportion of species in each size category. This method of estimating MAP using leaf area is known as leaf area analysis (LAA; Table 1). The standard error for ln(MAP) for LAA is 0.359 (Wilf et al., 1998).

Following the work of Wilf et al. (1998), the relationship between leaf area and MAP has been tested on a series of floras from Bolivia and predominately Northern Hemisphere

temperate regions (Gregory-Wodzicki, 2000), floras from equatorial Africa (Jacobs, 1999; 2002), and floras from North America, Central America, South America, Asia, and Oceania (Peppe et al., 2011) (Fig. 2). These correlations have been used to develop several additional LAA equations to estimate MAP (Table 1, Fig. 2; Jacobs, 1999; Gregory-Wodzicki, 2000; Jacobs, 2002; Peppe et al., 2011). Using a dataset of sites from equatorial Africa and Bolivia, Jacobs and Herendeen (2004) also documented a significant relationship between leaf area and precipitation during the three wettest months, which they used to develop a proxy for wet month precipitation (Table 1).

Although the relationship between leaf area and mean annual precipitation is significant, LAA estimates of MAP are not accurate and the uncertainties are relatively large. Peppe et al. (2011) used a jackknife-type approach for a dataset of 92 globally distributed sites to gauge the accuracy of LAA, and found that LAA tended to underestimate MAP at sites with relatively high precipitation and overestimate MAP at sites with relatively low precipitation. These results and the original work of Wilf et al. (1998) suggest that LAA is not a precise estimator of MAP and instead is primarily a useful tool for roughly estimating MAP.

Leaf size is also influenced by a variety of other factors including temperature, elevation, soil fertility, and leaf life-span (e.g., Webb, 1968; Dolph and Dilcher, 1980a, b; Givnish, 1984; Wolfe, 1995; Halloy and Mark, 1996; McDonald et al., 2003; Peppe et al., 2011) confounding the relationship between MAP and leaf size leading to the low accuracy and precision of MAP estimates made using LAA. Additionally, available water appears to be the main control on leaf size (Givnish, 1984). In addition to precipitation, plant available water is influenced by many factors such as rates of evapotranspiration, temperature, seasonality, the position of the water table, and hydrologic conductance within the soil. As a result, MAP may not be a good proxy for available water in many situations, which perhaps explains the relatively poor accuracy and precision of LAA.

Although LMA, and to a lesser extent LAA, have been widely adopted by the paleobotanical community and the fossil leaf based MAT and MAP estimates made using the methods are often considered some of the most robust estimates for terrestrial paleoclimates, both methods rely on single characters. Leaf size and shape is remarkable diverse and many aspects of leaf physiognomy vary with climate (e.g., Wolfe, 1993, 1995; Royer et al., 2008; Royer et al., 2009b; Schmerler et al., 2012). Additionally, in at least some cases, multiple leaf physiognomic traits appear to co-vary with climate variables (Dolph and Dilcher, 1980a, b; Peppe et al., 2011). Further, although LMA and LAA commonly agree with other climate proxy reconstructions, in many cases, these proxies provide cooler and drier estimates of MAT and MAP than other proxies (e.g., Liang et al., 2003; Fricke and Wing, 2004; Wing et al., 2009; Adams et al., 2011). Because LMA and LAA are univariate approaches, the incorporation of additional leaf characters may lead to improvements in paleoclimate estimates.

Leaf physiognomic methods – multivariate approaches: In an attempt to improve on the shortcomings of univariate leaf physiognomic methods, Wolfe (1990; 1993, 1995) developed a multivariate method called Climate-Leaf Analysis Multivariate Program (CLAMP), which currently uses 31 categorical leaf physiognomic traits (see Spicer, 2016). In CLAMP the leaf character scores and climate data from a modern training set are analyzed using canonical correspondence analysis (CCA; Wolfe, 1995; Kovach and Spicer, 1996). The resultant eigenvectors for the climate and leaf physiognomic variables are projected onto the major axes of variation, which roughly correlate with temperature (first axis) and moisture (second axis) (Wolfe, 1995). A second-order polynomial fit for a climate variable to the eigenvector is then used to develop a predictive equation for that climate variable, which can then be applied to a fossil flora (Wolfe, 1995). In practical terms, this means that the leaf character scores of a fossil flora are projected onto each of the climate variable vectors in the CLAMP calibration dataset and those scores are used to estimate each climate variable. CLAMP estimates MAT, warm

month mean temperature, cold month mean temperatures, growing season length, growing season precipitation, mean monthly growing season precipitation, precipitation in the three wettest and three driest months, relative humidity, specific humidity, and enthalpy (Wolfe, 1995; Spicer, 2016). The standard errors for CLAMP climate estimates are small (Wolfe, 1993, 1995; Spicer et al., 2005); however, the errors are only based on the analytical uncertainty of CCA and do not account for any additional uncertainties related to the leaf character states, character scoring, precision in the climate variables of the calibration data set, or factors that potentially confound leaf character-climate relationships. Thus, the standard errors reported for CLAMP considerably underestimate uncertainty and are artificially precise. For example, at minimum, the uncertainties in MAT estimates made using CLAMP are similar to, if not larger than those for leaf margin analysis (see Figure 1 in Royer, 2012a).

CLAMP was originally calibrated with 106 sites with a limited global coverage, and since has been expanded to two primary calibration datasets primarily derived from floras from the Northern Hemisphere: (1) PHYSG3BR, which includes 144 temperature Northern Hemisphere sites, and (2) PHYSG3AR, which includes 173 Northern Hemisphere sites that include sites that experience very cold winter temperatures (e.g., Wolfe, 1993, 1995; Wolfe and Spicer, 1999; Spicer et al., 2004; Spicer, 2016). Since then Spicer and colleagues (see Spicer, 2007, 2016) have assessed regional differences in the relationship between climate and CLAMP characters in South America (Gregory-Wodzicki, 2000; Kowalski, 2002), South Africa (Stear et al., 2011), New Zealand and Australia (Kennedy et al., 2002; Kennedy et al., 2014) and expanded the calibration datasets to include floras in regions that experience a monsoon climate (Jacques et al., 2011; Khan et al., 2014), floras from the Southern Hemisphere (Kennedy et al., 2014), and floras from temperate and high latitudes in the Northern and Southern Hemispheres (Yang et al., 2015). The CLAMP modern calibration originally used climate data from local climate stations (Wolfe, 1993, 1995), but more recent studies follow Spicer et al. (2009) and use climate data extracted from the New et al. (2002) global, gridded climate model. CLAMP analyses were

originally performed using a series of spreadsheets and conducting a CCA using the software package CANACO 4.5 (Microcomputer Power, Ithaca, NY, USA). CLAMP analyses can now be performed online (Yang et al., 2011) through the CLAMP website:

http://clamp.ibcas.ac.cn/CLAMP_Run_Analysis.html.

Although CLAMP has been widely applied (reviewed in Spicer, 2007, 2016), the method has several shortcomings that have been reviewed many times (e.g., Jordan, 1997; Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1998; Green, 2006; Peppe et al., 2010; Jordan, 2011). The most notable criticisms are that (1) based on the character distributions, CCA may not be the most appropriate technique for predicting climate (Green, 2006; Peppe et al., 2010), (2) at least some of the leaves in the original calibration dataset were scored incorrectly (Peppe et al., 2010), (3) many of the CLAMP character states are at least partially ambiguous and the original scoring procedures were poorly defined (Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1998, 1999; Green, 2006), (4) the CLAMP characters are discrete and categorical despite the fact that leaf traits are continuous (i.e., number of teeth, leaf size) and many of the continuous traits correlate strongly with temperature and/or precipitation (Huff et al., 2003; Royer et al., 2005; Royer et al., 2008; Peppe et al., 2011), and (5) some CLAMP character states only correlate weakly to climate and/or have no physiological explanations for climate causality.

One of the underlying assumptions of CCA is that the variables are unimodally distributed (ter Braak, 1986). However, Green (2006) and Peppe et al. (2010) showed that many of the CLAMP leaf character distributions were not unimodally distributed. Following this work, Teodoridis et al. (2011) developed transformations of the CLAMP PHYSG3BR and PHYSG3AR calibration datasets that could be used as “correction coefficients” to account for the non-normality of the CLAMP leaf character state data.

Peppe et al. (2010) rescored a subset of Wolfe's (1993, 1995) original calibration sites and demonstrated that the site-mean leaf area of 38 sites in the CLAMP calibration and the leaf area scores of the species in each site were considerably underestimated relative to digitally

measured leaf area. When the influence of this underestimation of leaf area was accounted for, it added a considerable amount of uncertainty to all CLAMP climate estimates (Peppe et al., 2010). Spicer and Yang (2010) assessed the influence of leaf size on MAT and enthalpy estimates made using CLAMP and found that when the leaf size character state was removed it increased uncertainty, but caused only relatively small changes in MAT and enthalpy. This result indicates that leaf size contributes relatively little information when predicting at least some climate variables with CLAMP and suggests that some climate predictions could be improved by changing the leaf character states used in CLAMP. Spicer and Yang (2010) only indirectly addressed the main criticism of Peppe et al. (2010), that the leaf area scores in the CLAMP calibration dataset are underestimated, by suggesting that the measured leaf area bias was the result of measuring leaf area directly rather than using the CLAMP leaf area template. This is an important distinction because it means that when performing a CLAMP analysis, leaf area can only be scored using the CLAMP leaf area template and if leaf area is measured directly, even if it is more accurate, it will add considerable uncertainty to the CLAMP estimates.

