Quantification of large uncertainties in fossil leaf paleoaltimetry

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[1] Estimates of paleoelevation potentially constrain geodynamic models of continental deformation and inform interpretations of landscape and climate evolution. One widely used, paleobotanical approach reconstructs paleoelevation from the difference in estimated atmospheric enthalpy between a known sea level and a targeted, coeval, elevated fossil floral site. Enthalpy is estimated using Climate-Leaf Analysis Multivariate Program (CLAMP) on 31 leaf size and shape variables that have been calibrated in living forests. Errors related to CLAMP are significantly greater than often reported, and there are many sources of large potential error related to this method that are either difficult to quantify or unquantifiable and are thus not documented. Here, we quantify one significant bias, toward underestimation of leaf area in the CLAMP data set (~50%), that affects all CLAMP climate estimates, including enthalpy. Crucially, errors in paleoelevation when the leaf size bias is included are in the range of ±2 km or more, at least 2 times the previous estimates, and exceeding the plausible paleoelevations of many fossil sites. Previously published paleoelevations derived from this technique are unlikely to be accurate either in magnitude or in estimated error. **Citation:** Peppe, D. J., D. L. Royer, P. Wilf, and E. A. Kowalski (2010), Quantification of large uncertainties in fossil leaf paleoaltimetry, *Tectonics*, *29*, TC3015, doi:10.1029/2009TC002549.

1. Introduction

[2] There is considerable interest in constraining past elevations to refine interpretations of climatic, biotic, tectonic, and geomorphic evolution. Although many proxies for past elevations have been proposed, most have large (>1 km) or unconstrained errors, and there is often extreme disparity between independent estimates from the same sites [e.g., *England and Molnar*, 1990; *Molnar and England*, 1990; *Meyer*, 1992, 2001; *Chamberlain et al.*, 1999; *Garzione et al.*, 2000; *Gregory-Wodzicki*, 2000b; *Rowley et al.*, 2001; *Sahagian et al.*, 2002; *McElwain*, 2004; *Mulch et al.*, 2004;

Ghosh et al., 2006; *Kohn and Dettman*, 2007; *Riihimaki and Libarkin*, 2007; *Rowley*, 2007; *Ehlers and Poulsen*, 2009].

[3] Traditionally, paleobotanists estimated paleoelevation using mean annual temperature (MAT) estimates for two fossil floral sites (a sea level and a target, elevated site) that were coeval and from the same paleolatitude and region [e.g., *Axelrod*, 1965, 1968, 1997; *Gregory and Chase*, 1992; *Meyer*, 1992, 2001, 2007; *Wolfe*, 1992; *Gregory*, 1994; *Gregory-Wodzicki*, 2000b; *Gregory and McIntosh*, 1996; *Gregory-Wodzicki et al.*, 1998]. The difference in temperatures between the two sites was assumed to be due to the elevation difference, and present-day lapse rates were used to estimate the paleoelevation of the target site. However, modern lapse rates of MAT vary geographically from <4.0°C km^{-1} to >8.0°C km^{-1}, which can result in elevation estimates that differ by more than a factor of 2 [*Meyer*, 1992, 2007; *Wolfe*, 1992]. Furthermore, increases or decreases in temperatures associated with regional climate change during evolution of mountain belts can considerably affect elevation estimates [*Ehlers and Poulsen*, 2009].

[4] Because of the large geographic variation in MAT lapse rates, *Forest et al.* [1995, 1999] developed a model that uses moist static energy to estimate paleoelevation from fossil leaves. They argued that moist static energy has three key advantages over MAT lapse rates for estimating paleoelevation: first, unlike the MAT lapse rates model, it has a theoretical basis; second, moist static energy is conserved along air masses and thus is usually constant along latitude; and third, because moist static energy is constrained by thermodynamics, moist enthalpy, which is the combination of internal and latent heat energies, should only vary with altitude unlike temperature lapse rates, which vary considerably spatially and temporally due to variations in water vapor content. The *Forest et al.* [1995, 1999] model uses the difference between moist enthalpy estimates (which are related to moist static energy, see equation (1)) derived from leaves (living or fossil) at a sea level site and at a target site. The method estimates enthalpy using Climate-Leaf Analysis Multivariate Program (CLAMP) [*Wolfe*, 1993, 1995; *Wolfe and Spicer*, 1999], which utilizes a multivariate data set of modern foliar physiognomy (i.e., leaf size and shape characters) to predict climatic variables such as enthalpy (*H*), mean annual temperature (MAT), specific humidity (*q*), and growing season precipitation (GSP).

[5] This approach, which we will refer to as the paleoenthalpy method, is considered by many to be one of the most precise ways to estimate paleoelevation, with errors based on the internal variance in the calibration data of ±<1 km [*Forest et al.*, 1995, 1999; *Forest*, 2007]. It has been used to estimate Eocene and Oligocene elevations in the western United States [*Forest et al.*, 1995; *Gregory-Wodzicki*, 1997; *Wolfe et al.*, 1998], Miocene elevations of the U.S. Basin and Range

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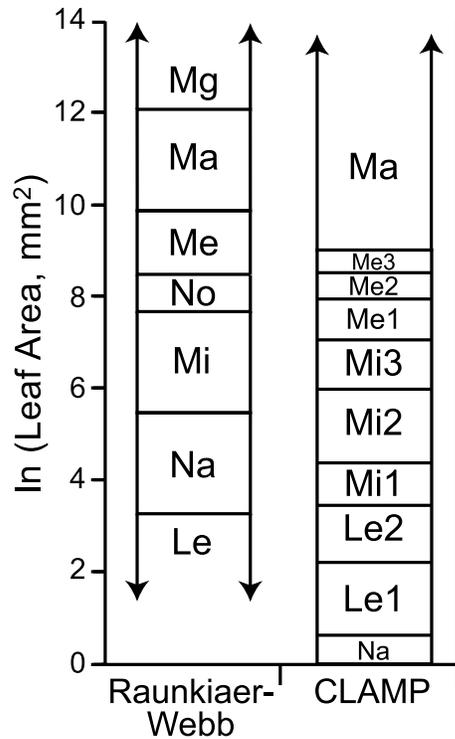
Figure 1. Two systems of leaf classifications shown on a natural log scale: Raunkiaer-Webb [*Raunkiaer*, 1934; *Webb*, 1959] and CLAMP [*Wolfe*, 1993; R. A. Spicer, 2009] (modified from *Wilf et al.* [1998]). CLAMP sizes were digitally measured from template by R. A. Spicer (2009). Le, leptophyll; Na, nanophyll; Mi, microphyll; No, notophyll; Me, mesophyll; Ma, macrophyll; Mg, megaphyll. Note that (1) the largest CLAMP category is a medium-sized leaf [*Raunkiaer*, 1934; *Webb*, 1959] and yet there are no leaves of this size category in the CLAMP data set [*Wolfe*, 1993; R. A. Spicer, 2009] and (2) the extreme compression of the three CLAMP "mesophyll" categories, making scoring error much more likely.

Province [*Wolfe et al.*, 1997], and, in a hybrid form, Miocene elevation of the Tibetan Plateau [*Spicer et al.*, 2003]. The resulting estimates, many of which are much higher than previously thought for the areas studied, have been extensively discussed for their impacts on tectonic, paleoclimatic, and paleontological interpretations [e.g., *House et al.*, 1998, 2001; *Dettman and Lohmann*, 2000; *Hay et al.*, 2002; *Morrill and Koch*, 2002; *Currie et al.*, 2005; *Wang et al.*, 2005; *Horton and Chamberlain*, 2006; *McMillan et al.*, 2006; *Crowley et al.*, 2008; *Davis et al.*, 2009].

[6] The relationship between leaf area and moisture variables, such as precipitation and humidity, has long been noted [*Raunkiaer*, 1934; *Webb*, 1959; *Givnish*, 1984; *Wolfe*, 1993, 1995; *Wilf et al.*, 1998]; however, the largest leaf size category in the CLAMP scoring system is a medium-sized leaf [e.g., *Raunkiaer*, 1934; *Webb*, 1959; *Wilf et al.*, 1998; *Jacobs*, 2002] (Figure 1) and large leaves appear not to be scored in the CLAMP data set [*Wilf et al.*, 1998, 1999]. The bias toward smaller leaves suggests that CLAMP is insensitive to varia-

tion in the upper range of leaf size, and that CLAMP incorrectly estimates climate variables related to moisture (i.e., H, q, GSP) [*Wilf et al.*, 1998, 1999]. This implies that fossil sites measured following CLAMP methodology [e.g., *Wolfe et al.*, 1997; *Kennedy et al.*, 2002; *Spicer et al.*, 2003] would also be variably biased to underestimate leaf area, and thus also incorrectly estimate climate variables. This bias, in addition to many previously documented sources of error discussed in section 3, suggests that the errors associated with the paleoenthalpy method, affecting many published paleoeolevations [e.g., *Forest et al.*, 1995; *Gregory-Wodzicki*, 1997; *Wolfe et al.*, 1997, 1998; *Spicer et al.*, 2003], are considerably larger than ±<1 km as advocated by *Forest et al.* [1999] and *Forest* [2007].

