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Mean annual temperature estimation based on leaf morphology: a test from tropical South America

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Abstract

Are models that predict mean annual temperature (MAT) from leaf morphology applicable globally? Fifteen models that predict MAT from leaf morphology were tested on thirty floral samples from tropical South America to determine the degree to which models based on published data that are primarily from other regions are applicable to floras from tropical South America. The models included are based on regional data from North America, South America, and Asia. Of the fifteen models tested, five are simple linear regressions, six are multiple linear regressions, two are canonical correspondence analyses, and two are correspondence analyses followed by nearest neighbor analyses. For the seven modern floras with $\text{MAT} \leq 21^\circ\text{C}$, every model overestimates MAT. For the 23 modern floras with $\text{MAT} > 21^\circ\text{C}$, all models produce variable results without a systematic error. The range of average model errors is $2.7\text{--}7.3^\circ\text{C}$, while the absolute extremes of error are 0 and 15.1°C . Average 95% predictive confidence intervals range from 1.6 to 6.9°C . Predicted MAT falls within the published standard error of the model for 0–67% of the South American test floras. Evaluating the seven sites with $\text{MAT} \leq 21^\circ\text{C}$ separately from the 23 sites with $\text{MAT} > 21^\circ\text{C}$ shows that no equation accurately estimates MAT of the majority of low-temperature sites, but that four equations accurately estimate $> 50\%$ of high-temperature sites. The results suggest that at least for sites of unknown or high elevation, mean annual temperature of fossil floras from tropical South America may be better predicted from models based on the leaf morphology of tropical South American floras.

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1. Introduction

In the eleventh century, Shen Kuo described the paleoclimate of Shansi Province, China, based on fossil plants that he found in the region (Li, 1981). From this early beginning, the use of fossil floras

to interpret paleoclimate has become a much-used technique. Modern study of the correlation between paleoclimate and plant fossils, especially the morphology of fossil leaves, started in the early 1900s with an investigation of the relationship between climate and extant plants. At that time, Bailey and Sinnott (1915, 1916) noted that temperate climates have proportionately more species with toothed-margined leaves than do tropical, frigid, or desert climates, and used this

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qualitative relationship to infer climate from Cretaceous and Tertiary fossil leaf assemblages. Wolfe (1979) first quantified a relationship between leaf margin and temperature using modern floras from east Asia.

In addition to margin type, other aspects of leaf morphology, such as apex shape and leaf size, are thought to vary based on environmental conditions (e.g. Parkhurst and Loucks, 1972; Givnish, 1987; Uhl and Mosbrugger, 1999). The relationship between leaf morphology and climatic conditions is thought to reflect the convergent adaptation of leaf form to climate regime (e.g. Parkhurst and Loucks, 1972; Wolfe, 1978; Uhl and Mosbrugger, 1999). The same or similar combinations of characters tend to be common in floras living in similar climates (Givnish, 1987), even those that are widely separated spatially and compositionally (Wolfe, 1978; Halloy and Mark, 1996). However, the amount of morphologic change is limited in some respects by phylogeny (Givnish, 1987; Bongers and Popma, 1990). Phylogenetic constraints may conserve the morphologic composition of species in any given flora even when climate changes, and thus the relationship between climate and morphology, should vary geographically based on differences in taxonomic composition.

Quantifying the modern relationship between leaf morphology and climate allows the creation of predictive equations that are used to reconstruct paleoclimate using fossil leaves. Many published methods detail the relationship between leaf morphology and several different climatic parameters, including mean annual temperature (MAT), mean annual precipitation, mean annual range of temperature, and cold month mean temperature, among others. This paper concentrates on the relationship between leaf morphology and MAT.

Four different methods have been used to quantify the relationship between leaf morphology and MAT: simple linear regression (SLR), multiple linear regression (MLR), canonical correspondence analysis (CCA), and nearest neighbor analysis (NN). These four methods are the basic techniques from which over 20 separate equations, or models, have been constructed. Many published equations that predict MAT

rely on the CLAMP database (Gregory and Chase, 1992; Wing and Greenwood, 1993; Gregory, 1994; Gregory and McIntosh, 1996; Wilf, 1997; Wiemann et al., 1998), a database of modern climate and leaf morphological characters from North America and the Pacific compiled by Wolfe (1993, 1995). Other published equations are derived from data from the Western Hemisphere (Wilf, 1997), Bolivia (Gregory-Wodzicki, 2000), and eastern Asia (Wolfe, 1978, 1979). While it is reasonable to assume that these equations accurately predict MAT from leaf morphology in the area from which the data sets are derived, the applicability of these models to other geographical areas is not known.

Many published models that predict MAT have been used previously in geographical regions other than the region from which the data set was derived, with varied results. While some studies have shown that published equations accurately predict MAT of sites from outside the geographical range of that equation's database (Jacobs and Deino, 1996; Gregory-Wodzicki, 2000; Burnham et al., 2001), other studies have shown estimates of MAT that are off by as much as 7°C (Burnham, 1997; Jordan, 1997; Stranks and England, 1997; Wiemann et al., 1998), and it has been suggested that the relationship between leaf morphology and temperature is not consistent between widely different regions (Wolfe, 1995; Greenwood, 2001). Clearly, geographic variation exists in the relationship between climate and leaf morphology. Thus, models used to predict MAT from leaf morphology must be tested using modern regional floras before they are applied to fossil floras from those regions.