Several studies have documented issues with the ambiguity of CLAMP character states and original scoring procedures (Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1998, 1999; Green, 2006; Peppe et al., 2010). Recently, Spicer (2016) updated the character state definitions and scoring protocol in an attempt to eliminate the ambiguities. To test these revisions, Spicer and Yang (2010) had students collect and score leaves from a forest reserve near Beijing, China and found that the resulting CLAMP climate estimates were different, though reasonably similar, suggesting the revised CLAMP scoring protocol and character definitions have helped eliminated some of the problems with the original method.

Although there has been recent work to expand the CLAMP calibration datasets to a wider range of biogeographic regions and climate regimes (e.g., Jacques et al., 2011; Kennedy et al., 2014; Yang et al., 2015), the inherent issues with using categorical variables and leaf characters that are not physiologically linked to climate have not been addressed. Furthermore,

many studies have demonstrated that climate estimates made using CLAMP are similar to, or less accurate than, estimates made using LMA and LAA (e.g., Wilf, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000; Kowalski, 2002; Kowalski and Dilcher, 2003; Hinojosa et al., 2006a; Hinojosa et al., 2006b; Dilcher et al., 2009; Royer, 2012a; Smith et al., 2012; West et al., 2015).

Rather than apply CCA, several researchers have used the CLAMP calibration datasets or comparable datasets using the CLAMP characters to develop multiple linear regressions models for paleoclimate (e.g., Wing and Greenwood, 1993; Gregory, 1994; Gregory and McIntosh, 1996; Jacobs and Deino, 1996; Stranks and England, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000; Kowalski and Dilcher, 2003; Lielke et al., 2012). However, these methods have not been widely adopted. Further, because they utilize the CLAMP calibration dataset and leaf character states, they suffer from many of the same problems as CLAMP.

Given the potential problems with CLAMP, and in particular the subjectivity of scoring leaf traits, Huff et al. (2003) proposed digital leaf physiognomy (DiLP), which is a method for measuring leaf traits digitally. The benefits of DiLP are that it increases the reproducibility of leaf character scores and that it measures continuous variables, such as number of teeth and tooth size, that have functional or physiological links to climate. In their preliminary study of three floras, Huff et al. (2003) found that continuous variables related to tooth number and tooth shape varied between floras and with temperature, demonstrating that the incorporation of continuous variables had the potential to improve fossil leaf based paleoclimate models. A subsequent study by Royer et al. (2005) showed that leaves in cold climates are more highly dissected and have more, larger teeth. Using data from 17 sites from the east coast of the United States and Panama, Royer et al. (2005) developed a preliminary multiple linear regression model for predicting MAT that was more accurate and precise than LMA and CLAMP. However, the study was based on sites from a relatively limited range in biogeography and precipitation. Peppe et al. (2011) quantified DiLP leaf physiognomic variables and climate using 92 globally distributed and climatically diverse sites and noted the same patterns between

leaf traits and MAT as observed by Huff et al. (2003) and Royer et al. (2005) and also that leaves in wet climates were larger and had fewer, smaller teeth. Using these relationships, Peppe et al. (2011) developed multiple linear regression models for MAT and MAP (Table 1):

$$\text{(Eq. 7) } \text{MAT} = 0.210(E) + 42.296(FDR) + 2.609(T:IP) - 16.004$$

$$\text{(Eq. 8) } \ln(\text{MAP}) = 0.298 \ln(A) - 2.71 \ln(PR) + 0.279 \ln(T:IP) + 3.033$$

where E is the proportion of species at the site with entire margins, FDR is feret's diameter ratio (Diameter of a circle with the same area as the blade area (cm)/ longest measurable line across blade area (cm)), $T:IP$ is the number of teeth to internal perimeter (number of teeth/perimeter of the leaf after teeth are removed (cm)), A is leaf area, and PR is perimeter ratio (perimeter of the leaf blade/internal perimeter (cm) / perimeter of the leaf after teeth are removed (cm)). The leaf character states used in these models are defined in Peppe et al. (2011). The standard error for the MAT model is ± 4.0 °C and for the MAP model is 0.60.

DiLP estimates of MAT and MAP are significantly more accurate than MAT estimates made using LMA and marginally better than MAP estimates using LAA (Peppe et al., 2011). DiLP MAT estimates made for several fossil floras are also in better agreement with other proxy reconstructions of MAT than LMA estimates (Peppe et al., 2011). This suggests that the DiLP method potentially offers improvements over other existing leaf physiognomic methods. DiLP also offers three additional advantages over CLAMP, LMA, and LAA: (1) it minimizes ambiguity in leaf character scoring because computer algorithms process most of the measurements; (2) the DiLP models use mostly continuous variables, such as feret's diameter ratio and number of teeth:internal perimeter; and (3) the leaf characters used in the DiLP models have a functional connection to climate and include traits that display phenotypic plasticity between growing seasons (Royer et al., 2009b) indicating the traits can respond quickly to climate change.

Despite its advantages, a major limitation of DiLP is that some of the characters used in the DiLP MAT and MAP models (feret's diameter ratio and leaf area) require relatively complete preservation of leaves. Unfortunately, fossil leaves are typically fragmented (e.g., Greenwood,

1992, 2005, 2007; Spicer et al., 2005), which means that it may not be possible to score all DiLP characters for all fossil taxa. In an sensitivity experiment using modern leaves, Royer et al. (2005) tested the effect of fragmentary leaves on LMA and DiLP and found that in all cases fragmentary leaves led to less precise climate estimates, but when leaves were 50% intact, LMA estimates of MAT had larger errors than estimates made with DiLP. Additionally, Royer et al. (2005) found that while multiple specimens should be scored when possible, only one specimen per species needed to be digitally score to provide an accurate MAT estimate using DiLP. These results suggest that although there is some information lost when leaves are fragmentary, DiLP may still able to provide reasonable estimates of paleoclimate when fragmentary leaves are scored. In an attempt to address the fact that fossil leaves are commonly incomplete, Peppe et al. (2011) developed a detailed protocol for processing incomplete leaves. In practice DiLP characters can be scored in most fragmentary leaves, provided that at least 25% of the leaf is preserved and the fragment preserves both the margin and the mid-vein. Additionally, recent work documented a strong relationship between leaf vein density and leaf size (e.g. Sack et al., 2012), and was used to develop a “vein scaling” transfer function for estimating leaf area from fragmentary fossils (Merhofer et al., 2015). The incorporation of leaf area estimates made using vein scaling also has the potential to increase the number of fragmentary fossil specimens that can be used to reconstruct MAT and MAP.

DiLP has been successfully applied to several fossil floras (Peppe et al., 2011; Flynn et al. 2016), which suggests that the method has great potential to be more widely applied. However, there are some examples in which the climate estimates made using DiLP were unreasonable based on other lines of evidence (Peppe et al., 2011). For example, estimates for the Laguna del Hunco flora from Argentina, were cooler and drier than expected (Peppe et al., 2011), based on the habitat preference of some of the species present in the flora (Wilf et al., 2009). This discrepancy may be because the physiognomic-climate space of South America is not fully characterized in the current DiLP calibration.

There are also some floras to which DiLP cannot be applied. Peppe et al. (2011) recommend using CCA as an initial check to confirm that a fossil floras physiognomic space is captured by the calibration data. Peppe et al. (2001) and Peppe (unpublished data) have analyzed two floras that plotted outside the calibrated physiognomic space: Bonanza, an Eocene flora from North America, and Rusinga R3, a Miocene flora from Kenya (Fig. 3). Peppe et al. (2011) argued that the Bonanza flora was likely an outlier because the fossil flora was a mixture of two habitats resulting in a unique site mean physiognomic space. There are no modern floras from Africa in the current DiLP calibration, and thus the Rusinga R3 flora from Kenya likely samples a currently uncalibrated physiognomic space (Fig. 3). Future work expanding the calibration dataset to more sites from the Southern Hemisphere, and particularly from Africa, may help improve DiLP so that the method can be applied to a wider range of floras.

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Shortcomings and limitations of physiognomic methods: Although leaf physiognomic methods of reconstructing paleoclimate have been widely applied and generate reasonably accurate and precise estimates, they are not without their inherent disadvantages. There are a variety of factors that affect and confound the relationships between leaf physiognomy and climate. In this review, we will briefly discuss three of the important factors that limit leaf physiognomic methods: life history, phylogeny, and plant ecology. For a review of some of the other confounding factors, such as taphonomy, local water availability, position in the canopy, soil fertility, and nutrient availability, see the recent reviews by Greenwood (2007), Jordan (2011), and Royer (2012).