2. Paleoenthalpy Paleoaltimetry Method

[7] *Forest et al.* [1995, 1999] and *Forest* [2007] fully describe the enthalpy paleoaltimetry method. Briefly, moist static energy (h, J kg^{-1}) is the sum of moist enthalpy (H, kJ kg^{-1}) and the gravitational potential energy per unit mass (gZ), where g is gravitational acceleration (J m^{-1} kg^{-1}) and Z is altitude (m):

$$h = H + gZ \qquad (1)$$

The derivation of H is

$$H = c'_p T + L_v q \qquad (2)$$

where c'_p is the specific heat capacity at constant pressure of moist air (J kg^{-1} K^{-1}), T is temperature (K), L_v is the latent heat of vaporization of water (J kg^{-1}), and q is specific humidity (g kg^{-1}); c'_p is derived from two constants, with a slight adjustment for specific humidity (q). The L_v term also is derived from constants, with a minor adjustment for temperature (T). Thus, enthalpy is a function of temperature and specific humidity, and moist static energy is a function of enthalpy and altitude.

[8] The method assumes that moist static energy does not vary significantly across a region with longitude (including in the deep past). Thus, if the enthalpies for two coeval sites (a sea level and a higher elevation site) within the same latitudinal band are known, equations (1) and (2) can be solved for altitude (Z):

$$Z = \frac{H_{sealevel} - H_{high}}{g} \qquad (3)$$

A paleoelevation estimate is thus wholly dependent on the two enthalpy estimates (equation (3)), each derived from a fossil leaf assemblage with a temperature and specific humidity component (equation 2).

3. Climate-Leaf Analysis Multivariate Program

[9] Enthalpy is estimated with CLAMP, which uses a multivariate calibration data set composed of 31 categorical leaf size and shape characters, each measured for a site as the among-species average percentage of woody dicotyledonous

angiosperms that have the character. The method is currently calibrated for extant vegetation collected from 144 sites with associated climate data [*Wolfe*, 1993, 1995; *Wolfe and Spicer*, 1999; R. A. Spicer, CLAMP, climate leaf analysis multivariate program, September 2008 to May 2009, available at http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html, updated 1 May 2009, hereafter referred to as R. A. Spicer, 2009]. The leaf size and shape information and the climate data are processed together using canonical correspondence analysis (CCA) [*Wolfe*, 1995]. The resultant eigenvectors for the climate and leaf physiognomic variables are projected onto the major axes of variation [*Wolfe*, 1993, 1995]. These axes roughly correlate with temperature (first axis) and moisture (second axis) [*Wolfe*, 1993, 1995]. For example, the vectors for MAT and the leaf character state "untoothed margins" are closely aligned (i.e., untoothed leaf margins correlate to warm MATs), as are the character states for leaf size and climatic variables related to moisture such as GSP, relative humidity, and q (i.e., large leaf size correlates to high levels of moisture) [*Wolfe*, 1993, 1995]. A second-order polynomial fit for a climate variable, such as H, to the eigenvector scores from the leaf size and shape character scores is then used to develop a predictive formula for the given climate parameter that can be used on a fossil leaf sample [*Wolfe*, 1995].

[10] Designed for comparisons of species data and environmental variables [*ter Braak*, 1986; *ter Braak and Prentice*, 1988], CCA is attractive for evaluating the relationship between climate and leaf physiognomic characters. However, a fundamental assumption of CCA is that the variables are unimodally distributed; the method is prone to spurious results if characters are distributed in more complex ways, such as bimodally [*ter Braak*, 1986]. Although there may be reasons to assume that some leaf physiognomic characters have unimodal distributions along environmental gradients, this assumption is probably invalid for some characters such as leaf apices [*Green*, 2006]. We tested this assumption by plotting the distributions of the 31 character states for the 144 CLAMP sites and found that the character distributions were usually not unimodal (Figure S1 in the auxiliary material).[1] Thus, CCA may not be the most appropriate technique for predicting climate from leaf physiognomy.

[11] Several additional problems with CLAMP are well documented. In most cases, the sources of error in CLAMP are potentially large but are either unquantified or unquantifiable in terms of their effect on climate and elevation estimates. Below we review several of these sources of error.

[12] First, many of the CLAMP character states are at least partly ambiguous, and the scoring procedure is not sufficiently well defined that different investigators can reproduce the same scores from the same leaves, even for apparently straightforward characters [*Wilf*, 1997; *Wiemann et al.*, 1998; *Green*, 2006]. Four examples highlight this issue: (1) *Wilf* [1997] and *Wolfe* [1993] scored several characters from the same leaves from a site (Barro Colorado Island, Panama) differently; (2) one leaf base character from CLAMP was subject to a blind test with eight paleobotanists and was found

to be unreliable [*Wilf*, 1997]; (3) *Wilf et al.* [1998, 1999] noted that CLAMP samples apparently did not include large leaves, resulting in a bias toward smaller leaf area scores; and (4) leaf size categories used in CLAMP, which were defined using hand-drawn overlay templates without assigned numerical values [*Wolfe*, 1993], have been measured by different researchers to have at least three different sets of values [*Wilf et al.*, 1998; *Gregory-Wodzicki*, 2000a; *Jacobs*, 2002].

[13] Second, CLAMP characters are discrete and categorical, and thus they are likely to be less precise than continuous measurements. For example, continuous variables such as tooth size, number of teeth, and area:perimeter ratios correlate significantly with temperature [*Huff et al.*, 2003; *Royer et al.*, 2005]; however, CLAMP cannot differentiate between leaves with contrasting numbers and sizes of teeth, does not measure area accurately (see section 5.1), and does not quantify perimeter.

[14] Third, some of the CLAMP characters correlate very weakly to climate and/or lack any physiological explanations for climate causality. A tacit assumption of CLAMP is that all leaf size and shape variables are informative for all climate variables; this assumption has not been tested or validated. Phylogenetic signal from inheritance of leaf morphological traits may be equally, or much more important than climate selection in many cases [*Jordan*, 1997; *Doyle*, 2007; *Little et al.*, 2008]. This is particularly important because fossil floras compositionally resemble extant floras less and less going back in time, and there is differential speciation and extinction in, for example, obligately toothed and untoothed lineages for reasons unrelated to climate, altering the empirical correlations observed today. Finally, topographically low riparian, wetland, and lakeshore vegetation, which comprises the closest environmental analogs for most fossil leaf deposits, has been observed to have a significantly higher prevalence of toothed species than adjacent forests, biasing temperature estimates made using leaf teeth characters [e.g., *Burnham et al.*, 2001; *Kowalski and Dilcher*, 2003; *Greenwood*, 2005; *Royer et al.*, 2009].

[15] In sum, the noise associated with the CLAMP leaf character states and their scoring probably exceeds the potential gain in climate signal from the numerous (31) leaf size and shape characters that must be measured. Many studies have documented that climate estimates made using CLAMP are no better than, and are often poorer than, estimates made using univariate methods [e.g., *Wilf*, 1997; *Wiemann et al.*, 1998; *Gregory-Wodzicki*, 2000a; *Kowalski*, 2002; *Kowalski and Dilcher*, 2003; *Liang et al.*, 2003; *Royer et al.*, 2005; *Dilcher et al.*, 2009].

[16] The CLAMP method has primarily been used to estimate MAT and GSP [e.g., *Kennedy et al.*, 2002]. *Forest et al.* [1999] suggested that CLAMP could be used to estimate H either by using the leaf size and shape eigenvector scores directly, or by using equation (2) to calculate enthalpy using the MAT and q estimates made by CLAMP. In both cases, estimated H is strongly climate dependent and relies on the precision of the foliar signals for MAT and q [*McElwain*, 2004]. The MAT estimate is strongly influenced by the leaf margin (i.e., presence or absence of leaf teeth; absence of teeth correlates with warmth), leaf size (correlates with warmth), and emarginate (notched) apices (presence of char-

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[1]Auxiliary materials are available in the HTML. doi:10.1029/2009TC002549.

acter correlates with warmth in CLAMP) [*Wolfe*, 1993, 1995; *Forest et al.*, 1999]. The q estimate is strongly positively dependent on leaf size, attenuate apices, and long narrow leaf shape [*Forest et al.*, 1999]. Thus, because H is dependent on both MAT and q, its estimate is strongly affected by leaf margin and size, and by the other features listed.