Many of the published predictive models may not accurately estimate MAT in South America because South American sites are poorly represented in the databases used to construct the models (except Gregory-Wodzicki, 2000). Much of South America lies within the tropics (Fig. 1), where proportions of entire-margined species are high (Bailey and Sinnott, 1915; Wolfe, 1971). In fact, none of the modern floras used here has a percentage of entire-margined species below 60% (Appendix 1), in contrast with the Northern Hemisphere sites from the CLAMP database, in

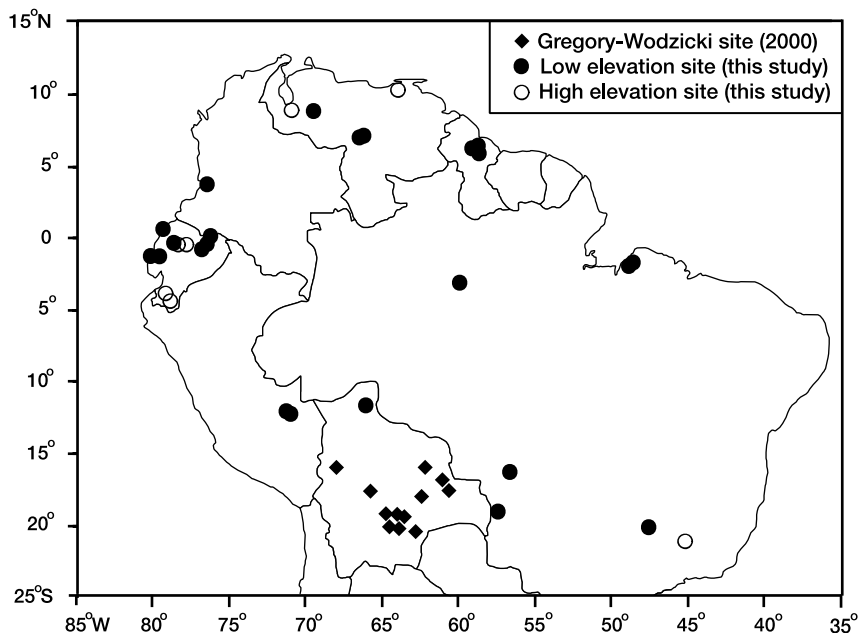


Fig. 1. Location of 30 modern neotropical floras (circles) used to test models of MAT–leaf morphology correlation and 12 Bolivian sites (diamonds) discussed in the text from Gregory-Wodzicki (2000). Open circles are the seven low-temperature sites mentioned in the text, Baeza, La Montaña, Laguna de Cocos, Loja–non-ridge, Loja–ridge, Pasochoa, and Rio Grande. Filled circles are high-temperature, lowland sites.

which 70% of the sites have fewer than 60% entire-margined species (Wolfe, 1995). Predictive models based heavily on leaf margin and derived from areas with a wider range of entire-margin percentages may overestimate the MAT of modern tropical South American sites because of the skew toward higher percentages of entire-margined leaves in tropical sites. In this paper, 30 tropical South American floras are used to test 15 leaf morphology–MAT relationships based on data from other continents as well as South America, in order to assess the applicability of these models to tropical South American vegetation.

2. Materials and methods

2.1. Floral localities

Thirty modern sites located in northern South America (Fig. 1; Appendix 2) were used in this study. Sites were chosen if located within the neo-

tropics of South America between 9°N and 21°S latitudes and if the flora at the site contained 20 or more species. MAT of these sites ranges from 11 to 26.9°C, and mean annual precipitation ranges from 65 to 553 cm (Appendix 2). Sites have varying degrees of seasonality of temperature and precipitation. Sites experience 0–8 dry months per year (Appendix 2) and consist of a variety of vegetation types (Appendix 3). MAT values were taken from the literature or from the nearest climate station (CODESUR, 1979; FAO, 1985; Global Historical Climatology Network, 1999). Location, elevation, and length of climatic records for each site are listed in Appendix 2.

Species lists for each site were taken from the literature. Appendix 3 lists the number of species reported and the area and type of individual sampled for each flora. Species listed for each site were studied from herbarium specimens at the herbaria of the University of Michigan, the Field Museum, and the Pontificia Universidad Católica del Ecuador as well as a reference collec-

tion of R.J. Burnham housed at the University of Michigan. The location and elevation of each specimen as listed on the herbarium specimen were recorded. Specimens collected at the inventoried site were used to score 10% of all species scored. When no site-voucher was available, specimens were scored that had been collected geographically close to the inventoried site and from a similar elevation, so that the specimen scored came from a climatically similar area. Number of leaves per herbarium specimen varied from one to approximately 50.

Specimens were scored for the presence of 31 leaf characters after Wolfe (1993) and Wolfe and Spicer (1999). In the original CLAMP database only 29 characters were scored per site (Wolfe, 1993). Later versions split the smallest and largest size categories into two size classes each. None of the equations tested here rely on either of the size classes that were split. The percentage of each character state among all species at each site is listed in Appendix 1. In total, 1823 specimens were scored representing 1233 species. A total of 208 species from the original floral lists was not scored because the species were not present at the herbaria visited. The number of species scored for each site is listed in Appendix 3. Species totals for all sites exceed the minimum 20 species recommended to predict MAT from leaf morphology (Wolfe, 1993; Povey et al., 1994). As the number of species scored decreases, error increases because each individual species contributes a larger

proportion of the total. Twenty species is suggested as the minimum number of species necessary to ensure that each species does not over-contribute to the total.

2.2. MAT models

Four methods, SLR, MLR, CCA, and NN, were tested on the 30 modern floras using appropriate character percentages listed in Appendix 1. Fifteen models were tested: five SLR, six MLR, two CCA and two NN. Both the SLR and MLR methods have been extensively used by previous workers and the resulting models vary according to which database was used to derive predictive equations. MLR equations also vary due to the choice of leaf characters used in the equation. The regression equations are numbered 1–11 for reference, the CCA and NN methods are not numbered. The number of original data points, standard error, R^2 and p values of each equation, if reported, are listed in Table 1.

The following abbreviations are used throughout this section: SE, standard error; E , percent of flora with entire-margined leaves; BR , base round; W_1 , length to width ratio < 1 ; AE , apex emarginate; L_2 , leptophyll 2; M_2 , microphyll 2; W_2 , length to width ratio 1–2:1; Lo , lobed; BA , base acute. Leaf morphologic characters follow Wolfe (1993). All leaf characters are reported as proportions, and MAT is reported in °C.