The original leaf margin analysis calibration data and most subsequent calibrations, as well as most of the calibration data that underlies CLAMP and DiLP, are primarily derived from

Northern Hemisphere temperate floras (e.g., Wolfe, 1979; Wolfe, 1993, 1995; Wilf, 1997; Kowalski and Dilcher, 2003; Su et al., 2010; Peppe et al., 2011). However, the relationship between leaf physiognomy and climate, and particularly between the presence of leaf teeth and MAT, is distinctly different in the Southern Hemisphere where floras typically have a higher percentage of untoothed species than their Northern Hemisphere counterparts (e.g., Wolfe, 1979; Upchurch and Wolfe, 1987; Gregory-Wodzicki, 2000; Kowalski, 2002; Greenwood et al., 2004; Hinojosa et al., 2006a; Aizen and Ezcurra, 2008; Hinojosa et al., 2011; Steart et al., 2011; Kennedy et al., 2014). Further, in Africa, Australia, and New Zealand the correlation between leaf size and MAT is as strong, if not stronger, than between leaf margin and MAT (Webb, 1968; Greenwood, 1992, 1994; Jacobs, 1999; Jacobs, 2002).

These hemispheric differences could be due to regional differences in environment, such as thermal seasonality or soil fertility, phylogenetic differences, leaf life-span (i.e., lack of temperate deciduous forests in the Southern Hemisphere), or differences in plant ecology (e.g., Upchurch and Wolfe, 1987; Wolfe and Upchurch, 1987; Jordan, 1997; Greenwood et al., 2004; Jordan, 2011; Peppe et al., 2011). Researchers have also found that there are considerable differences between physiognomy and climate when comparing the CLAMP PHYSG3BR and PHYSG3AR to regional floras in South America, Australia, and New Zealand (e.g., Gregory-Wodzicki, 2000; Kennedy et al., 2002; Kowalski, 2002; Hinojosa et al., 2006a; Steart et al., 2011; Kennedy et al., 2014). There are also notable differences in the relationship between leaf physiognomy and climate in some of the DiLP characters (e.g., number of teeth vs. temperature and leaf area vs. temperature) between sites from the different hemisphere, and particularly from Australia and New Zealand (Peppe et al., 2011). Finally, although much research has focused on the regional differences in the relationships between climate and physiognomy, most of the regional datasets have not been added to the larger calibration dataset or used to develop new models (e.g., Steart et al., 2011 from South Africa). As a result, most LMA regressions and the most commonly used CLAMP calibration datasets PHYSG3BR and

PHYSG3AR have few to no floras from Africa, South America, and Oceania. The net effect is the most leaf physiognomic models do a relatively poor job reconstructing the paleoclimate of Southern Hemisphere floras (Kowalski, 2002; Greenwood et al., 2004; Hinojosa et al., 2006a; Peppe et al., 2011).

Two of the hypothesized explanations for the differences between Northern and Southern Hemisphere floras, phylogeny and plant ecology, likely play a role in their differences and also strongly influence the relationships globally. Although there is evidence that leaves can phenotypically respond to climate change rapidly (Royer et al., 2009b; Chitwood et al., 2016), there is clearly a genetic control on leaf shape and tooth characters (reviewed in Chitwood and Sinha, 2016). Additionally, there are many families of plants that are overwhelmingly toothed (e.g., Betulaceae, Juglandaceae) or untoothed (Lauraceae, Myrtaceae). However, in *Viburnum* there are evolutionary correlated shifts in leaf shape and leaf tooth morphology that are coincident with climate (Schmerler et al., 2012), suggesting that in at least some taxa, leaf physiognomy responds to climate on evolutionary timescales.

More generally, the phylogenetic composition of a flora strongly can strongly influence leaf physiognomy (Little et al., 2010). There appears to be a significant phylogenetic signal in the relationship between leaf margin and MAT (Jones et al., 2009; Little et al., 2010; Hinojosa et al., 2011) and, using a restricted dataset of 17 sites from the eastern United States and Central America, in the relationship between DiLP characters and MAT as well (Little et al., 2010). Little et al. (2010) also found that phylogenetic generalized least squares analysis that included phylogenetic information improved the ability to predict margin state (toothed vs. entire) from MAT, but with much larger uncertainty and a flatter regression slope. Based on these results, Little et al. (2010) argue that LMA is so strongly affected by phylogenetic bias that it should not be used. However, although there is phylogenetic signal in leaf traits, there is a global relationship between leaf traits and climate (Peppe et al., 2011; Yang et al., 2015) suggesting there is likely geographic and evolutionary sorting of taxa and preferred plant morphology

relative to climate. Further, recent work by Lawing et al. (2016) suggests that the work of Little et al. (2010) may be affected by phylogenetic autocorrelation and that their conclusions may not be valid unless the geographic distribution of tree species also has strong phylogenetic inertia, which seems unlikely given the rapid movement of plants in response to changing climate in the Quaternary and today (e.g., Comes and Kadereit, 1998; Davis and Shaw, 2001; Kelly and Goulden, 2008). However, if plant communities and/or species are in climate disequilibrium (e.g., Svenning and Sandel, 2013; Rokataorinivo et al., 2013), there is the potential for paleoclimate to have influenced modern plant distributions, and thus modern leaf trait-climate relationships, which would considerably confound leaf physiognomic based paleoclimate estimates. Regardless, phylogenetic history likely plays an important role in influencing climate-leaf physiognomy relationships, and future work should focus on incorporating phylogeny into future leaf physiognomic methods.

Plant growth habit and leaf life-span also influences leaf physiognomy. In particular, deciduous taxa are more likely to be toothed than evergreen taxa (Peppe et al., 2011; Royer et al., 2012) and leaf life-span (deciduous vs. evergreen) also influences tooth size and number (Peppe et al., 2011). Thus, the growth habits of species within a plant community likely has a strong influence on leaf physiognomy. As an example, floras from the Southern Hemisphere tend to have more species that are evergreen relative to Northern Hemisphere floras; therefore, it is possible that leaf life-span plays a significant role in driving the higher percentage of untoothed species in the Southern Hemisphere (e.g., Upchurch and Wolfe, 1987; Greenwood et al., 2004; Peppe et al., 2011). Using a data set of species, instead of sites which all of the leaf physiognomic calibrations are optimized for, Royer et al. (2012) found that the inclusion of leaf thickness and deciduousness with other DiLP variables and a multiple linear regression model of leaf thickness, deciduousness, and leaf margin reduced the standard errors of both models predictions of MAT. Leaf thickness and deciduousness are not measureable in fossils, but leaf mass per area, which is a proxy for leaf life-span (Royer et al., 2007), can be estimated. The

incorporation of leaf mass per area into a model with other DiLP characters also reduces the standard error of the models prediction of MAT (Royer et al., 2012). These preliminary results suggest that although plant ecology clearly has an effect on leaf physiognomy, its incorporation into paleoclimate models might improve the accuracy and precision of the paleoclimate models.

Nearest living relative methods: The geographic distributions of plants are strongly influenced by their environmental and climatic tolerances (e.g., Merriam, 1894; Kchler, 1964; Holdridge, 1967; Whittaker, 1975). Under the assumption that the climatic tolerances of fossil taxa and fossil plant assemblages are similar to their modern “nearest living relatives” (NLR), for more than 100 years paleobotanists have used this information to estimate ancient climate based on fossil plant assemblages (e.g., Heer, 1870, 1878b, a, 1882; Chaney, 1938; Axelrod, 1948, 1952; MacGinitie, 1953; Axelrod and Bailey, 1969; Hickey, 1977; Kerhsaw and Nix, 1987; Mosbrugger and Utescher, 1997). Probably beginning with the work of Heer (e.g., 1870, 1878b, a, 1882), numerous NLR qualitative and quantitative methods have been developed and applied primarily to Cenozoic floras. Both qualitative and quantitative NLR methods use the climatic and ecological requirements of extant plant taxa, which means that these methods rely upon accurate taxonomic identification of plant fossil material. Additionally, NLR methods are not limited to woody dicot angiosperm leaves alone, and any reliably identified plant organ can be utilized.

Qualitative NLR methods rely on individual indicator taxa to derive paleoclimate and paleoenvironment from a fossil flora. For example, the occurrence of palms in a fossil flora would be used to infer warm and wet conditions with cold months above freezing because the palm family Arecaceae is found predominately in tropical to sub-tropical regions with limited to no winter freezing (e.g., Larcher and Winter, 1981; Wing and Greenwood, 1993; Greenwood and Wing, 1995). However, a considerable limitation of these qualitative NLR approaches is

that they do not provide quantitative estimates of paleoclimate (i.e., a MAT or MAP prediction) and the accuracy of the paleoclimate interpretation can be strongly influenced by taphonomic removal of important indicator taxa as well as the level of taxonomic identification of the indicator taxa.