[17] The paleoenthalpy method presently does not account for any of the problems with CLAMP discussed above. Each of these issues probably significantly affects both the climate variable estimates made using CLAMP and any paleoelevation inferences. In addition, there are other important uncertainties associated with estimating paleoelevation from fossil floras (see discussion by *McMillan et al.* [2006]), such as the currently untestable but key assumption that enthalpy did not vary with longitude in the past, and the near impossibility of constraining two fossil floras, separated by distance, as precisely coeval. Fossil floras are typically dated to ca. 10^5–10^6 year precision, but short-term, orbitally forced climatic variations are significant and occur on much shorter time scales of 10^4–10^5 years [e.g., *Zachos et al.*, 2001]. For example, to estimate the Miocene elevation of the southern Tibetan Plateau, *Spicer et al.* [2003] compared the estimated enthalpy of low elevation Miocene floras from Japan with a target ~15 Ma fossil flora from Tibet. However, in addition to unknown and unquantified errors associated with comparing (via a climate model) the temperatures and enthalpies of floras that are more than 3000 km apart and widely separated in latitude, one of the Japanese floras (Noroshi) is significantly older than 15 Ma, with published isotopic age determinations indicating ages of ~16–22 Ma, and most probably >17 Ma (unit 2 of *Kano et al.* [2002] (also K. Kano, personal communication, 2003)). The age mismatch with the Tibetan sample is especially problematic during a time of significant regional environmental change [*Kano et al.*, 2002] and global climate change [e.g., *Zachos et al.*, 2001].

[18] Although the error sources reviewed above are potentially quite large, they are also for the most part unquantified or unquantifiable in terms of the effect on elevation estimates. Herein, for the first time we quantify the effect of the leaf area bias, finding that it alone has a major impact on climate estimates made using the CLAMP methodology and on paleoelevation estimates made using the paleoenthalpy approach. Although in theory this leaf area bias could be corrected with significant effort, our view is that its magnitude is representative of the many other sources of error that cannot be quantified or eliminated, and thus we do not recommend further use of the CLAMP paleoenthalpy method.

4. Materials and Methods

[19] The 58 extant floras used in this study (Tables 1 and S1) come from three sources: 38 sites from the CLAMP data set, 3 sites sampled in central Connecticut, and 17 sites from the eastern United States and Panama published by *Royer et al.* [2005]. The 38 CLAMP sites were chosen from the 144 floras in the CLAMP data set primarily for collection quality and diversity in geographic location and climate space. The collections, made by Jack Wolfe and collaborators [see *Wolfe*, 1993], are currently housed in the Division of Paleobotany, National Museum of Natural History, Smith-

sonian Institution, Washington, DC. Each site in our data set is composed of between 16 and 53 woody dicotyledonous species. For each site, a subsample of 1–3 leaves (or leaflets in the case of compound leaves) per species with complete or nearly complete margins was digitally photographed and the leaf areas calculated using Image-J (http://rsbweb.nih.gov/ij/) following the protocols of *Huff et al.* [2003] and *Royer et al.* [2005]. The grand mean of the average leaf areas for each species at a site was recorded as the site-mean leaf area. Using the digitally measured leaf areas, we also determined the CLAMP size category (R. A. Spicer, 2009) scores for each site. To do this, we determined the proportion of species that had digitally measured leaf areas that fell between the minimum and maximum leaf area of each size category and thus turned our continuous leaf area measurements into categorical, leaf area scores.

[20] The leaf areas as published for these same 38 sites were taken directly from the CLAMP calibration data set "PHYS3GAR" (R. A. Spicer, 2009), which is an updated version of the data published by *Wolfe* [1993]. All meteorological data for these sites are from the CLAMP calibration data set "MET3AR" (R. A. Spicer, 2009), also an update of *Wolfe* [1993]. The CLAMP leaf areas are based on proportional scores in nine leaf area categories. Therefore, we had to convert the proportional scores to actual area to allow comparison to the digitally measured leaf areas. We made this transformation in three different ways, using: the mean natural log, the arithmetic mean, and the maximum area of each leaf area category (Table S1). Because the CLAMP system is modified from the logarithmic Raunkiaer-Webb category system (Figure 1) [*Raunkiaer*, 1934; *Webb*, 1959], we primarily use the mean natural log transformation throughout the paper. The maximum area of each category is an extreme conservative test for the leaf area bias because it assumes that the leaf area of each species is equal to the maximum area of its category. This transformation obviously estimates considerably larger areas than the natural log or arithmetic mean; however, it is probably not a realistic depiction of how most users score leaf area with CLAMP.

[21] We conducted CLAMP analyses following the protocols described by R. A. Spicer (2009). As suggested by *Wolfe* [1995], the CCA was conducted using the software CANOCO (Canoco 4.5, Microcomputer Power, Ithaca, New York [see *ter Braak*, 1987]). For all analyses, we used the calibration data sets based on 144 sites (i.e., PHYS3BR and MET3BR, see R. A. Spicer (2009)) to estimate climate variables. We treated each of the 38 CLAMP sites as an unknown fossil site; thus, the sites were analyzed passively in the CCAs because we did not input their environmental variables. We conducted two sets of CCAs. In the first set (CCA1), excepting the leaf area scores, we used all of the CLAMP character scores from the calibration sheets (see R. A. Spicer, 2009). For leaf area, we changed the scores to the digitally measured leaf areas. We then conducted CCAs following standard CLAMP methodology (e.g., R. A. Spicer, 2009) to estimate MAT, GSP, q, and H. In the second set of analyses (CCA2), we used all of the CLAMP character scores for each site without change from the calibration sheets, and conducted CCAs to estimate these variables at each of the 38 sites.