Table 1
Number of sites, SE, R^2 and p -value, if reported, for each of the published regression equations tested

| Equation number and source | Number of sites | SE | R^2 | p -value |
|---|-----------------|-----|-------|------------|
| (1) Wilf, 1997 | 9 | 2.0 | 0.94 | < 0.0005 |
| (2) Wilf, 1997 | 106 | 3.4 | 0.76 | < 0.0005 |
| (3) Wilf, 1997 | 74 | 2.1 | 0.84 | < 0.0005 |
| (4) Wolfe, 1979; Wing and Greenwood, 1993 | 34 | 0.8 | 0.98 | < 0.001 |
| (5) Gregory-Wodzicki, 2000 | 12 | 1.6 | 0.89 | N/A |
| (6) Wiemann et al., 1998 | 144 | N/A | 0.90 | N/A |
| (7) Wing and Greenwood, 1993 | 106 | 2.0 | 0.86 | N/A |
| (8) Gregory and Chase, 1992 | 86 | 1.5 | 0.94 | N/A |
| (9) Gregory, 1994 | 84 | 1.5 | 0.94 | N/A |
| (10) Gregory and McIntosh, 1996 | 106 | 2.3 | 0.75 | N/A |
| (11) Gregory and McIntosh, 1996 | 74 | 1.5 | 0.92 | N/A |

Multiple regression equations have a p -value associated with each variable, therefore p -values are not listed for multiple regression equations.

2.2.1. Simple linear regression

Five SLR equations that predict MAT from the percentage of species with entire-margined leaves were tested. The first three equations were originally published in a study on the use of leaf margin as a robust correlate of MAT (Wilf, 1997). Though not suggested for use as predictive equations, these equations are published SLR equations derived from the CLAMP database or sites from both North and South America, so they were tested for their predictive value here. Wilf (1997) compiled a data set of nine sites from the Western Hemisphere ranging from Bolivia to Pennsylvania. His equation relating the percentage of species with entire-margined leaves and MAT is:

$$\text{MAT} = 28.6E + 2.24 \quad (1)$$

Two of the SLR equations are based on data from the 1993 CLAMP database (Wilf, 1997). The database used in this equation includes 106 sites, primarily from North America:

$$\text{MAT} = 29.1E - 0.266 \quad (2)$$

An abundance of cold sites in the CLAMP database increases the slope of the regression line and lowers the value of the y -intercept. The result is that MAT is often underestimated for warm sites when using a regression equation based on the entire database. To eliminate the bias introduced by high numbers of cold sites, Wilf (1997) included a relationship in which the coldest 32 sites, those with cold month mean temperatures below -2°C , were removed from the database used above prior to calculating the following regression:

$$\text{MAT} = 24.4E + 3.25 \quad (3)$$

The original regression that quantified the relationship between leaf margin and temperature is based on 34 sites from eastern Asia (Wolfe, 1979). Wing and Greenwood (1993) published the following equation based on the graph of the original data from Wolfe (1979):

$$\text{MAT} = 30.6E + 1.14 \quad (4)$$

An equation from Gregory-Wodzicki (2000) is based on data from 12 sites in Bolivia, along with two South American sites taken from Wilf (1997). This equation is unique in that the data come only from South America:

$$\text{MAT} = 31.6E - 0.059 \quad (5)$$

2.2.2. Multiple regression

Six MLR equations were tested. The equations use varying numbers of sites from different versions of the CLAMP database to quantify the relationship between leaf morphology and MAT. Wiemann et al. (1998) derived an equation from the CLAMP 3B database:

$$\text{MAT} = 0.207E - 0.058BR - 0.202W_1 + 9.865 \quad (6)$$

Wing and Greenwood's (1993) equation is based on 106 CLAMP sites primarily from North America. The values used to derive the equation were first transformed by taking the arcsine in degrees of the square root of the proportion represented by each percentage value before the regression analysis, to stabilize the variance of bounded data (Sokal and Rohlf, 1995):

$$\text{MAT} = 17.372E + 2.896AE - 8.592W_1 + 2.536 \quad (7)$$

Gregory (1994; Gregory and Chase, 1992; Gregory and McIntosh, 1996) has published several different regression equations based on the CLAMP data set. Four are included here. Data used in the following four equations have undergone arcsine transformation as described above. The following equation (Gregory and Chase, 1992) is based on 86 CLAMP sites:

$$\text{MAT} = 10.4E - 15.0L_2 - 8.68W_1 + 4.74AE - 5.13M_2 + 16.1 \quad (8)$$

The following equation from Gregory (1994) is based on 84 of the sites used in the previous equa-