Quantitative NLR methods build on the indicator taxa approach to quantitatively estimate paleoclimate. Originally quantitative NLR methods used a few selected fossil taxa and assessed their overlapping climate preferences, which resulted in broad “coexistence intervals” that were used to estimate paleoclimate (e.g., Grichuk, 1969; Hickey et al., 1988; Zagwijn and Hager, 1987). This approach was modified independently first as bioclimatic analysis (Kerhsaw and Nix, 1987; Greenwood et al., 2003, 2005), and then as the coexistence approach (CA) of Mosbrugger and Utescher (1997). Other NLR methods also use the same fundamental premise, but assess the climatic ranges and/or distributions differently (e.g., Thompson et al., 2012; Harbert and Nixon, 2015). All NLR methods have four primary assumptions: (1) there are modern taxa that are systematically closely related to identified fossil taxa (i.e., their “nearest living relative”); (2) the climate requirements of the fossil taxon are similar to those of the nearest living relatives; (3) the climate tolerances of the nearest living relatives can be derived from its modern distribution; and (4) the climate data for the nearest living relatives is good quality (Mosbrugger and Utescher, 1997; Utescher et al., 2014).

In CA all identified fossil taxa are conferred to nearest living relatives. The climatic tolerances of each fossil's nearest living relative are then compared to find an interval where all nearest living relatives could coexist (Fig. 4). The climatic ranges of many vascular plant taxa have been compiled in the Palaeoflora Database (PFDB; www.palaeoflora.de), which is the dataset used for CA. Individual taxa that do not overlap with the rest of the taxa from a site are considered outliers and are removed from the analysis. This subjective removal of outliers has come under criticism (Grimm and Denk, 2012; Grimm et al., 2015; Grimm and Potts, 2016). CA

has been used to reconstruct seven different aspects of temperature and precipitation: MAT, warm month mean temperature, cold month mean temperature, MAP, monthly minimum precipitation, monthly maximum precipitation, and warm month mean precipitation and has a reported precision of 0.1 °C and 1 mm precipitation (Mosbrugger and Utescher, 1997). This uncertainty is only the analytical uncertainty of the CA calculation for the coexisting climatic range, and thus is artificially precise and considerably underestimates the total uncertainty of the climate estimate.

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Another quantitative NLR method is Bioclimatic Analysis (Kershaw and Nix, 1987; Kershaw, 1997). Just as in CA, in Bioclimatic Analysis fossil taxa are conferred the nearest living relatives, which are compared to determine the climate interval where all of the nearest living relatives could coexist originally using the PFDB and more recently using climatic ranges of taxa using the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>) and the WorldClim global climate models (Hijmans et al., 2005). However, unlike CA, which uses the entire climatic range of all taxa to calculate a climatic variable, Bioclimatic Analysis initially limited coexistence intervals to the 10th (lower limit) to 90th (upper limit) or 5th to 95th percentile values of the total climatic range for all of the nearest living relative taxa (Kershaw and Nix, 1988; Kershaw, 1997; Greenwood et al., 2003, 2005). Subsequent iterations of bioclimatic analysis, however, calculated the estimate as the mean value of the 10th and 90th percentile of the maximum and minimum values across all taxa recorded in a sample, with the total range between these plotted as an “error bar” (e.g., Greenwood, et al., 2005; Eldrett et al., 2009, 2014; Pross et al., 2012; Smith et al., 2012; Reichgelt et al., 2013).

701 The mutual climatic range (MCR) method estimates paleoclimate from the present
702 climatic tolerance ranges of the nearest living relative of fossil taxa and originally was
703 methodologically nearly identical to CA (Sinka and Atkinson, 1999; Sharpe, 2002). More
704 recently, Thompson et al. (2012) modified the method and currently MCR uses factor-analysis
705 based climate space to plot coldest month temperature against coldest month precipitation and
706 warmest month temperature against warmest month precipitation and the estimated
707 temperature and precipitation for a given time of year (i.e., coldest month, warmest month) is
708 made based on where the climate space overlaps. The MCR method can only be applied to the
709 Quaternary and has only been applied to a few fossil assemblages (Thompson et al., 2012).
710 Applications to modern coleopteran assemblages demonstrates the estimates made using MCR
711 are conservative when compared to meteorological data, but that the method has systematic
712 biases (winter estimates too warm, summer estimates too cool in Britain) (Thompson et al.,
713 2012). Additionally, if neither the absence nor proportion of taxa in the flora can be used to
714 delimit a smaller climatic range, MCR estimates an overly large climatic range (Thompson et al.,
715 2012).

716 Climate Reconstruction Analysis using Coexistence Likelihood Estimation (CRACLE) is
717 a new quantitative NLR method that uses global scale specimen collection data to infer species
718 climate tolerance by calculating the maximum joint likelihood of species coexistence (Harbert
719 and Nixon, 2015). CRACLE uses species distribution data from specimen collections obtained
720 from the GBIF and the WorldClim global climate models (Hijmans et al., 2005) to determine
721 species-climate tolerance profiles. When compared to other quantitative NLR methods, MAT
722 estimates made using CRACLE are more accurate and precise suggesting this method may
723 offer considerable improvements over other NLR approaches. However, unless modified,
724 CRACLE is only applicable to the Holocene and late Pleistocene because it requires modern
725 geographic distributions of fossil taxa to make climatic estimates. Additionally, a major limitation
726 of CRACLE is that for it to be applied to the fossil record, it assumes realized niche stasis, which

has been demonstrated to be invalid (e.g., Jackson and Overpeck, 2012; Veloz et al., 2012), and that plant communities are in equilibrium with climate, which also may not always be a valid assumption (e.g., Svenning and Sandel, 2013; Rokataorinivo et al., 2013).

Shortcomings and limitations of nearest living relative methods: All NLR methods rely heavily on accurate climate data for the distribution of the living relative, and precise taxonomic identification. However, resolution of climate estimates decreases at higher taxonomic levels: species-level analyses tend to produce narrow climate intervals, while family-level analyses tend to produce wide climate intervals. Additionally, species turnover within a genus that leads to niche shifts and changes in realized niches through time (e.g., Veloz et al., 2012), are not captured by this approach. This is a problem when trying to apply NLR methods to the fossil record because while younger fossil floras, such as those from the Quaternary, often have a NLR identified at the genus or even species level, older fossil floras, such as those from the Paleogene and Neogene, are often associated with a NLR at the genus or family level where climate intervals are larger and assumptions about the relative stasis of modern climatic distributions of a genus or family may not be appropriate. As a result, NLR methods are typically restricted to Cenozoic floras, though the methods have sometimes been used on assemblages from the late Cretaceous (e.g., Mosbrugger and Utescher, 1997; Utescher et al., 2014; Fletcher et al., 2014).

Although NLR methods, and in particular CA, have been applied to a large number of Cenozoic floras (e.g., Utescher et al., 2014), they have recently come under major criticism based on their assumptions about species distributions, the lack of statistical framework, and how climate variables are calculated for past plant communities based on modern plant distributions (Grimm and Potts, 2016). Additionally, there are significant issues with the PFDB, which is used in CA. Studies by Grimm and Denk (2012), Grimm et al. (2015) and Grimm and

Potts (2016) have shown that the MAT ranges in the PFDB are incorrect when compared to climate stations or WorldClim (Hijmans et al., 2005) and even when using corrected climate data the precision of MAT ranges was between 5-10 °C (Grimm and Denk, 2012). These criticisms raise major questions about the ability of quantitative NLR methods to accurately and precisely reconstruct the paleoclimate of ancient plant communities.

LEAF TRAITS AND ECOLOGY

In addition to a relationship between leaf traits and climate, there are a suite of leaf structural and functional traits that are correlated to each other and to environmental gradients. This covariation of leaf traits is known as the leaf economic spectrum (LES; Wright et al., 2004; Wright et al., 2005; Reich, 2014). The LES is a framework for organizing leaf functional ecology, which reflects a series of trade-offs among leaf traits that are related to carbon balance. Plants on the “fast-return” end of the spectrum, characterized by rapid resource acquisition, typically have a short leaf life-span (less than 12 months), high photosynthetic and respiration rates, low leaf mass per area (M_A), high nutrient concentrations (principally nitrogen and phosphorus), and fast growth rates, while the inverse is true for plants with slow resource acquisition on the “slow-return” end of the spectrum (Reich et al., 1997; Westoby et al., 2002; Diaz et al., 2004; Wright et al., 2004; Wright et al., 2005; Reich, 2014). The interrelationships between these traits are largely independent of phylogeny in seed plants (Ackerly and Reich, 1999), have been observed in all vascular plant groups (Wright et al., 2004; Karst and Lechowicz, 2007; Peppe et al., 2014) and probably reflect evolutionary trade-offs in leaf design to maximize resource acquisition vs. performance for the environment in which a plant is living (Shipley et al., 2006).

Recently, researchers have suggested that venation networks are linked to the LES either as the underlying determinant of leaf mass per area, leaf life-span, carbon assimilation

rate, and nitrogen concentration ("vein origin" hypothesis; Blonder et al., 2011; Blonder et al., 2013; Blonder et al., 2014a) or that venation networks are only one axis of many that determine hydraulic conductance and carbon economics, and in turn the plant's relative growth rate ("flux trait network" hypothesis; Sack and Scoffoni, 2013; Sack et al., 2013; Sack et al., 2014). Regardless of which hypothesis is correct, both highlight the importance of vein networks in the LES.