Table 1. Sites Used for Analyses of Leaf Area Bias

State or Province and Country	Latitude (°N)	Longitude (°E)	Species Used	Elevation (m)	Digitally Measured Leaf Area (mm^2)	Reference[a]
CLAMP Floral Sites						
Alamos, Sonora, Mexico	27.07	−108.97	35	400	1316.50	1, 2
Bandon, Oregon	43.13	−124.40	27	16	1977.73	1, 2
Borinquen, Puerto Rico	17.97	−66.87	41	140	1028.81	1, 2
Buena Vista, Puerto Rico	18.17	−66.99	39	655	1596.69	1, 2
Cabo Rojo, Puerto Rico	17.95	−67.19	30	10	1735.04	1, 2
Cabo San Lucas, Baja California, Mexico	22.88	−109.88	36	8	407.30	1, 2
Cape Blanco, Oregon	42.83	−124.55	24	33	2097.41	1, 2
Childs, Arizona	34.35	−111.70	23	810	632.94	1, 2
Chuzenji-ko, Honshu, Japan	36.72	139.47	43	1300	4596.82	1, 2
Clearwater, Washington	47.58	−124.30	20	25	2729.05	1, 2
Emaplme, Sonora, Mexico	27.950	−110.850	24	10	251.4	1, 2
Government Camp, Oregon	45.32	−121.75	28	1210	1619.06	1, 2
Guajataca, Puerto Rico	18.41	−65.97	38	250	5391.54	1, 2
Guanica, Puerto Rico	17.92	−55.91	30	10	2145.13	1, 2
Half Moon Bay, California	37.43	−122.44	24	30	1733.46	1, 2
Hood River, Oregon	45.71	−121.55	27	155	1870.62	1, 2
Keka, Fiji	−16.75	178.98	35	150	4781.76	1, 2
Ketchikan, Alaska	55.32	−131.60	23	31	3376.67	1, 2
Monte Guilarte, Puerto Rico	18.16	−66.81	33	1075	2856.74	1, 2
Nagakubo, Yakushima, Japan	30.35	130.67	53	10	2942.53	1, 2
Nestucca River, Oregon	45.04	−122.97	17	5	3850.33	1, 2
North Bend, Oregon	43.42	−124.25	26	12	2575.54	1, 2
Parkdale, Oregon	45.51	−121.57	32	465	2821.83	1, 2
Placerville, California	38.71	−120.76	23	575	2295.37	1, 2
Portal, Arizona	31.88	−109.22	38	1640	664.98	1, 2
Powers, Oregon	42.87	−124.09	29	65	2625.33	1, 2
Red Fleet, Utah	40.55	−109.33	23	1660	617.83	1, 2
Republic, Washington	48.65	−121.14	28	775	2773.14	1, 2
Santa Cruz, California	36.98	−121.92	25	21	1349.77	1, 2
Suganuma, Honshu, Japan	36.81	139.38	16	1770	3354.03	1, 2
Talkeetna, Alaska	62.31	−150.11	27	123	1931.42	1, 2
Three Lynx, Oregon	45.13	−122.08	27	335	2760.16	1, 2
Toro Negro, Puerto Rico	18.17	−66.57	43	1285	2445.81	1, 2
Wolf Creek, Colorado	37.48	−106.86	21	2875	796.93	1, 2
Yakusugi (1080 m), Yakushima, Japan	30.30	130.58	26	1080	1818.26	1, 2
Yakusugi (1350 m), Yakushima, Japan	30.30	130.54	17	1350	2714.02	1, 2
Yakusugi (260 m), Yakushima, Japan	30.31	130.63	43	260	3035.14	1, 2
Yakusugi (800 m), Yakushima, Japan	30.31	130.59	32	800	2577.96	1, 2
Central Connecticut Floral Sites						
George Dudley Seymour State Park (swamp site), Connecticut	41.50	−72.55	13	3	3656.85	7
George Dudley Seymour State Park (river site), Connecticut	41.51	−72.54	19	3	3059.67	7
Hurd State Park (upland site), Connecticut	41.52	−72.54	14	120	2678.47	7
Royer et al. [2005] and Kowalski and Dilcher [2003] Floral Sites						
Allegheny National Forest, Pennsylvania	41.88	−78.70	47	503	4415.74	3, 4, 5
Archbold Biological Station, Florida	27.18	−81.35	18	50	1404.21	5, 6
Barro Colorado Island, Panama	9.17	−79.85	135	<100	6648.43	1, 3, 4, 5
Big Hammock Natural Area and Wildlife Management Area, Georgia	31.86	−82.11	26	55	2536.26	5, 6
Cockaponset State Forest, Connecticut	41.40	−72.50	26	100	3490.49	5
Dilcher's Woods lowland, Florida	29.60	−82.20	24	20	2704.93	5, 6
Dilcher's Woods upland, Florida	29.60	−82.20	22	20	1759.41	5, 6
Duke Forest, North Carolina	35.98	−78.91	27	150	4433.97	5
Harvard Forest, Massachusetts	42.50	−72.20	27	356	3513.76	5
Hawk Mountain Sanctuary, Pennsylvania	40.63	−75.85	24	15	5148.84	5
Hubbard Brook Experimental Forest, New Hampshire	43.90	−71.80	15	400	4010.10	5
E. N. Huyk Preserve and Biological Research Station, New York	42.67	−74.49	24	465	3589.47	5
Institute for Ecosystem Studies, New York	41.83	−73.75	31	400	5288.33	5
Florida Panther National Wildlife Refuge, Florida	26.17	−81.34	18	128	2521.88	5, 6
Little Pee Dee State Park, South Carolina	34.18	−79.38	27	30	1865.03	5
Smithsonian Environmental Research Center, Maryland	38.52	−76.33	25	11	5297.47	5
York County, Pennsylvania	39.92	−76.75	56	118	4128.56	3, 4, 5

[a]References: 1, *Wolfe* [1993]; 2, R. A. Spicer (2009); 3, *Wilf et al.* [1998]; 4, *Huff et al.* [2003]; 5, *Royer et al.* [2005]; 6, *Kowalski and Dilcher* [2003]; 7, D. L. Royer (unpublished data, 2006).

Table 2. Enthalpy Estimates for a Subset of High and Low Elevation Sites Used to Estimate Elevation[a]

Sites	Elevation (m)	Enthalpy Estimates (kJ kg^{-1})	
		CLAMP Leaf Areas	Digitally Measured Leaf Areas
Cabo Rojo, Puerto Rico	10	333.0	339.3
Chuzenji-ko, Honshu, Japan	1300	300.9	312.4
Empalme, Mexico	10	316.1	318.4
Government Camp, Oregon	1210	294.5	298.5
Monte Guilarte, Puerto Rico	1075	327.7	339.9
Nagakubo, Yakushima, Japan	10	318.5	332.4
Nestucca River, Oregon	5	298.3	307.3
North Bend, Oregon	12	301.9	309.9
Portal, Arizona	1640	308.3	311.5
Powers, Oregon	65	302.1	309.3
Red Fleet, Utah	1660	294.6	297.6
Suganuma, Honshu, Japan	1770	290.5	301.7
Toro Negro, Puerto Rico	1285	322.3	332.2
Wolf Creek, Colorado	2875	290.5	295.1
Yakusugi (1350 m), Yakushima, Japan	1350	299.1	309.6
Yakusugi (260 m), Yakushima, Japan	260	309.3	319.8

[a]See Table 3. Standard error is 3.2 kJ kg^{-1}.

[22] In both cases, we did not remove single sites from the 144 site calibration data set when estimating a site's climate variables because this variably changed the eigenvector scores of the data sets, which in turn considerably affected the second-order polynomial regressions. This resulted in marked differences in climate estimates, making it impossible to compare the results among sites. Thus, our reported differences between the digitally measured (CCA1) and unmodified (CCA2) climate estimates are probably conservative. Additionally, this suggests that the CLAMP model is unstable, and slight changes to the calibration data set will have major impacts on climate estimates.

[23] The second group of sampled floras comes from three sites in central Connecticut (two sites from George Dudley Seymour State Park and one site from Hurd State Park) (Table 1). Leaves from between 13 and 19 native woody dicotyledonous species at each site were collected, pressed, and dried by D. L. Royer in May and June 2006. A subsample of 2–6 leaves (or leaflets) was digitally photographed and processed for each species (Table 1). Leaf area estimates were made on the same leaves that were digitally measured using both the CLAMP leaf area templates of R. A. Spicer (2009), following the protocols of *Wolfe* [1993] and R. A. Spicer (2009), and Raunkiaer-Webb leaf area templates [*Ellis et al.*, 2009] by D. J. Peppe (Table S1).

[24] The third group of sampled floras comes from the 17 sites from the eastern United States and Barro Colorado Island, Republic of Panama, that were used by *Royer et al.* [2005] (see *Royer et al.* [2005, and references therein] for site details). Here, up to six leaves per species were photographed and digitally processed as described in section 2 (Table 1). Planimeter measurements were made by E. A. Kowalski on 10 leaves per species to estimate leaf areas for 14 of these floras (Table S1). The CLAMP leaf size and shape characters were scored on a subset of leaves from 14 of the sites [*Kowalski and Dilcher*, 2003; E. A. Kowalski, unpublished data, 2003] (Table S1). Leaf area estimates for four of these sites were also made using the Raunkiaer-Webb classification system by *Wilf et al.* [1998] (Table S1). All

measurements were based on random subsets of the same voucher specimens.

[25] To test elevation estimates, we focused on nine CLAMP sites from the 38 site cluster (see above) that have elevations >1 km above sea level and seven neighboring sites from near sea level (Table 2). Three high elevation sites are from Japan, four are from the western United States (Arizona, Colorado, Utah, and Oregon), and two are from Puerto Rico. For the low elevation sites, two are from Japan, three are from the western United States (Oregon), one is from Mexico (northern Baja California), and one is from Puerto Rico (Tables 2 and 3). Each Japanese high elevation site was coupled separately with the two Japanese low elevation sites so that each high elevation site has two elevation estimates (Table 3). The high elevation sites from Colorado, Utah, and Oregon were each coupled with each of the three low elevation sites from Oregon, resulting in three elevation estimates for each high elevation site (Table 3). This resulted in 18 total elevation estimates (Table 3). In all cases, the sea level site and the corresponding high elevation site are from relatively restricted latitude bands (<10°) approximately equivalent to the moist static energy bands of *Forest et al.* [1999].

5. Results and Discussion

5.1. Leaf Area Bias

[26] At all 38 sites, CLAMP underestimates site-mean leaf area relative to digitally measured leaf area (Figure 2). This bias exists whether CLAMP leaf areas are estimated using the mean natural log leaf area of each area class (average bias across sites is 57.2%; range is 33.5%–77.0%), the mean leaf area of each area class (53.0%; 28.0–74.2%), or the maximum leaf area of each area class (34.9%; 2.2–63.0%) (Tables 1 and S1). Underlying this, the leaf areas of sites' constituent species are underestimated by 50–60% (Figure S2).