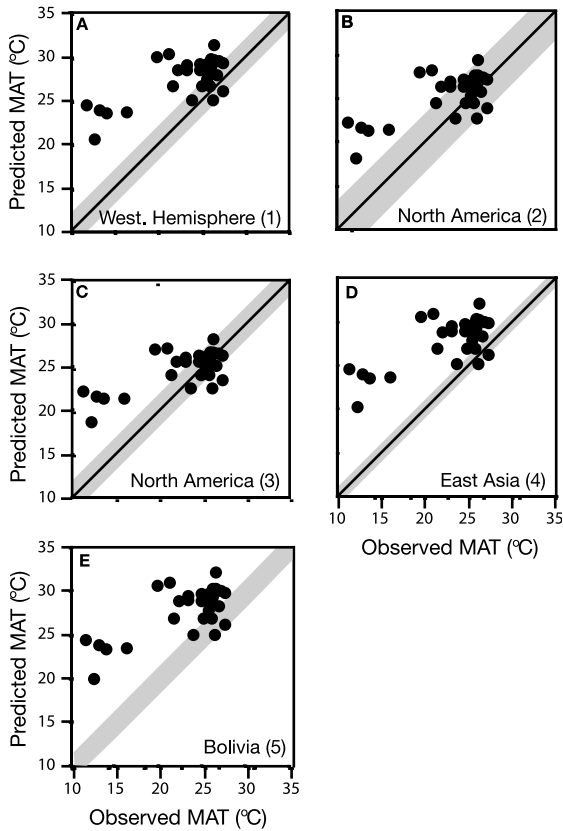


Fig. 2. Results of simple linear regression equations. Results are plotted as predicted MAT vs. observed MAT. The diagonal line in each graph is the line of unity of predicted MAT with observed MAT. The SE (when reported) of the predictive equation is indicated by gray shading. Predicted MAT values result from the use of the following models: (A) Eq. 1 (Wilf, 1997); (B) Eq. 2 (Wilf, 1997); (C) Eq. 3 (Wilf, 1997); (D) Eq. 4 (Wolfe, 1979); (E) Eq. 5 (Gregory-Wodzicki, 2000).

tion. The two coldest sites were removed to eliminate any bias toward cold temperatures:

$$\text{MAT} = 10.34E^2 + 5.48AE - 15.32W_1^2 - 15.29L_2 - 5.79M_2 + 15.32 \quad (9)$$

Gregory and McIntosh (1996) proposed two relationships, one is based on the 106-site CLAMP database, and the other removes 32 sites with cold month mean temperatures below -2°C . All data were transformed by adding 0.005 to the

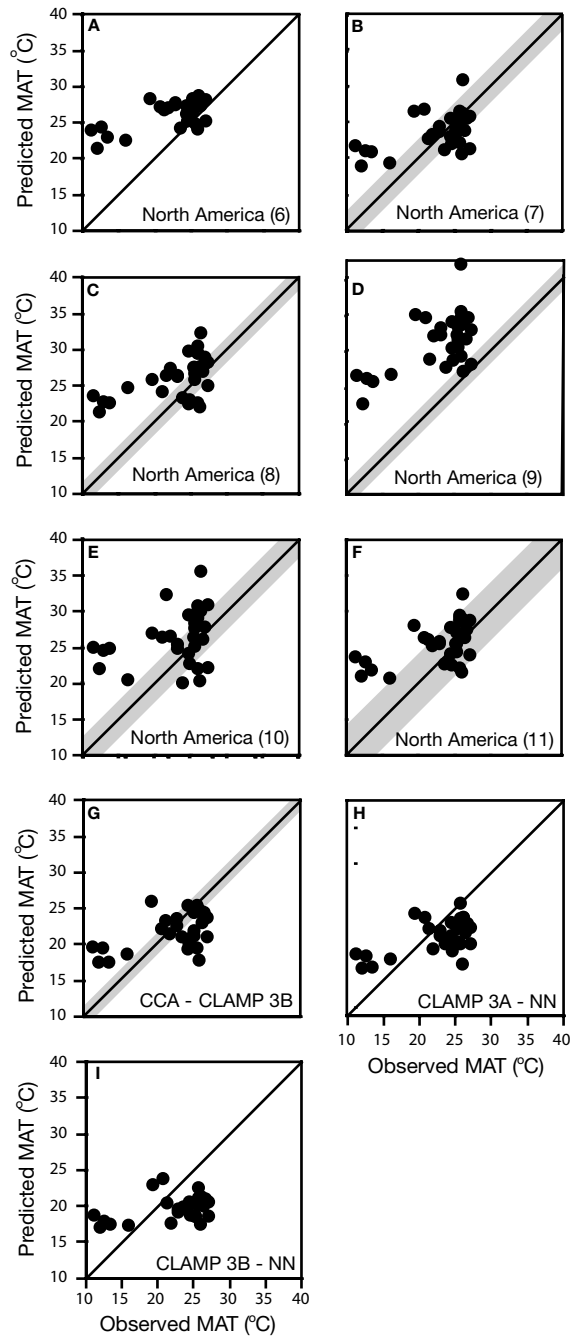


Fig. 3. Results of MLR equations, CCA and NN. Results are plotted as in Fig. 2. (A) Eq. 6 (Wiemann et al., 1998); (B) Eq. 7 (Wing and Greenwood, 1993); (C) Eq. 8 (Gregory and Chase, 1992); (D) Eq. 9 (Gregory, 1994); (E) Eq. 10 (Gregory and McIntosh, 1996); (F) Eq. 11 (Gregory and McIntosh, 1996); (G) CCA, CLAMP 3B (Wolfe, 1993, 1995); (H) NN3A; (I) NN3B.

Table 2

Observed and predicted MAT (°C) for each site and model and the average error for all models for each tropical South American site