While in modern leaves these LES variables are easily measured, they cannot be directly measured in fossil leaves. Instead a series of different proxies based on features that are measureable in fossil leaves, such as leaf area, petiole width, and vein density, have been developed to estimate leaf mass per area M_a , leaf life-span (LLS), carbon assimilation rate, and respiration rate (e.g., Brodribb et al., 2007; Royer et al., 2007; Boyce et al., 2009; Brodribb and Feild, 2010; Royer et al., 2010; Blonder et al., 2011; Feild et al., 2011b; Royer et al., 2012; Sack and Scoffoni, 2013; Sack et al., 2013; Blonder and Enquist, 2014; Peppe et al., 2014; Sack et al., 2014). These reconstructed LES variables can then be used to reconstruct aspects of the paleoecology of the fossil plant (e.g., leaf life-span, hydraulic conductance), as well as other features of the ecosystem and environment in which the plant lived. Since the majority of these methods are developed based on relationships within the LES, they are applicable across a variety of plant groups and can be used throughout the geologic record (e.g., Royer et al., 2007; Boyce et al., 2009; Brodribb and Feild, 2010; Royer et al., 2010; Blonder et al., 2011; Feild et al., 2011b; Royer et al., 2012; Blonder et al., 2014b; Crifo et al., 2014; Peppe et al., 2014), though some aspects of the LES, such as carbon assimilation and respiration rates are probably heavily dependent on past levels of atmospheric CO_2 and O_2 (e.g., De Boer et al., 2012; McElwain et al., 2016).

Methods of paleoecological reconstruction

Most leaf economic spectrum traits cannot be directly measured in fossils. However, a proxy for M_a , which is a core LES character and also correlates strongly with leaf thickness and leaf life-span (Wright et al., 2004; Royer et al., 2012), has been developed that is applicable to fossil plants (Royer et al., 2007; Royer et al., 2010; Peppe et al., 2014). The method uses the scaling relationship between petiole width (PW), leaf area (A), and M_a . The relationship between PW and A to M_a is based on the biomechanics of the leaves since heavier leaves need more support, which necessitates larger, thicker petioles (Royer et al., 2007; Royer et al., 2010; Peppe et al., 2014). Leaves with high M_a are more commonly evergreen and thicker, which in addition to providing structural support also allows long-term nutrient transport (Wright et al., 2004).

Proxies for leaf mass per area have been developed for all woody dicot angiosperms (Royer et al., 2007), herbaceous angiosperms and broadleaf gymnosperms (Royer et al., 2010), and ferns (Peppe et al., 2014). Each of these groups has significantly different scaling relationships between PW and A to M_a and the relationships in angiosperms and broadleaf gymnosperms are explained by a different biomechanical model than ferns. The relationships between area normalized PW and M_a in angiosperms and broadleaf gymnosperms are best explained by modeling a leaf as a pole supporting a singular mass and assumes that the cross-sectional area of the petiole is proportional to leaf mass (Royer et al., 2007; Royer et al., 2010). The relationships between PW and A to M_a in ferns are best explained by a cantilever beam model that assumes the petiole width and length are independent, that petiole shape is relatively invariant, and that the leaf mass is proportional to the flexural rigidity of the entire petiole (Peppe et al., 2014).

The M_a of fossil leaves can be used to estimate a number of paleoecological variables. First, greater M_a is correlated with longer leaf life-span and can be used to reconstruct the leaf life-span of a fossil flora (Royer et al., 2007; Royer et al., 2010; Peppe et al., 2014). Fossil

leaves with a $M_a < \sim 87 \text{ g m}^{-2}$ can be broadly categorized as deciduous and those with a $M_a > \sim 129 \text{ g m}^{-2}$ can be broadly categorized as evergreen, with the transition between predominately deciduous to predominately evergreen occurring at $\sim 111 \text{ g m}^{-2}$ (Royer et al., 2007). The variance in M_a and leaf life-span can also be used to infer seasonality in paleoecosystems with greater variance in M_a in plant populations related to greater seasonality (Wright et al., 2005). Additionally, the distribution of M_a of a flora also appears to be environmentally specific (Royer et al., 2010), suggesting that the distribution of M_a in a fossil flora can be compared to modern distributions and used as a proxy for environment. Finally, M_a correlates with leaf nitrogen content (Royer et al., 2005), and could potentially be used as a proxy for percent nitrogen, which could be used to infer nutrient cycling in fossil forest ecosystems.

The interaction of plants and their herbivores has a long geologic record and can be used to infer a variety of ecological variables (Labandeira and Currano, 2013). Reconstructions of M_a combined with measurements of insect-plant interactions via their feeding traces can be used to reconstruct aspects of plant ecology such as nutrient content and ecosystem disturbance (Royer et al., 2007; Currano et al., 2008; Currano et al., 2011). Leaves with greater M_a have lower diversity, lower density, and lower area removed by insect herbivores when compared to leaves with low M_a (Coley, 1983; Royer et al., 2007). This relationship between insect damage and M_a is probably because leaves with high M_a are typically thicker and/or tougher, possess a greater amount and concentration of chemical deterrents, and have lower leaf nitrogen content, which makes them less nutritious and less palatable for insect herbivores (Coley, 1983; Royer et al., 2007). Additionally, changes in the diversity and density of insect feeding traces can be used to infer large-scale changes in ecology following ecological disturbances, including changes in climate and recovery after mass extinction events (e.g. Wilf et al., 2006; Currano et al., 2008; Currano et al., 2011; Donovan et al., 2016).

Recent studies have suggested a link between vein networks and the LES (Blonder et al., 2011; Blonder et al., 2013; Blonder et al., 2014); however, this remains controversial (e.g.,

Sack and Scoffoni, 2013; Sack et al., 2013; Sack et al., 2014; Li et al., 2015). If there is a relationship between vein networks and the leaf economic spectrum, measurements of vein networks in fossil plants could be used to reconstruct other LES variables, such as leaf life-span and M_a , which in turn would allow for paleoecological reconstruction. These proxies are in development, but offer considerable promise. In addition to its relationship to the LES, vein networks, and specifically vein density, is a proxy for water use efficiency and gas exchange, making it a powerful tool for assessing gas and water exchange capacity of plants (Sack et al., 2005; Sack and Frole, 2006; Brodribb et al., 2007; Boyce et al., 2009; Brodribb and Feild, 2010). For example, angiosperms have much higher vein densities than plants from all other groups, living or extinct, which allows angiosperms to have much higher rates of transpiration (Boyce et al., 2009). This connection between high vein density and high rates of transpiration in angiosperms has been used to infer that the evolution of angiosperms and their increase in maximum leaf vein density through the Cretaceous enabled the evolution and expansion of tropical rain forests, because transpiration rates in other plant groups are too low to maintain the precipitation abundance and evenness necessary for tropical rainforest ecosystems (Boyce et al., 2009; Boyce et al., 2010; Feild et al., 2011a). The distribution of vein densities within a flora differs significantly between canopy and understory plants and between sites with different forest structures (Crifo et al., 2014). Thus, it is possible to infer ancient forest structure, and its constituent understory and canopy taxa, from the range of vein densities within a fossil flora (Crifo et al., 2014).

Shortcomings and limitations of paleoecological methods

Methods of paleoecological reconstruction are very powerful tools for assessing aspects of plant ecology (e.g., leaf life-span, hydraulic conductance) and a ecosystem's environment (e.g., ecosystem disturbance, forest structure); however, these methods are relatively new and have been not been widely applied. The primary reason for this is that they require excellent

preservation of venation (vein density proxies), and the entire leaf area and at least part of the leaf petiole (M_A proxies). Due to taphonomic constraints, these proxies cannot be applied to many fossil floras, or in some cases, can only be applied to the best preserved specimens within a flora such that the reconstructed ecological variables may not be representative of the entire flora. As an example, Blonder et al. (2014b) were only able to analyze <20% of more than 6,000 collected fossil specimens, suggesting the potential for significant taphonomic biases in leaf vein density analyses. Additionally, though there appears to be a relationship between leaf vein density and forest structure (Crifo et al., 2014) and M_A and environment (Royer et al., 2010), these relationships are based on relatively limited datasets with small sample sizes. Thus, it's unclear if these relationships are representative globally and to all ecosystems.

APPLICATION OF PALEOCLIMATE AND PALEOECOLOGICAL PROXIES

Leaf physiognomic methods for reconstructing paleoclimate have been applied hundreds, if not thousands of times to fossil floras from the Cretaceous through the Quaternary, and leaf trait methods for reconstructing paleoecology have begun to be applied to fossil plants through Earth history. The following is a brief example of an application of these methods for reconstructing paleoclimate and paleoecology by Michel et al. (2014) that made it possible to reconstruct the climate and to determine the climatic, environmental, and ecological biome of the fossil site. The study of Michel et al. (2014) documented a diverse assemblage of fossil vertebrates, leaves, and tree stump and root casts and used the fossil data to reconstruct the paleoclimate and paleoenvironment of the Early Miocene R3 fossil site on Rusinga Island, western Kenya. The R3 fossil site is of particular interest because of the co-occurrence of multiple species of Early Miocene catarrhines, including *Dendropithecus macinnesi* and *Ekemboheseloni*, as well as several vertebrate fossil taxa that suggest a more closed environment. Prior to the work of Michel et al. (2014), the paleoenvironment of the site was relatively poorly constrained. Michel et al. (2014) mapped a series of fossil tree stump casts of varying diameter

preserved within the same stratigraphic layer across the R3 site. Based on the density of the tree stump casts across the landscape, they reconstructed the ecosystem as a dense, closed-canopy, multi-storied forest. Abundant fossil leaves were found in a thin mudstone layer stratigraphically directly above the fossil tree stump casts. The flora was made up of 29 morphotypes, which can be considered a rough proxy for biological species (see Ash et al., 1999 and Peppe et al., 2008 for a review of the morphotype method), representing 27 dicotyledonous (dicot) and 2 monocotyledonous angiosperms. The dicots were used to reconstruct the paleoclimate and paleoecology of the site.