[27] The leaf area bias is consistent across all leaf area classes (Figure S3): we compared the proportional number of species in each CLAMP leaf area class using the digitally

Table 3. Elevation Estimates Made Using CLAMP and Digitally Measured Leaf Areas

High Elevation Site (Low Elevation Site)	Elevation of High Site (m)	Estimation of High Elevation Site (m)		Elevation Bias[a] (m)
		CLAMP Leaf Areas	Digitally Measured Leaf Areas	
Chuzenji-ho, Japan (Nagakubo, Japan)	1300	1794.3	2036.5	−242.2
Chuzenji-ho, Japan (Yakasugi, 260 m, Japan)	1300	856.0	750.9	105.1
Government Camp, Oregon (Nestucca River, Oregon)	1210	378.2	894.7	−516.5
Government Camp, Oregon (North Bend, Oregon)	1210	746.4	1157.1	−410.7
Government Camp, Oregon (Powers, Oregon)	1210	773.2	1100.9	−327.7
Portal, Arizona (Empalme, Mexico)	1640	800.5	701.4	99.1
Red Fleet, Utah (Nestucca River, Oregon)	1660	377.4	984.1	−606.7
Red Fleet, Utah (North Bend, Oregon)	1660	745.5	1246.5	−501.0
Red Fleet, Utah (Powers, Oregon)	1660	772.3	1190.3	−417.9
Suganuma, Japan (Nagakubo, Japan)	1770	2850.9	3124.1	−273.2
Suganuma, Japan (Yakasugi, 260 m, Japan)	1770	1912.6	1838.5	74.1
Wolf Creek, Colorado (Nestucca River, Oregon)	2875	794.5	1246.7	−452.2
Wolf Creek, Colorado (North Bend, Oregon)	2875	1162.6	1509.1	−346.4
Wolf Creek, Colorado (Powers, Oregon)	2875	1189.4	1452.8	−263.4
Yakusugi, 1350 m, Japan (Nagakubo, Japan)	1350	1971.9	2317.6	−345.7
Yakusugi, 1350 m, Japan (Yakasugi, 260 m, Japan)	1350	1033.6	1032.0	1.6
Monte Guilarte, Puerto Rico (Cabo Roja, Puerto Rico)	1075	544.1	−60.5	604.6
Toro Negro, Puerto Rico (Cabo Roja, Puerto Rico)	1285	1093.4	728.8	364.6

[a]Elevation bias is elevation estimate based on CLAMP leaf area minus elevation estimate based on digitally measured leaf area (see equation (14), section 5.3).

measured and CLAMP leaf areas, and we found that CLAMP overestimates the proportional number of species in the smaller size classes (nanophyll, leptophyll-1, leptophyll-2, microphyll-1) and underestimates the number of species in the larger size classes (mesophyll-1, -2, and -3) (Figure S3). Because they represent much larger leaves, the underestimation in the large size classes has a much stronger impact on the total leaf area bias than the smaller size classes. Thus, the underestimated proportions of species in the largest leaf area classes are the main reason for the bias in site-mean leaf area, consistent with the observations of *Wilf et al.* [1998, 1999].

[28] The published CLAMP leaf area scores are presumably based on all vouchered leaves, but we only sampled one to three leaves per species; thus, it is possible that we preferentially photographed large leaves. To examine this possibility, we compared leaf area estimates made with the CLAMP template to digital measurements made on the same leaves for the three central Connecticut sites (Table S1). Here, the site-mean underestimation of leaf area in CLAMP is 60.3% (range is 35.2%–76.7%) (Figure 2b).

[29] It is possible that the observed leaf area bias is more related to user bias than to actual leaf area differences. To test for this potential bias, we compared leaf area estimates made by one of us (E. A. Kowalski) using both the CLAMP template and a planimeter for 14 sites from eastern United States. We also digitally measured the leaf areas at all of these sites. In all cases, the leaf area estimates made using the CLAMP template are considerably smaller than the planimeter-measured (42.3%; 11.5%–77.3%) leaf areas (Table S1) and the digitally measured (Figure 2b) (mean is 45.7%; range is 7.2%–78.1%).
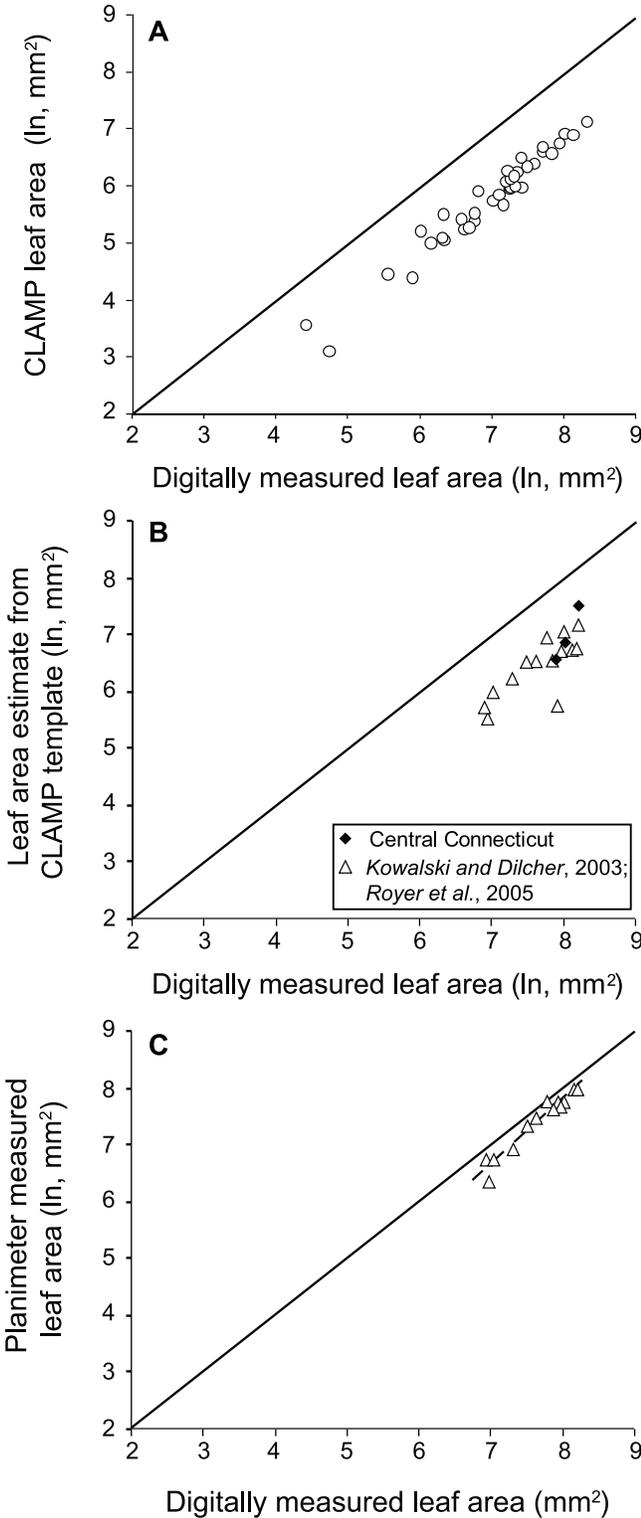
[30] To assess the reproducibility of the digital measurements, we compared the digitally measured leaf areas at the 14 eastern U.S. sites with the planimeter leaf area measurements discussed above. Because planimeters are designed to the measure the area of an arbitrary two-dimensional shape,

their measurements likely reflect the true area of each leaf. Importantly, the digital and planimeter estimates of leaf area are approximately the same (slope of 1.15 [+0.18, −0.16], $r^2 = 0.95$) (Figure 2c and Table S1), demonstrating that our digital measurements are both accurate and reproducible.

[31] Together, these results suggest leaf area estimates made using the CLAMP template are consistently underestimated by ∼45–60%, and that this error in CLAMP is due to a scoring bias rather than a collection bias. Moreover, our observations of the CLAMP vouchers do not show any collection bias against large leaves. To explore whether this leaf area bias is specific to the CLAMP template or, instead, is a more pervasive problem with categorical systems of leaf area, we scored leaves from the three Connecticut sites using another categorical system (Raunkiaer-Webb). Here, the site-mean leaf areas are 25.3% smaller than the digitally measured leaf areas (Figure S4). We also compared leaf areas that were digitally measured with leaf areas that had been estimated using the Raunkiaer-Webb system for four sites from the eastern United States and Panama [*Wilf et al.*, 1998]. At these sites, site-mean leaf areas using the Raunkiaer-Webb templates are 7.5% smaller than the digitally measured leaf areas. This suggests that there is a consistent but unpredictable bias with these categorical systems, but that the bias with CLAMP is probably larger than with Raunkiaer-Webb, which uses more evenly proportional categories, especially in the upper ranges of leaf size (Figure 1).