| Site | Alto Ivan | Rio Grande | Conquista | Corumbá | Belém--igapó forest | Belém--terra firme | Rio Claro | Mamaus | Alto Yunda | Loja--non-ridge | Loja--ridge | Pasochoa | Baeza | Rio Palenque | El Pechiche | Cuyabeno | Añanagu--floodplain | Añanagu--unflooded | Jaunche | Cerro Mutiles | Guyana--mora consociation | Guyana--Morabukea | Guyana--mixed forest | Pakisa, Manu NP Plot 1 | Pakisa, Manu NP Plot 3 | La Montaña | Laguna de Coeos | Corozal--Guiana Shield | Corozal--woody savanna | Délgadito Creek |
|---|-----------|------------|-----------|---------|---------------------|--------------------|-----------|--------|------------|-----------------|-------------|----------|-------|--------------|-------------|----------|---------------------|--------------------|---------|---------------|---------------------------|-------------------|----------------------|------------------------|------------------------|------------|-----------------|------------------------|------------------------|-----------------|
| Observed MAT | 26.8 | 19.6 | 23.7 | 24.6 | 26.2 | 26.2 | 25.8 | 26.6 | 21.5 | 11.5 | 12.4 | 13.8 | 16.2 | 22.1 | 24.8 | 24.6 | 25.4 | 25.4 | 25.3 | 25.5 | 25.9 | 25.9 | 23.1 | 23.1 | 13.0 | 21.0 | 27.2 | 27.2 | 26.1 | |
| Predicted MAT | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Western Hemisphere (1) | 28.9 | 29.4 | 24.4 | 26.8 | 30.8 | 29.1 | 26.1 | 27.4 | 26.1 | 23.9 | 19.9 | 23.0 | 23.0 | 27.8 | 26.1 | 28.6 | 26.9 | 28.6 | 27.9 | 27.7 | 29.2 | 28.2 | 29.1 | 27.9 | 28.4 | 23.3 | 29.7 | 28.7 | 25.4 | 24.4 |
| North America/CLAMP-106 sites (2) | 26.9 | 27.4 | 22.3 | 24.8 | 28.8 | 27.1 | 24.0 | 25.3 | 24.0 | 21.8 | 17.7 | 20.8 | 20.9 | 25.8 | 24.0 | 26.6 | 24.8 | 26.5 | 25.9 | 25.6 | 27.1 | 26.2 | 27.0 | 25.9 | 26.4 | 21.2 | 27.7 | 26.7 | 23.3 | 22.3 |
| North America/CLAMP-74 sites (3) | 26.0 | 26.5 | 22.1 | 24.8 | 27.7 | 26.2 | 23.6 | 24.7 | 23.6 | 21.7 | 18.3 | 20.9 | 21.0 | 25.1 | 23.6 | 25.8 | 24.3 | 25.7 | 25.2 | 25.0 | 26.2 | 25.4 | 26.1 | 25.2 | 25.6 | 21.2 | 26.7 | 25.8 | 23.0 | 22.1 |
| East Asia (4) | 29.7 | 30.2 | 24.8 | 27.5 | 31.7 | 29.9 | 26.6 | 28.0 | 26.6 | 24.3 | 20.0 | 23.3 | 23.4 | 28.5 | 26.6 | 29.4 | 27.5 | 29.3 | 28.6 | 28.4 | 29.9 | 29.0 | 29.8 | 28.6 | 29.2 | 23.7 | 30.5 | 29.5 | 26.0 | 24.8 |
| Bolivia (5) | 29.4 | 30.0 | 24.4 | 27.1 | 31.5 | 29.6 | 26.3 | 27.6 | 26.3 | 23.9 | 19.5 | 22.8 | 22.9 | 28.2 | 26.3 | 29.1 | 27.2 | 29.1 | 28.3 | 28.1 | 29.7 | 28.7 | 29.6 | 28.3 | 28.9 | 23.2 | 30.3 | 29.2 | 25.6 | 24.4 |
| North America/CLAMP 3B (6) | 27.4 | 27.9 | 23.8 | 25.0 | 28.3 | 28.0 | 24.5 | 26.9 | 26.3 | 23.5 | 21.0 | 22.6 | 22.2 | 26.6 | 24.9 | 26.9 | 26.0 | 27.9 | 26.7 | 27.1 | 27.9 | 27.2 | 27.8 | 27.0 | 27.3 | 24.0 | 26.8 | 27.7 | 24.8 | 23.7 |
| North America/CLAMP-106 sites (7) | 25.3 | 26.3 | 21.1 | 21.9 | 30.6 | 26.1 | 22.0 | 23.7 | 22.5 | 21.6 | 18.9 | 20.8 | 19.3 | 23.2 | 21.9 | 25.4 | 22.2 | 24.7 | 23.7 | 23.5 | 26.3 | 25.2 | 26.0 | 23.6 | 24.3 | 20.9 | 26.6 | 25.6 | 21.2 | 20.4 |
| North America/CLAMP-86 sites (8) | 28.2 | 25.1 | 22.6 | 21.2 | 31.5 | 26.8 | 21.9 | 26.3 | 25.7 | 22.9 | 20.6 | 21.9 | 24.0 | 26.7 | 22.3 | 29.0 | 25.9 | 26.8 | 26.7 | 25.1 | 29.7 | 28.7 | 28.7 | 25.5 | 25.6 | 22.1 | 23.4 | 27.4 | 24.3 | 21.3 |
| North America/CLAMP-84 sites (9) | 33.5 | 34.0 | 26.7 | 28.0 | 41.3 | 33.1 | 28.3 | 30.6 | 27.9 | 25.7 | 21.8 | 24.8 | 25.8 | 31.1 | 27.7 | 33.1 | 29.5 | 32.3 | 31.2 | 30.4 | 34.4 | 32.6 | 33.5 | 31.2 | 32.2 | 25.2 | 33.6 | 31.9 | 27.2 | 26.2 |
| North America/CLAMP-106 sites (10) | 27.5 | 26.6 | 19.9 | 22.6 | 35.1 | 29.6 | 21.8 | 25.8 | 31.9 | 24.7 | 21.8 | 24.5 | 20.3 | 26.1 | 22.4 | 29.2 | 24.8 | 27.3 | 26.0 | 28.0 | 30.3 | 28.7 | 29.7 | 25.1 | 24.5 | 24.3 | 26.0 | 30.5 | 21.9 | 20.1 |
| North America/CLAMP-77 sites (11) | 27.3 | 27.9 | 22.6 | 23.0 | 32.2 | 28.7 | 22.1 | 26.2 | 25.9 | 23.5 | 20.9 | 21.7 | 20.7 | 25.0 | 22.4 | 27.6 | 24.2 | 26.8 | 25.4 | 25.3 | 29.3 | 28.4 | 28.8 | 25.3 | 25.7 | 22.9 | 26.2 | 28.6 | 23.9 | 21.5 |
| CCA | 23.7 | 25.1 | 20.3 | 19.2 | 23.9 | 24.0 | 18.8 | 23.0 | 22.8 | 18.9 | 16.7 | 16.8 | 18.3 | 19.7 | 19.4 | 25.0 | 21.2 | 23.8 | 20.5 | 20.6 | 24.1 | 24.0 | 25.8 | 22.0 | 22.8 | 18.8 | 23.2 | 23.1 | 20.2 | 17.2 |
| NN3A | 22.7 | 24.1 | 19.9 | 21.0 | 23.5 | 23.5 | 20.0 | 21.5 | 22.1 | 18.5 | 16.6 | 16.8 | 17.8 | 19.2 | 19.0 | 22.8 | 22.1 | 20.1 | 25.3 | 20.2 | 22.6 | 23.4 | 25.5 | 21.0 | 21.8 | 18.3 | 23.6 | 22.2 | 19.9 | 17.2 |
| NN3B | 20.5 | 22.5 | 19.4 | 20.1 | 20.8 | 20.7 | 19.7 | 19.6 | 20.0 | 18.3 | 16.6 | 17.1 | 16.9 | 17.2 | 18.3 | 19.7 | 18.2 | 19.9 | 18.2 | 18.1 | 20.1 | 20.7 | 22.0 | 18.7 | 19.1 | 17.5 | 23.3 | 20.1 | 18.2 | 19.1 |
| Average error of predicted MAT per site | 2.4 | 7.8 | 2.1 | 2.8 | 5.2 | 2.6 | 3.1 | 2.3 | 3.8 | 10.9 | 6.9 | 7.5 | 4.9 | 4.3 | 2.7 | 3.3 | 2.3 | 2.8 | 2.7 | 2.7 | 3.3 | 2.5 | 2.6 | 3.4 | 3.5 | 8.9 | 5.8 | 2.6 | 4.0 | 4.5 |