PLACE FIGURE 5 ABOUT HERE; WIDTH = ONE PANEL

The mean annual temperature and mean annual precipitation of the site was reconstructed using LMA and LAA, respectively (Fig. 5). Mean annual temperature reconstructed using the LMA regressions of Wolfe (1979), Miller et al. (2006), Kowalski and Dilcher (2003), and Peppe et al. (2011) ranged between 22.6 °C and 34.5 °C (Fig. 5). Mean annual precipitation reconstructed using the LAA regression of Wilf et al. (1998), Gregory-Wodzicki (2000), Jacobs and Herendeen (2004) and Peppe et al. (2011) ranged from 1,394 mm to 2,618 mm (Fig. 5). Wet month precipitation estimates using the method of Jacobs and Herendeen (2004) indicate that there was relatively little precipitation during the dry season. This evidence for seasonality is also supported by analyses of the paleosols at the R3 site. The paleoclimate reconstructions for the site indicate a tropical seasonal forest biome (Fig. 5; Whittaker, 1975). Interestingly, the forest density evidence for the R3 site are very similar to modern tropical seasonal forests that support medium and large bodied primate communities, such as Barro Colorado Island (BCI), Panama and Ituri Forest, Democratic Republic of Congo. Only univariate methods were utilized on the R3 flora because, as discussed above, the leaf physiognomic space of the fossil flora is not captured by the modern DiLP dataset (Fig. 3). This

demonstrates one of the limitations of the existing multivariate methods, and the difficulty of reconstructing the paleoclimate of African fossil floras.

PLACE FIGURE 6 ABOUT HERE; WIDTH = TWO PANELS

Leaf mass per area was reconstructed for seventeen of the twenty seven dicot morphotypes from R3 (Fig. 6, 7). Leaf mass per area reconstructions for the flora indicate that the species were predominantly evergreen, but that there was an important component of deciduous taxa (Fig. 6). The distribution of M_a at the site is most similar to non-riparian sites (Fig. 7), which is unsurprising given the sedimentological and paleosols evidence from the site. The paleoclimate reconstructions for the flora are most similar to BCI site (MAT = 26.5 °C, MAP = 2620 mm), and the distribution of M_a at the sites is similar, though BCI has a higher proportion of species low M_a than the R3 flora (Fig. 7D). The R3 flora is also somewhat similar to the non-riparian, wet tropical rainforest of Buena Vista, Puerto Rico, though the wet tropics site has a larger proportion of species with much higher M_a than reconstructed for the R3 flora (Fig. 7E). Similar to the paleoclimate estimates, the M_a reconstructions for R3 also suggest a non-riparian tropical seasonal forest or tropical rainforest biome.

PLACE FIGURE 7 ABOUT HERE; WIDTH = TWO PANELS

The paleoclimate and paleoecological reconstructions for the R3 fossil site using fossil leaves indicate a tropical seasonal forest biome and a warm and seasonally wet climate (Fig. 5, 6, 7). These results are also in agreement with reconstructions of the forest density and paleoenvironmental reconstructions based on the paleosols at the site and the composition of the vertebrate fauna. Together, the multiproxy evidence presented by Michel et al. (20014) indicates that the R3 fossil locality sampled a widespread, dense, multistoried, closed-canopy

tropical seasonal forest set in a warm and seasonally wet climate. When combined with the primate fossil record from the R3 site, the paleoclimate and paleoecological results of Michel et al. (2014) demonstrate the importance of forested environments in the evolution of early apes in Africa. The Michel et al. (2014) study is an example of the power and utility of combining fossil leaf based estimates of paleoclimate and paleoecology to reconstruct a terrestrial ecosystem, and is a good model for fossil leaf based research focused on terrestrial ecosystem and climate reconstruction.

FUTURE RESEARCH DIRECTIONS

Fossil plants, and particularly fossil leaves, are powerful tools for reconstructing paleoclimate and paleoecology. However, despite the power of the paleoclimate and paleoecology methods that can be applied to fossils, they have important limitations.

One of the most important potential shortcomings of leaf physiognomic methods is the possible influence of phylogeny and life history on leaf trait-climate relationships. Recently, the vertebrate paleontology community has begun to develop a series of trait-based approaches that use relationships between functional traits and environment to reconstruct climate and assess the responses of faunal communities to environmental change called ecometrics (e.g., Eronen et al., 2010a; Eronen et al., 2010b; Polly et al., 2011; Lawing et al., 2012; Polly and Sarwar, 2014; Lawing et al., 2016). These methods have addressed potential issues related to phylogenetic influences on functional traits by resampling techniques and by applying phylogenetic corrections to the datasets (Eronen et al., 2010b; Lawing et al., 2012; Polly and Sarwar, 2014; Lawing et al., 2016). The utilization of these types of methods when revising and developing new leaf physiognomic methods for reconstructing paleoclimate has considerable potential and is an important future research direction. Additionally, as noted above, the leaf physiognomic-climate relationships are different between the Northern and Southern

Hemispheres. The development of new calibration datasets that incorporate more floras from the Southern Hemisphere, and particularly Africa and South America, and from tropical regions will add phylogenetic diversity to the calibration datasets and may make it possible to ascertain the driver behind the hemispheric differences, especially if phylogenetic corrections are applied to the datasets.

Leaf life-span also has an important effect on leaf trait-climate relationships. Royer et al. (2012) found that the incorporation of leaf thickness, deciduousness, and M_A into species-specific leaf physiognomic models reduced the standard errors of the models. However, this result was based on a species-based dataset, instead of a site-based calibration, on which all leaf physiognomic models are based. Thus, it's uncertain if these results are broadly applicable to existing leaf physiognomic models. Using a dataset of taxa from 17 floras from a range of MATs, Blonder and Enquist (2014) demonstrated a relationship between vein density and MAT, which they used to develop a predictive model for MAT. However, the relationships between vein density and MAT were different in temperate and tropical floras, such that they developed one model with different parameter values for temperate floras and tropical floras. Taken together, the results of Royer et al. (2012) and Blonder and Enquist (2014) suggest that the incorporation of functional traits, such as vein density and M_A , into leaf physiognomic models could improve their precision and accuracy and are an interesting research direction to pursue.

In addition to potential shortcomings with the methods, making the measurements necessary to apply paleoclimate and paleoecological proxies can be time consuming and trait scoring can be ambiguous. Recently, there has been a push to develop computer-based algorithms that are automated to measure and score leaf traits and to identify plants using leaves (e.g., Cope et al., 2012; Corney et al., 2012a; Corney et al., 2012b; Price et al., 2012; Green et al., 2014; MacLeod and Steart, 2015; Wilf et al., 2016). Automated measurements of leaf size and shape would eliminate ambiguities in leaf trait scoring, increase scoring throughput, make it easier to measure continuous variables, and potentially help aid in the

identification of fossil plants. The potential of automated or semi-automated leaf trait scoring and identification is an exciting new development that has the potential to revolutionize the way leaf traits are scored and help to significantly improve leaf trait-climate and ecological proxies.

One of the fundamental shortcomings of leaf-based climate reconstruction is that we still do not understand the physiological and/or evolutionary mechanisms that drive the empirical relationships observed between leaf physiognomy and climate. As a result leaf physiognomic proxies are empirically derived and traits used for extrapolation may not have a direct functional link to climate or ecology and/or may be strongly driven by phylogeny and life history. This might lead to biased paleoclimate and paleoecological estimates, particularly in deep time. Research focused on the evolution of leaf form and on the genetic underpinnings of leaf shape and development is making significant strides towards addressing this shortcoming (e.g., Pérez-Pérez et al., 2010; Schmerler et al., 2012; Edwards and Donoghue, 2013; Chitwood et al., 2014; 2016; Dkhar and Pareek, 2014; Rodriguez et al., 2014; Vaughan, 2015; Chitwood and Sinha, 2016; Coneva et al., 2017). A more complete understanding of the genetic controls on leaf size and shape and the drivers of leaf shape evolution will make it possible for us to better understand how environment and climate influence leaf physiognomy, as well as provide a basis for understanding plant species' distributions on climatic gradients. This will allow for the development of phylogenetically and physiologically informed plant-based paleoclimatic and paleoecological proxies, which has the potential to revolutionize the field and our ability to reconstruct ancient climate and ecology.