[32] Finally, to examine if the CLAMP leaf area bias is the result of noise introduced when continuously measured leaf area is quantified using discrete categories, we replaced our digitally measured leaf areas with the appropriate CLAMP size categories and compared them to the original digitally measured areas. In this case, the leaf areas filtered through CLAMP are almost identical to the digitally measured leaf areas (average difference is 1.39%, $r^2 = 0.99$) (Figure S5). Together, our data suggest that the leaf size bias is probably

caused by an error when humans use these categorical templates, perhaps analogous to similar user errors observed in other categorical systems [e.g., *Bell et al.*, 1985]. Consequently, we strongly recommend using continuous digital measurements instead of categorical templates to measure leaf area.

Figure 2. Leaf area bias. Solid black lines indicate 1:1. (a) Comparison of site-mean digitally measured leaf areas to site-mean leaf areas for leaf samples from the 38 CLAMP sites [*Wolfe*, 1993; R. A. Spicer, 2009] used in this study. (b) Comparison of site-mean digitally measured leaf areas to site-mean leaf areas estimated using the CLAMP template for eastern U.S. sites not in the CLAMP data set. For the three sites from central Connecticut, the same leaves were used for both measurements. For the five sites from *Kowalski and Dilcher* [2003] and *Royer et al.* [2005] an unbiased subset of the voucher specimens from each site was used for each analysis. (c) Comparison of site-mean digitally measured leaf areas [*Royer et al.* 2005] to leaf areas calculated using a planimeter for 14 sites from the eastern United States. An unbiased subset of the same voucher specimens from each site was used for each analysis. Dashed black line indicates standardized major axis regression ($y = 1.12x - 143.2$).
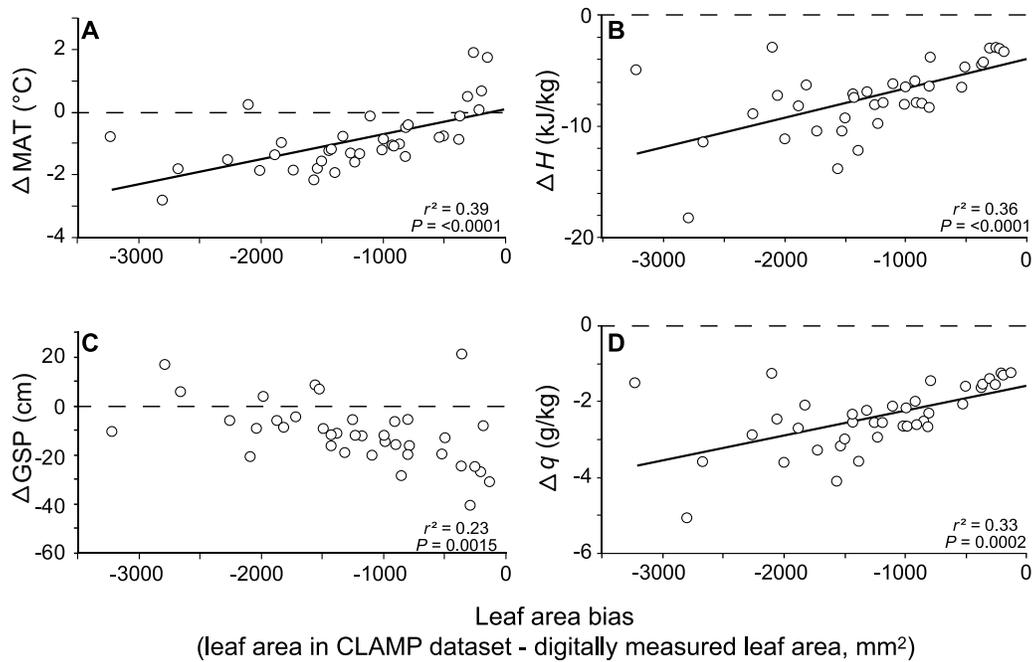
5.2. Effect of Leaf Area Bias on Climate Estimates

[33] Because climate estimates are dependent on leaf size, it is important to know how climate estimates made using CLAMP will be affected, assuming leaf area is estimated correctly in an unknown (fossil) sample. We compared climate variable estimates (MAT, GSP, q, H) made for each of the 38 CLAMP sites using the CCA1 versus CCA2 scenarios (see section 4; Figure 3 and Table S2). The climate estimates from CCA1 are considerably different from those of CCA2 (Figure 3 and Table S2). As expected, the sizes of the differences in MAT, q, and H positively correlate to the magnitude of leaf size bias, although for GSP the differences weakly correlate negatively. In all cases, there is a great deal of variance in the correlations, which is presumably because the climate estimates are variously affected by the interactions of the nine leaf size categories to the other 22 physiognomic variables in the data matrix.

[34] The MAT estimates made using the CLAMP leaf areas (CCA2) are 7.2% (or −0.95°C) lower than the estimates made using the digitally measured leaf areas (CCA1); the average magnitude of the offset among these 38 test sites is 8.6% (or 1.2°C) (Figure 3a and Table S2). Growing season precipitation estimates made using the CLAMP leaf areas are 17.0% (or −12.4 cm) lower than the estimates made using the digitally measured leaf areas. The average magnitude of change is 19.4% or 15.4 cm (Figure 3c and Table S2). In both cases, the estimates usually increased when using the larger digitally measured leaf areas; however, they decreased in some cases. The q and H estimates made using the digitally measured leaf areas are always higher than the estimates using the CLAMP leaf area (mean increase is 2.6% or 2.5 g kJ^{-1} and 2.5% or 7.9 kJ kg^{-1}, respectively) (Figures 3b and 3d and Table S2). Increases in the values of climate variables when using the larger, digitally measured leaves are expected because higher MAT, GSP, q, and H values all correlate with larger leaf areas [e.g., *Wolfe*, 1995]

[35] In summary, based on these results, if leaf areas in a fossil floral assemblage are measured correctly and are evaluated by CCA using the published CLAMP calibration, MAT, GSP, q, and H estimates will tend to be higher than if the leaf areas were measured with the CLAMP template.

Figure 3. Effects of leaf area biases in CLAMP on climate estimates are large, mostly unpredictable, and nonuniform. For each of the 38 CLAMP sites used in this study (data points), the effects are shown on that site's climate estimates when using corrected versus uncorrected site-mean leaf size, using the standard CLAMP methodology and full data set for each [e.g., *Wolfe*, 1993, 1995; R. A. Spicer, 2009]. In all cases, the horizontal axis is the leaf area bias (Δ_{area} of equation (5)), which for each site is the digitally measured leaf area subtracted from the leaf area in the CLAMP data set and is (empirically) always negative. The vertical axes are climate biases, which are calculated by subtracting the climate estimates based on the digitally measured leaf areas (estimated in CCA1; see text) from the climate estimates based on the CLAMP leaf areas (estimated in CCA2; see text); climate biases were usually negative, although in some cases, MAT and GSP biases were positive. All four variables are used in, or are relevant to, paleoelevation estimates (e.g., equations (2) and (6)–(13)): (1) mean annual temperature (MAT), (2) enthalpy (H), (3) growing season precipitation (GSP), and (4) specific humidity (q).

However, in some cases MAT and GSP estimates can be lower (Figures 3a and 3c and Table S2). Although the differences in climate estimates are correlated to the leaf area bias, we do not recommend using correlations like those shown in Figure 3 as corrective tools. The effects of the leaf area bias are large, unpredictable, and nonuniform. Because the leaf area estimates made using the CLAMP template nonuniformly underestimate leaf area, it is probable that climate estimates for a fossil floral assemblage that were measured following CLAMP methodology would also be inconsistently affected.

[36] It is potentially possible to correct the leaf area bias by digitally remeasuring the remaining species-site pairs in the CLAMP data set; however, we do not advocate this approach. As discussed in sections 1 and 3, in addition to the leaf area bias there are other fundamental problems with CLAMP, such as ambiguities in scoring leaf characters and using CCA as a predictive tool, that probably add unquantified errors. Even if the errors associated with the leaf area bias were minimized, these other errors remain. We have presented the leaf area bias as an illustration of the errors that can be quantified, and because this bias affects numerous published paleoelevations, discussed next.