Equation numbers correspond to the text. Sites with MAT $\leq 21^\circ\text{C}$ are in bold type.

Table 3

Published SE and percent of floras within the published SE or within 2.0°C, average 95% predictive confidence interval, and range, median and average error of predicted MAT produced by each equation for 30 tropical South American floras

| Method | Equation number and source | SE of equation (± °C) | % floras within SE of equation | % floras within 2.0°C | Average 95% predictive interval (°C) | Range of error (°C) | Median error (°C) | Average error (°C) |
|--------|---|--------------------------|--------------------------------|-----------------------|---|------------------------|----------------------|-----------------------|
| SLR | (1) Wilf, 1997 | 2.0 | 26.7 | – | 5.1 | 0.3–12.4 | 3.2 | 4.3 |
| | (2) Wilf, 1997 | 3.4 | 66.7 | – | 6.9 | 0.1–10.3 | 1.9 | 2.9 |
| | (3) Wilf, 1997 | 2.1 | 60.0 | – | 4.4 | 0.0–10.2 | 1.7 | 2.7 |
| | (4) Wolfe, 1979; Wing and Greenwood, 1993 | 0.8 | 0 | 20.0 | 1.6 | 0.8–12.8 | 4.0 | 4.8 |
| | (5) Gregory-Wodzicki, 2000 | 1.6 | 13.3 | 26.7 | 3.4 | 0.5–12.9 | 3.7 | 4.6 |
| MLR | (6) Wiemann et al., 1998 | N/A | N/A | – | 4.1 | 0.1–12.0 | 2.2 | 3.5 |
| | (7) Wing and Greenwood, 1993 | 2.0 | 50.0 | – | 6.5 | 0.1–10.1 | 2.3 | 3.1 |
| | (8) Gregory and Chase, 1992 | 1.5 | 30.0 | 30.0 | – | 0.2–11.9 | 2.8 | 3.7 |
| | (9) Gregory, 1994 | 1.5 | 6.7 | 6.7 | – | 0.0–15.1 | 6.9 | 7.3 |
| | (10) Gregory and McIntosh, 1996 | 2.3 | 53.0 | – | 5.4 | 0.6–13.2 | 3.9 | 4.6 |
| | (11) Gregory and McIntosh, 1996 | 1.5 | 30.0 | 30.0 | 3.8 | 0.1–12.0 | 2.9 | 3.7 |
| CCA | CCA, Wolfe, 1995; Wolfe and Spicer, 1999 | 1.0 | 13.3 | 33.3 | – | 0.1–9.0 | 3.4 | 3.6 |
| NN | NN3A, Stranks and England, 1997 | N/A | N/A | 16.7 | – | 0.4–8.9 | 3.7 | 3.9 |
| | NN3B, Stranks and England, 1997 | N/A | N/A | 6.7 | – | 0.7–9.0 | 5.3 | 5.2 |

raw percentage value, followed by arcsine transformation:

$$\text{MAT} = 23.258E - 16.099W_1 - 12.211L_2 + 11.484W_2 + 10.282Lo - 7.022BA - 11.262 \quad (10)$$

$$\text{MAT} = 16.656E - 9.2L_2 - 5.594W_1 + 5.137BA + 4.879AE + 1.768 \quad (11)$$

2.2.3. Multivariate statistical techniques

CCA on the CLAMP database was carried out for this study using CANOCO Version 3.12 (ter Braak, 1991), an ordination program used here to quantify the association between climatic variables and leaf morphologic characters. The axis scores resulting from the ordination are converted to absolute temperature values through multiple regression equations. Both CLAMP 3A, a 173-site

CLAMP database, and CLAMP 3B, a 144-site CLAMP database that excludes 29 alpine and scrub outliers (Wolfe, 1995; Wolfe and Spicer, 1999), were analyzed with CCA. Only the results from the CLAMP 3B analysis are reported. Both the CLAMP database and the regression equations are available online from Jack A. Wolfe (University of Arizona, Tucson, AZ).