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FIGURE CAPTIONS

Fig.1. Examples of modern and fossil leaves of woody dicotyledonous angiosperms with entire (A,C) and toothed (B,D) margins. (A) Cleared and stained leaf of *Calophyllum calabea* with an entire margin (NCLC4372). (B) Cleared and stained leaf of *Tilia heterophylla* with a toothed margin (NCLC5403). (C) Unidentified Paleocene fossil leaf from the Fort Union Formation, Williston Basin, North Dakota, USA with an entire margin (YPM52359). Black arrow indicate location of petiolar attachment. (D) *Davidia antiqua*, Paleocene fossil leaf from the Fort Union Formation, Powder River Basin, Montana, USA with a toothed margin (DMNH28307). Large black arrow indicates the leaf's petiole. Small black arrow in upper left indicates one of the leaf's teeth.

Fig. 2. Univariate leaf physiognomic models for estimating mean annual temperature (MAT) and mean annual precipitation (MAP). (A) Relationship between the proportion of untoothed species in a flora and MAT for 1488 globally distributed sites. Linear regression fit shown ($r^2 = 0.43$, $F = 1113$, $P < 0.001$). Data from Wolfe (1979, 1993), Midgley et al. (1995), Wilf (1997), Kennedy, (1998), Jacobs, (1999, 2002), Burnham et al. (2001), Greenwood et al. (2004), Royer et al. (2005), Hinojosa et al. (2006), Aizen and Ezcurra (2008), Su et al. (2010), Peppe et al. (2011), Chen et al. (2014), Yang et al. (2015). (B) Relationship between mean leaf area and MAP for 184 globally distributed sites. Linear regression fit shown ($r^2 = 0.41$, $F = 126$, $P < 0.001$). Data from Wilf et al. (1998), Jacobs (1999, 2002), Gregory-Wodzicki (2000), and Peppe et al. (2011).

Fig. 3. Canonical correspondence analysis plot of the digital leaf physiognomy (DiLP) calibration dataset and fossil sites based on leaf physiognomy from Peppe et al. (2011) with modern biomes mapped onto plot. Extant sites indicated by circles and fossil sites indicated by squares. Site from the Northern Hemisphere are indicated by white symbols and sites from the Southern Hemisphere by gray symbols. The Rusinga R3 fossil site, which is indicated by a red square, falls well outside the leaf physiognomic space of the extant floras in the current DiLP calibration demonstrating a limitation of the applicability of the method.

Fig. 4. Coexistence Approach analysis of the latest Eocene Florissant Fossil Beds flora (Baumgartner and Meyer, 2014). The orange dashed line indicates the estimated coexistence interval using the full range of climate data, while the solid blue line indicates the estimated coexistence interval between the 10-90th percentiles. Both coexistence intervals are limited by *Abies* and *Cathaya*; these MAT intervals are estimated as 13.4 – 18.0 °C (solid line) and 13.9 – 16.2 °C (dashed line). The age of the flora precludes assigning nearest living relatives at the species level and some genera (i.e. *Betula* and *Alnus*) have relatively large climatic ranges for MAT. There are no outliers.

Fig. 5. Climatic reconstruction for the Rusinga R3 fossil site from Michel et al. (2014). Black circle is the average is of all mean annual temperature and mean annual precipitation estimates. Shaded square is the range of all climate estimates. Biomes follow Whittaker (1975). Area shaded in light gray indicates mean annual temperatures higher than recorded today. The dashed lines represent projections of biomes outside of modern climate space.

Fig. 6. Estimated leaf mass per area (M_a) for Rusinga R3 flora and comparison to extant vegetation. (A) M_a and leaf lifespan for 678 species of angiosperms, ferns, and gymnosperms modified from Royer et al. (2010). M_a and leaf lifespan data from Wright et al. (2004). M_a bin is 20 g/m^2 . Gray line at 129 g/m^2 indicates the upper bound of the transition between species whose leaves are predominately deciduous (leaf life-span <12 month) versus those that are predominately evergreen (leaf lifespan >12 months). (B) Estimated M_a for 17 morphotypes from the Rusinga R3 flora showing that the majority of morphotypes were likely evergreen (10 of 17 reconstructed). Errors are 95% prediction intervals. M_a data and morphotypes from Michel et al. (2014).

Fig. 7. Comparison of the reconstructed M_a distribution of the Rusinga R3 flora with extant sites from varying climate biomes and environments. M_a and climate data for extant sites from Peppe et al. (2011). The fossil and extant sites are comprised of exclusively wood dicot angiosperms. The M_a bin size is 20 g/m^2 . (A) Rusinga R3 (replicated in gray in all panels). (B) Connecticut River, near Middletown, Connecticut, USA. (C) Big Hammock Wildlife Refuge Area, Georgia, USA. (D) Pee Dee State Park, South Carolina, USA; (E) Barro Colorado Island, Panama. (F) Buena Vista, Puerto Rico.

Table 1. Leaf physiognomic models for climate from published literature

Method	Reconstructed climate variable	Equation	Region	r^2	n	SE	Authors
LMA	MAT	(1) $\text{MAT} = 0.306\text{E} + 1.141$	East Asia	0.98	34	0.80	(Wolfe, 1979; Wing and Greenwood, 1993)
LMA	MAT	(2) $\text{MAT} = 0.276\text{E} + 1.038$	China	0.79	50	1.90	(Su et al., 2010)
LMA	MAT	(3) $\text{MAT} = 0.223\text{E} + 6.68$	China	0.53	732	3.10	(Chen et al., 2014)
LMA	MAT	(4) $\text{MAT} = 0.2338\text{E} + 4.6321$	Japan	0.74	35	1.87	(Kennedy et al., 2014)
LMA	MAT	(5) $\text{MAT} = 0.314\text{E} + 0.512$	Europe	0.60	1835	1.70	(Traiser et al., 2005)
LMA	MAT	(6) $\text{MAT} = 0.291\text{E} - 0.266$	North, Central America and Japan	0.76	106	3.40	(Wilf, 1997)
LMA	MAT	(7) $\text{MAT} = 0.286\text{E} + 2.240$	North, Central and South America	0.94	9	2.00	(Wilf, 1997)
LMA	MAT	(8) $\text{MAT} = 0.363\text{E} + 2.233$	North America	0.80	10	3.60	(Kowalski and Dilcher, 2003)
LMA	MAT	(9) $\text{MAT} = 0.290\text{E} + 1.320$	North, Central America	0.91	84	-	(Miller et al., 2006)
LMA	MAT	(10) $\text{MAT} = 0.2471\text{E} + 2.3305$	North America	0.79	104	2.63	(Kennedy et al., 2014)
LMA	MAT	(11) $\text{MAT} = 0.250\text{E} + 3.42$	Temperate Northern Hemisphere	0.87	144	2.20	(Wolfe, 1993)
LMA	MAT	(12) $\text{MAT} = 0.275\text{E} + 1.36$	Temperate Northern Hemisphere	0.77	173	3.30	(Gregory-Wodzicki, 2000)
LMA	MAT	(13) $\text{MAT} = 0.249\text{E} + 3.53$	Temperate Northern Hemisphere (alpine excluded)	0.87	144	2.20	(Gregory-Wodzicki, 2000)
LMA	MAT	(14) $\text{MAT} = 0.2475\text{E} + 2.9066$	Northern Hemisphere	0.81	149	2.55	(Kennedy et al., 2014)
LMA	MAT	(15) $\text{MAT} = 0.759\text{E} - 0.013$	New Zealand, the Andes, the Alps	0.57	19	-	(Halloy and Mark, 1996)
LMA	MAT	(16) $\text{MAT} = 0.316\text{E} - 0.059$	South America	0.89	14	1.60	(Gregory-Wodzicki, 2000)
LMA	MAT	(17) $\text{MAT} = 0.385\text{E} - 10.24$	Tropical South America	0.47	30	3.40	(Kowalski, 2002)
LMA	MAT	(18) $\text{MAT} = 0.3825\text{E} - 10.9$	South America (isotherm)	0.73	16	-	(Aizen and Ezcurra, 2008)
LMA	MAT	(19) $\text{MAT} = 0.4236\text{E} - 11.37$	South America (cell)	0.54	16	-	(Aizen and Ezcurra, 2008)
LMA	MAT	(20) $\text{MAT} = 0.2603\text{E} + 1.31$	South America	0.82	51	2.80	(Hinojosa et al., 2011)