5.3. Effect of Leaf Area Bias on the Paleoenthalpy Method

[37] The paleoenthalpy method [*Forest et al.*, 1995, 1999; *Forest*, 2007] uses the enthalpy difference between a sea level and a target site to estimate elevation (equation (3)). Because the leaf area bias affects the enthalpy estimates, the standard error associated with the method is also affected. As defined by *Forest et al.* [1999], the standard error for paleoelevation (σ_Z) is obtained by combining the expected errors from the paleobotanical estimates of H, $\sigma_H = 5.5$ kJ kg^{-1} (one standard deviation of the calibration data), and the expected errors from zonal asymmetry [see *Forest et al.*, 1999], $\sigma_h = 4.5$ kJ kg^{-1}:

$$\sigma_Z = \sqrt{\frac{2\sigma_H^2 + \sigma_h^2}{g^2}} \qquad (4)$$

However, the leaf area bias discussed here adds an additional 7.9 kJ kg^{-1} of uncertainty (one standard deviation of the difference between the enthalpy estimates based on the CLAMP leaf areas and the digitally measured leaf areas at the 38 CLAMP sites) to all enthalpy estimates; thus, $\sigma_H = 13.4$ kJ

kg^{-1} (5.5 kJ kg^{-1} from *Forest et al.* [1999] plus 7.9 kJ kg^{-1} from leaf area bias). Using this σ_H, the standard error associated with the paleoenthalpy method more than doubles from ±0.91 km to ±1.98 km. These are in addition to numerous other sources of mostly unquantifiable error, discussed in section 3.

[38] We also directly examined the effect of the leaf area bias on elevation estimates made using the paleoenthalpy method on 18 high elevation–low elevation site couplets from the 38 CLAMP sites (Tables 2 and 3). First, we quantified the leaf area bias (Δ_{area}), which is always negative in our data set, as

$$\Delta_{area} = Area_{CLAMP} - Area_{digital} \qquad (5)$$
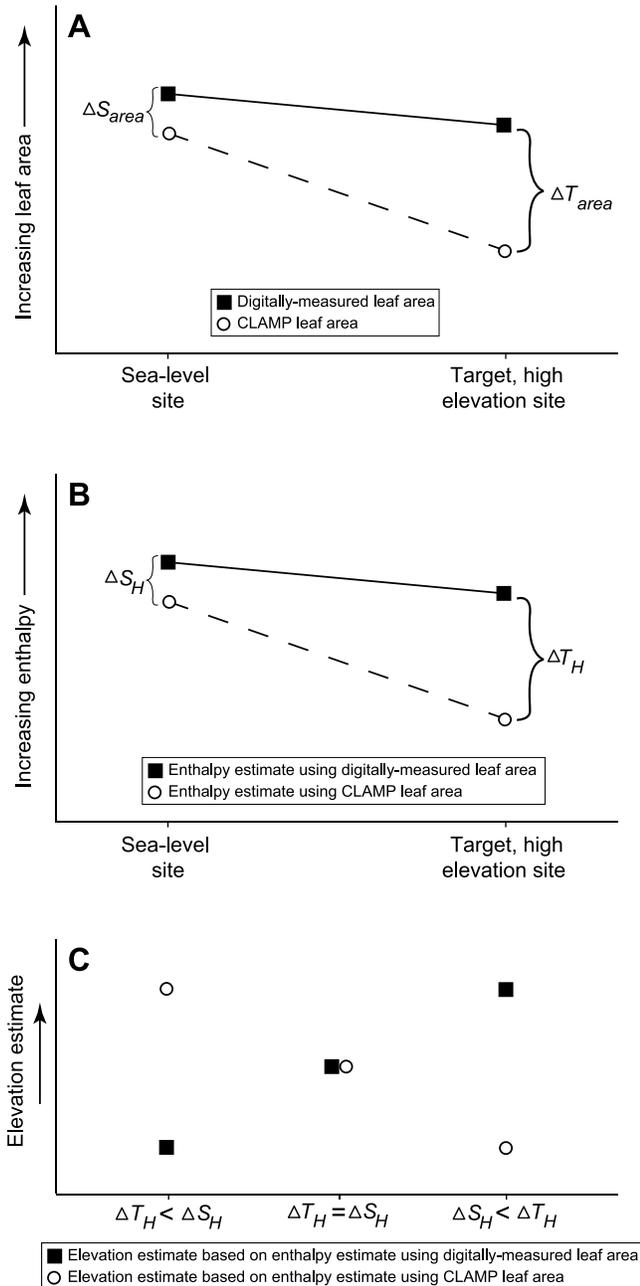
where $Area_{CLAMP}$ is CLAMP leaf area and $Area_{digital}$ is digitally measured leaf area.

[39] Because the paleoenthalpy method is affected by the leaf area at both a sea level site (S_{area}) and a target, high elevation site (T_{area}), Δ_{area} can be either more negative at the high elevation site (Figure 4a), meaning that CLAMP underestimates leaf area more at the elevated than the sea level site:

$$\Delta T_{area} < \Delta S_{area} \qquad (6)$$

more negative at the low elevation site, meaning that CLAMP underestimates leaf area more at the sea level site:

$$\Delta S_{area} < \Delta T_{area} \qquad (7)$$

or the same at both sites, meaning that CLAMP underestimates leaf area equally at both sites:

$$\Delta T_{area} = \Delta S_{area} \qquad (8)$$

[40] The leaf area bias (Δ_{area}) is not uniform (Figures 2 and 3), and therefore it is not possible to uniformly correct elevation estimates for the bias. Furthermore, any bias in the elevation estimates is directly related to how the leaf area bias influences the estimation of enthalpy. Calculations of enthalpy based on CLAMP leaf areas (H_{CLAMP}) will be lower than that based on digitally measured leaf areas ($H_{digital}$) (Figure 3b). The difference between H_{CLAMP} and $H_{digital}$,

Figure 4. Schematic illustrations of important possible biasing scenarios on paleoelevation estimates due to inaccurate CLAMP leaf size measurements in hypothetical fossil samples. (a) Illustration of leaf area bias (equation (6): $\Delta T_{area} < \Delta S_{area}$) depicting a more negative leaf area bias at a high target (T) than a low, sea level (S) elevation fossil site; that is, CLAMP underestimates leaf area more for T than for S. (b) Illustration of enthalpy (H) bias (equation (10): $\Delta T_H < \Delta S_H$) depicting a more negative enthalpy bias at T than at S; that is, CLAMP underestimates H more for T than for S. (c) Illustration of the three possible relationships between enthalpy bias and the paleoelevation estimate Z (equations (11)–(13)) when fossil leaf area is corrected (e.g., digitally measured). Recall that Z depends directly on $S_H - T_H$ (equation (3)). The three possibilities are as follows: (left) $\Delta T_H < \Delta S_H$; that is; CLAMP underestimates H more for T than for S. This scenario corresponds to Figure 4b. Because normally $S_H > T_H$ before correction and because the correction is greater for T_H than for S_H, Z decreases because $S_H - T_H$ decreases. (middle) $\Delta T_H = \Delta S_H$; that is, CLAMP underestimates H by the same amount for S and for T, no effect on Z. (right) $\Delta S_H < \Delta T_H$; that is, CLAMP underestimates H more for S than for T. Because normally $S_H > T_H$ before correction and because the correction is greater for S_H than for T_H, Z increases after correction because $S_H - T_H$ increases. See section 5.3 for a more detailed discussion.
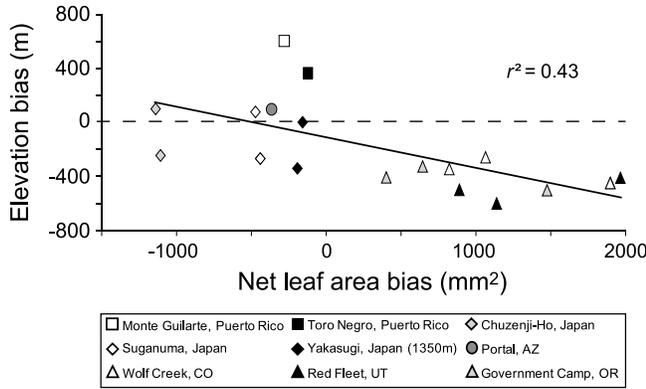
Figure 5. Relationship between net leaf area bias and elevation bias. Nine high elevation sites and seven neighboring sites from near or at sea level were used in this analysis. Three high elevation sites are from Japan, four are from the western United States (Arizona, Colorado, Utah, and Oregon), and two are from Puerto Rico. For the low elevation sites, two are from Japan, three are from the western United States (Oregon), one is from Mexico (northern Baja California), and one is from Puerto Rico. Each Japanese high elevation site was coupled with both of the Japanese low elevation sites, meaning that each high elevation site has two elevation estimates. The high elevation sites from Colorado, Utah, and Oregon were each coupled with the three low elevation sites from Oregon, resulting in three elevation estimates for each high elevation site. This resulted in 18 total elevation estimates (Table 3). Horizontal axis is net leaf area bias, defined for convenience as $\Delta T_{\text{area}} - \Delta S_{\text{area}}$, i.e., the leaf area bias at the sea level site (ΔS_{area}) subtracted from the leaf area bias at the target, high elevation site (ΔT_{area}) (see equations (5)–(8)). Both ΔS_{area} and ΔT_{area} are, empirically, negative numbers in the data analyzed here. When the net leaf area bias is negative, $\Delta T_{\text{area}} < \Delta S_{\text{area}}$, or CLAMP underestimates leaf area more for T than for S (see Figure 3a) and vice versa. When the net leaf area bias is positive, $\Delta S_{\text{area}} < \Delta T_{\text{area}}$, or CLAMP underestimates leaf area more for S than for T. The vertical axis is a site's difference between elevation estimates made using CLAMP leaf areas (Z_{CLAMP}) and elevation estimates made using digitally measured leaf areas (Z_{digital}) (equation (14)).