The final method tested is CCA, followed by a NN resemblance function. Canoco Version 3.12 was again used for the analysis. The first three axis scores resulting from the ordination were used to determine the twenty sites in the CLAMP database which are closest, using Euclidean distance, to the unknown site (Stranks and England, 1997). The MAT of the twenty nearest neighbors are then used as calibration data to determine the MAT of the test site, by calculating a regression equation from the axis scores. Both the 173-site CLAMP 3A and the 144-site CLAMP 3B databases were used with this method. The results of

Table 4

Range, median and average error of predicted MAT produced by each equation for the combined seven sites with MAT $\leq 21^\circ\text{C}$: Baeza, Loja–non-ridge, Loja–ridge, Laguna de Cocos, La Montaña, Pasachoa, and Rio Grande contrasted with the same values for the combined 23 sites with MAT $> 21^\circ\text{C}$

| Method | Equation number and source | SE of equation ($\pm^\circ\text{C}$) | % floras within SE of equation | % floras within 2.0°C | Range of error ($^\circ\text{C}$) | Median error ($^\circ\text{C}$) | Average error ($^\circ\text{C}$) |
|---------------------------------|---|--|--------------------------------|-------------------------------------|-------------------------------------|-----------------------------------|------------------------------------|
| SLR | (1) Wilf, 1997 | 2.0 | 34.8 | – | 0.3–5.7 | 2.6 | 2.8 |
| | | | 0.0 | – | 6.8–12.4 | 9.2 | 9.3 |
| | (2) Wilf, 1997 | 3.4 | 87.0 | – | 0.1–3.9 | 1.2 | 1.6 |
| | | | 0.0 | – | 4.7–10.3 | 7.0 | 7.1 |
| | (3) Wilf, 1997 | 2.1 | 78.3 | – | 0.0–4.2 | 1.2 | 1.4 |
| | | | 0.0 | – | 4.8–10.7 | 6.9 | 7.0 |
| | (4) Wolfe, 1979; Wing and Greenwood, 1993 | 0.8 | 0.0 | 26.0 | 0.8–6.4 | 3.3 | 3.4 |
| | | | 0.0 | 0.0 | 7.2–12.8 | 9.5 | 9.7 |
| | (5) Gregory-Wodzicki, 2000 | 1.6 | 17.4 | 34.8 | 0.5–6.1 | 3.0 | 3.1 |
| | | | 0.0 | 0.0 | 6.7–12.4 | 9.3 | 9.3 |
| | MLR | (6) Wiemann et al., 1998 | N/A | N/A | 60.9 | 0.1–4.8 | 1.9 |
| | | | N/A | 0.0 | 5.8–12.0 | 8.6 | 8.6 |
| (7) Wing and Greenwood, 1993 | | 2.0 | 65.2 | – | 0.1–6.0 | 1.6 | 2.0 |
| | | | 0.0 | – | 3.1–10.1 | 6.7 | 6.7 |
| (8) Gregory and Chase, 1992 | | 1.5 | 39 | 39.0 | 0.2–5.3 | 2.5 | 2.5 |
| | | | 0.0 | 0.0 | 2.4–11.4 | 8.1 | 7.5 |
| (9) Gregory, 1994 | | 1.5 | 8.7 | 8.7 | 0.0–15.1 | 6.4 | 5.9 |
| | | | 0.0 | 0.0 | 9.4–14.4 | | 12.2 |
| 11.9 | | | | | | | |
| (10) Gregory and McIntosh, 1996 | | 2.3 | 34.8 | – | 0.7–10.4 | 3.3 | 3.4 |
| | | | 0.0 | – | 4.1–13.2 | 9.4 | 8.7 |
| (11) Gregory and McIntosh, 1996 | 1.5 | 39.1 | 39.1 | 0.1–6.0 | 2.5 | 2.3 | |
| | | 0.0 | 0.0 | 4.5–12.0 | 8.3 | 8.1 | |
| CCA | CCA, Wolfe, 1995; Wolfe and Spicer, 1999 | 1.0 | 13.0 | 34.8 | 0.1–9.0 | 3.3 | 3.5 |
| | | | 14.3 | 28.6 | 0.3–7.4 | 4.3 | 4.0 |
| NN | NN3A, Stranks and England, 1997 | N/A | N/A | 17.4 | 0.4–8.9 | 3.6 | 3.9 |
| | | | N/A | 14.3 | 1.6–7.0 | 4.2 | 4.0 |
| | NN3B, Stranks and England, 1997 | N/A | N/A | 4.0 | 1.5–9.0 | 5.5 | 5.8 |
| | | | N/A | 14.3 | 0.7–6.8 | 3.3 | 3.5 |

Low-temperature sites in bold type. Percent of floras within SE is calculated from the number of floras in the group; 5 low-temperature sites and 25 high-temperature sites. Equations with a blank space in column 5 have a SE $\geq 2.0^\circ\text{C}$.

each analysis are referred to as NN3A and NN3B, depending on whether CLAMP 3A or 3B was used.

2.2.4. Error evaluation

Temperatures were calculated for each site using the 15 models detailed above. Predicted MAT was compared to observed temperature for each site. Absolute average, median, and range of error were calculated for each equation. In addition, the percentage of sites that are estimated within the SE of the equation and the average 95% predicted

confidence interval were calculated for each equation.

3. Results

3.1. General results

Each of the tested models gave different results (Figs. 2 and 3; Tables 2–4), but some trends do emerge. All equations overestimate the MAT of the same seven modern sites with an observed