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LMA	MAT	(21) $\text{MAT} = 0.4396\text{E} - 8.3637$	South America	0.93	14	1.73	(Kennedy et al., 2014)
LMA	MAT	(22) $\text{MAT} = 0.2399\text{E} + 3.6916$	Southern Africa	0.86	25	-	(Stear et al., 2010)
LMA	MAT	(23) $\text{MAT} = 0.1094\text{E} + 9.5173$	Southern Africa	0.37	14	2.30	(Kennedy et al., 2014)
LMA	MAT	(24) $\text{MAT} = 0.270\text{E} - 2.120$	Australia	0.63	74	-	(Greenwood et al, 2004)
LMA	MAT	(25) $\text{MAT} = 0.0862\text{E} + 17.6547$	Pacific Islands	0.35	6	1.33	(Kennedy et al., 2014)
LMA	MAT	(26) $\text{MAT} = 0.0571\text{E} + 16.4785$	Australia	0.06	21	2.34	(Kennedy et al., 2014)
LMA	MAT	(27) $\text{MAT} = 0.0239\text{E} + 10.561$	New Zealand	0.02	35	1.69	(Kennedy et al., 2014)
LMA	MAT	(28) $\text{MAT} = 0.257\text{E} - 1.8412$	Southern Hemisphere	0.40	90	4.83	(Kennedy et al., 2014)
LMA	MAT	(29) $\text{MAT} = 0.204\text{E} + 4.600$	North and South America, Japan, and Oceania	0.58	92	4.80	(Peppe et al., 2011)
LMA	MAT	(30) $\text{MAT} = 0.2039\text{E} + 3.6562$	Oceania, Japan, North America, South America, Southern Africa	0.57	239	3.97	(Kennedy et al., 2014)
LMA	MAT	(31) $\text{MAT} = 0.194\text{E} + 5.884$	Global	0.42	1488	4.54	this study
LAA	MAT	$\text{MAT} = 0.115\text{A} + 1.192$	New Zealand, the Andes, the Alps	0.87	19	-	(Halloy and Mark, 1996)
DiLP	MAT	$\text{MAT} = 0.210\text{E} + 42.296\text{D} - 2.609\text{I} - 16.004$	North and South America, Japan, and Oceania	0.70	92	4.00	(Peppe et al., 2011)
MLR	MAP	(1) $\text{MAP} = 167.948(\text{apex attenuate}) + 377.735(\text{mesophyll2}) + 11.489$	Temperate Northern Hemisphere	0.50	74	57.96	(Wing and Greenwood, 1993)
modified LAA	MAP	(2) $\text{MAP} = 6.18(\text{mesophyll1} + \text{mesophyll2}) + 47.5$	Temperate Northern Hemisphere	0.44	74	-	(Wilf et al., 1998)
LAA	MAP	(3) $\text{InMAP} = 0.484(\text{MnA}) + 1.78$	Temperate Northern Hemisphere	0.61	144	0.47	(Gregory-Wodzicki, 2000)
LAA	MAP	(4) $\text{InMAP} = 0.548(\text{MnA}) + 0.786$	North, Central and South America, Africa	50.0 0	50	0.36	(Wilf et al., 1998)
LAA	MAP	(5) $\text{InMAP} = 0.298(\text{MnA}) + 2.64$	Bolivia	0.52	12	0.22	(Gregory-Wodzicki, 2000)
LAA	MAP	(6) $\text{InMAP} = 1.369(\text{mesophyll1} + \text{mesophyll2}) + 3.982$	Africa and Bolivia	0.83	42	0.18	(Jacobs, 2002)
LAA	MAP	(7) $\text{InMAP} = 0.309(\text{MnA}) + 2.566$	Tropical Africa and Bolivia	0.73	42	-	(Jacobs and Heredeem, 2004)
MLR	MAP	(8) $\text{InMAP} = 0.6903(\text{mesophyll}) + 0.7059(\text{apex acuminate}) + 0.884(\text{apex acute}) + 0.7542\text{E} + 4.9415$	Africa	0.79	30	0.19	(Jacobs, 1999)

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MLR	MAP	(9) $\ln\text{MAP} = 1.274(\text{mesophyll1} + \text{mesophyll2}) - 1.013(\text{shape elliptic}) + 5.198$	Africa	0.81	30	0.18	(Jacobs, 2002)
modified LAA	MAP	(10) $\ln\text{MAP} = 1.321(\text{mesophyll1} + \text{mesophyll2}) + 4.018$	Africa	0.76	30	0.20	(Jacobs, 2002)
LAA	MAP	(11) $\ln\text{MAP} = 0.321(\text{MnA}) + 2.476$	Africa	0.66	30	0.24	(Jacobs, 2002)
LAA	MAP	(12) $\ln\text{MAP} (<260 \text{ cm}) = 0.354(\text{MnA}) + 2.167$	Tropical Africa, Bolivia, tropical to subtropical Western Hemisphere	0.71	79	-	(Jacobs, 2002)
LAA	MAP	(13) $\ln\text{MAP} = 0.429(\text{MnA}) + 1.705$	Western Hemisphere, Bolivia, Africa	0.71	92	0.34	(Jacobs, 2002)
LAA	MAP	(14) $\text{MAP} = 0.001\text{A} + 0.551$	New Zealand, the Andes, the Alps	0.71	19	-	(Halloy and Mark, 1996)
LAA	MAP	(15) $\ln\text{MAP} = 0.283(\text{MlnA}) + 2.92$	North and South America, Japan, and Oceania	0.23	92	0.61	(Peppe et al., 2011)
LAA	MAP	(16) $\ln\text{MAP} = 0.346(\text{MlnA}) + 2.404$	global	0.41	184	0.93	this study
DiLP	MAP	$\ln\text{MAP} = 0.298(\text{MlnA}) - 2.717(\ln\text{P}) + 0.279(\ln\text{I}) - 3.033$	North and South America, Japan, and Oceania	0.27	92	0.60	(Peppe et al., 2011)
MLR	GSP	(1) $\text{GSP} (<222 \text{ cm}) = 141.368(\text{mesophyll2}) - 136.340(\text{L:W} <1) + 93.936(\text{shape elliptic}) - 79.774(\text{base round}) - 52.386(\text{teeth acute}) + 48.050$	Temperate Northern Hemisphere	0.80	74	16.00	(Gregory and McIntosh, 1996)
MLR	GSP	(2) $\text{GSP} = -3.393(\text{leptophyll2}) + 2.40(\text{apex attenuate}) - 2.671(\text{base cordate}) + 2.360(\text{L:W } 2-3) + 3.122(\text{L:W } 3-4:1) + 31.6$	Temperate Northern Hemisphere (alpine excluded)	0.80	144	-	(Wiemann et al., 1998)
MLR	GSP	(3) $\text{GSP} (<222 \text{ cm}) = 1.60(\text{apex attenuate}) + 2.80(\text{L:W } 2-3) - 45.2$	Temperature Northern Hemisphere (alpine excluded)	0.63	144	27.00	(Gregory-Wodzicki, 2000)
MLR	Wet months precipitation	(1) $\ln \text{Wet Ppn} = 0.8368(\text{mesophyll}) + 0.819(\text{apex acuminate}) + 1.1718(\text{apex acute}) + 0.8246(\text{no teeth}) + 4.4993$	Africa	0.80	30	0.22	(Jacobs, 1999)
modified LAA	Wet months precipitation	(2) $\ln \text{Wet Ppn} = 1.546(\text{mesophyll1} + \text{mesophyll2}) + 6.112$	Africa	0.78	30	0.22	(Jacobs, 2002)
modified LAA	Wet months precipitation	(3) $\ln \text{Wet Ppn} = 1.601(\text{mesophyll1} + \text{mesophyll2}) + 3.777$	Africa and Bolivia	0.83	42	0.21	(Jacobs, 2002)

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modified LAA	Wet months precipitation	(4) $\ln \text{Wet Ppn} = 0.367(\text{MnA}) + 2.07$	Tropical Africa and Bolivia	0.75	42	-	(Jacobs and Heredeem, 2004)
MLR	Wet months precipitation	$3\text{-WET} = 110.841(\text{apex attenuate}) + 320.457 (\text{L:W } 2\text{-}3\text{:}1) + 179.775(\text{mesophyll2}) - 172.859$	Temperate Northern Hemisphere	0.58	74	47.23	(Wing and Greenwood, 1993)
MLR	Dry months precipitation	$3\text{-DRY} = 45.54(\text{apex attenuate}) + 38.186(\text{L:W } 2\text{-}3\text{:}1) - 24.489$	Temperature Northern Hemisphere	0.55	74	8.91	(Wing and Greenwood, 1993)

LMA = leaf margin analysis, LAA = leaf area analysis, MLR = multiple linear regression model, DiLP = digital leaf physiognomy, MAT = mean annual temperature, MAP = mean annual precipitation, GSP = growing season precipitation, wet months precipitation = precipitation during the three wettest months of the year, dry monts precipitation = precipitation during the three driest months of the year, E = percent of woody dicots with entire margins, A = leaf area, D = Feret's diameter ratio, I = number of teeth: internal perimeter, P = perimeter ratio, MnA = average leaf area of all dicot species

Table 2. Leaf mass per are models for woody dicot angiosperms, herbaceous angiosperms, broadleaf gymnosperms, and ferns

Taxonomic Group	Model	<i>a</i>	<i>b</i>	<i>r</i>²	Authors
woody dicot angiosperms	$\log(M_A) = a + b\log(PW^2/A)$	3.07	0.382	0.55	Royer et al. (2007)
herbaceous angiosperms	$\log(M_A) = a + b\log(PW^2/A)$	3.015	0.3076	0.44	Royer et al. (2010)
broadleaf gymnosperms	$\log(M_A) = a + b\log(PW^2/A)$	2.245	0.2204	0.32	Royer et al. (2010)
ferns	$\log(M_A) = a + b\log(PW^4/A)$	4.207	0.252	0.44	Peppe et al. (2014)

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