which is always negative (Figure 3b), can be expressed at the sea level site (ΔS_H) and at the target, high elevation site (ΔT_H), respectively, as

$$\Delta S_H = H_{\text{CLAMP(S)}} - H_{\text{digital(S)}} \qquad (9)$$

$$\Delta T_H = H_{\text{CLAMP(T)}} - H_{\text{digital(T)}} \qquad (10)$$

As with the leaf area bias, there are three possible relationships between ΔS_H and ΔT_H. ΔT_H can be more negative at the high elevation site (Figures 4b and 4c), meaning that CLAMP underestimates enthalpy more at the target, elevated than the sea level site:

$$\Delta T_H < \Delta S_H \qquad (11)$$

ΔS_H can be more negative at the low elevation site (Figure 4c), meaning that CLAMP underestimates enthalpy more at the sea level than at the target, elevated site:

$$\Delta S_H < \Delta T_H \qquad (12)$$

or ΔT_H and ΔS_H can be equal (Figure 4c), meaning that CLAMP underestimates enthalpy equally at both sites:

$$\Delta T_H = \Delta S_H \qquad (13)$$

[41] In turn, this enthalpy bias will affect elevation estimates (Z) made using the paleoenthalpy method (equation (3)): the elevation estimate made using H_{CLAMP} (Z_{CLAMP}) will be different from the elevation estimates made using H_{digital} (Z_{digital}). The difference in these estimates (elevation bias) can be expressed as

$$\text{Elevation bias} = Z_{\text{CLAMP}} - Z_{\text{digital}} \qquad (14)$$

[42] Because the elevation estimates made using the paleoenthalpy method are calculated directly from the difference in H between sea level and high elevation sites, the elevation bias will be affected by the relationship of ΔT_H and ΔS_H in the three ways shown in Figure 4c. If $\Delta T_H < \Delta S_H$, the elevation bias will be negative ($Z_{\text{CLAMP}} < Z_{\text{digital}}$). If $\Delta S_H < \Delta T_H$, the elevation bias will be positive ($Z_{\text{CLAMP}} > Z_{\text{digital}}$). If $\Delta T_H = \Delta S_H$, the elevation bias will be neutral ($Z_{\text{CLAMP}} - Z_{\text{digital}}$).

[43] Using the 18 sea level/high elevation site couplets, we quantified the magnitude of their elevation biases based on their outputs in CCA1 and CCA2: the biases range from −607 m to +605 m (mean is −217 m, $2\sigma = \pm646$ m) (Table 3 and Figures 5 and S6). The elevation bias correlates negatively to the net leaf area bias, $\Delta T_{\text{area}} - \Delta S_{\text{area}}$ (Figure 5): when $\Delta T_{\text{area}} < \Delta S_{\text{area}}$ (i.e., the target site has a more negative leaf area bias than that of the sea level site, and thus the net leaf area bias, as here defined, is positive), the elevation estimate made with the CLAMP leaf areas will probably underestimate elevation, and vice versa (Figure 5). However, the correlation is weak, making it difficult to correct for the elevation bias, even if it were possible to correct for the leaf area bias.

[44] As an additional example of uncertainties related to enthalpy estimates generated by CLAMP, our results also indicate that enthalpy estimates can vary considerably among sea level sites within a geographically restricted area (<500 km radius) (Table 2). This in turn considerably affects the elevation predictions of individual high elevation sites that are calculated from associated low elevation sites (Table 3) by as much as 1.2 km. Although the data set is small, it further indicates some of the uncontrolled variability that makes the method, in our view, unreliable.

[45] Together, our analyses demonstrate that the errors associated with the paleoenthalpy method are considerably larger than suggested by *Forest et al.* [1999] due to the effects

of leaf area bias alone, in addition to the numerous other unquantified errors discussed in section 3.

6. Conclusions

[46] We have documented a significant bias in the CLAMP data set that leads to an underestimation of leaf area (~50%). This bias has major implications for climate estimates made using CLAMP and for paleoelevation estimates made using the paleoenthalpy method. The cause of this bias is not clear, but it may result from human error when scoring leaves with a categorical template. For this reason, we strongly advocate the use of continuous, digital measurements of leaf size and shape categories rather than categorical templates, and suggest that future methods should focus on the use of continuously measured variables. Further, the paleoenthalpy method could be revisited if a better method or proxy for estimating moist static enthalpy is developed.

[47] The leaf area bias influences all climate variables estimated with CLAMP. Mean annual temperature estimates based on CLAMP leaf areas were on average 0.95°C cooler than estimates made using the digitally measured leaf areas, and the average magnitude of difference is 1.2°C. This suggests that the errors in MAT made using CLAMP should be at least ±3.0°C (±1.8°C standard error [*Forest et al.*, 1999] plus ±1.2°C from leaf area bias), which are more in line with univariate methods [*Wilf*, 1997; *Miller et al.*, 2006] and larger than multivariate models based on continuous, digital measurements [*Huff et al.*, 2003; *Royer et al.*, 2005]. These additional errors emphasize that CLAMP does not add any improvements over less complex, univariate methods [*Wilf*, 1997; *Wilf et al.*, 1998]. Further, these and the numerous other unquantified errors reviewed in section 3, suggest that uncertainties associated with climate estimates made using CLAMP are considerably larger than previously suggested [e.g., *Forest et al.*, 1999; *Spicer et al.*, 2005].

[48] Enthalpy estimates made from CLAMP leaf areas are always lower than estimates based on digitally measured leaf areas. The uncertainty in enthalpy from leaf area bias alone results in a more than doubling of the standard errors asso-

ciated with the paleoenthalpy technique from ±0.91 km to ±1.98 km. Moreover, in a small test study the leaf area bias in CLAMP led to differences in elevation predictions of ±600 m. As another example of uncertainty in CLAMP and the paleo-enthalpy method, enthalpy estimates of sea level sites can vary considerably even within a restricted geographic area (<500 km radius). This variation in estimates can result in very large differences in elevation predictions (up to 1.2 km). These analyses, coupled with additional errors reviewed here that are associated with the CLAMP methodology and with paleoelevation estimates made using fossil plants, suggest that the cumulative errors and uncertainties associated with the paleoenthalpy approach are large enough to make most estimates uninformative about true paleoelevation. Therefore, we do not recommend using CLAMP to estimate enthalpy, or the paleoenthalpy method to estimate elevation.

[49] Our analyses call into question the accuracy of previously published paleoelevation estimates made using the paleoenthalpy method [e.g., *Forest et al.*, 1995; *Gregory-Wodzicki*, 1997; *Wolfe et al.*, 1997; *Wolfe et al.*, 1998; *Spicer et al.*, 2003]. In many of these studies, the uncertainties associated with the paleoelevation estimates are equal to, and in some cases larger than, the estimates themselves. For example, seven of the 17 paleoelevation estimates made for the Miocene Basin and Range Province by *Wolfe et al.* [1997] are lower than the revised ±1.98 km standard error, from leaf size bias alone, associated with the paleoenthalpy method. We suggest that these, and other previously published paleo-elevation estimates made using the paleoenthalpy method, are unlikely to be accurate either in magnitude or estimated error.

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