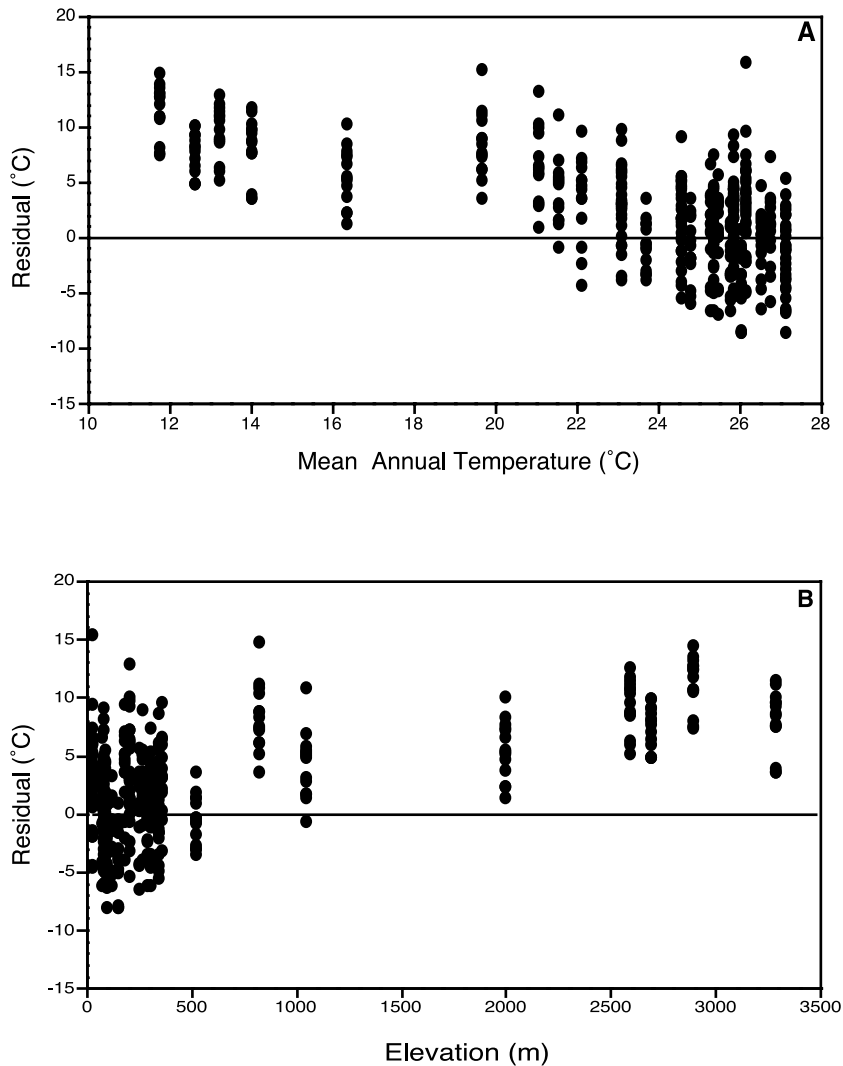


Fig. 4. Residuals of predicted MAT vs. MAT or elevation. Each point represents the residual of predicted MAT for one of the tested equations. (A) Residuals of predicted MAT vs. MAT. (B) Residuals of predicted MAT vs. elevation.

MAT $\leq 21^{\circ}\text{C}$ (Figs. 2–4; Tables 2–4). These sites are Loja–ridge, Loja–non-ridge, La Montaña, Paschoa, Baeza, Rio Grande, and Laguna de Cocos, and are distinguished by bold text (Appendices 2 and 3; Tables 2 and 4). For the 23 sites with an observed MAT above 21°C , predicted MAT values tend to form a tight but random scatter (Figs. 2 and 3). However, distinct sub-trends are present. SLR Eqs. 1, 4 and 5 overestimate MAT of the majority of the modern sites (Fig. 2A,D,E)

with almost identical predicted temperatures for each site.

The results of most MLR models follow the general pattern of the SLR equations, except Eq. 9, which overestimates MAT for all but one of the modern sites (Fig. 3D). Within the general MLR results are several noted patterns. MLR Eq. 10 produces high deviations in the higher-temperature sites (Fig. 3E). Removal of the coldest sites from the regression model results in Eq. 11 and

reduces the scatter in predicted temperatures (Fig. 3F). CCA and NN3B underestimate MAT at 21 of the 22 sites with a MAT above 22°C, and overestimate all eight sites with a MAT below 22°C (Fig. 3G,I). NN3A produces a similar result, the seven sites with MAT below 21°C are overestimated, and the rest are underestimated (Fig. 3H).

3.2. Standard error

The fitness of each model is determined from several estimates of error. The SE of each model is shown in Figs. 2 and 3 and listed in Table 3. The percentage of modern floras that have a predicted MAT within the reported SE of the given model ranges from 0% for Eq. 4 (Table 3) to 67% for Eq. 2 (Table 3). This measure of fitness is based on the magnitude of the SE of the equation so that, in general, if the SE of the model is large, more floras will be ‘accurately’ predicted. Wilf (1997) proposed that a minimum error of 2.0°C be used when the SE of the original equation is below 2.0°C to account for binomial sampling error. The ten models with reported SE below 2.0°C, or with no reported SE, were assigned the proposed minimum SE of 2.0°C for comparative purposes. The percentage of modern floras that have a predicted MAT within 2.0°C SE ranges from 6.7% NN3B (Fig. 3I) to 50% for MLR Eq. 7 (Fig. 3B).

3.3. Predictive confidence intervals

Ninety-five percent predictive confidence intervals were calculated for each predicted MAT for the 12 regression equations for which the primary data used to calculate the regression was available (Figs. 5 and 6). Predictive intervals are larger than the SE of the equation, and vary in magnitude depending on the relationship of the unknown site to the original data used to calculate the regression equation. The average 95% predictive confidence intervals for each equation are listed in Table 3. Eq. 4 has the smallest average predictive confidence interval while Eq. 2 has the largest. The magnitude of predictive confidence intervals can illustrate the potential resolution of temperatures calculated from each regression

equation. Predictive confidence intervals that overlap for all MAT indicate that the regression equation cannot significantly differentiate between predicted temperatures. Eqs. 4, 5 and 11 have several predictive confidence intervals that do not overlap, suggesting that these equations have higher ability to resolve different temperatures than the other equations. The best equation to predict MAT of South American data would have small predictive intervals that overlap the observed temperature for the majority of sites. None of the nine equations with calculated predictive confidence intervals have intervals that fit both criteria of small confidence intervals and observed temperatures that fall within the confidence interval, indicating that these equations are not entirely appropriate for predicting temperatures of the 30 tested South American sites.

3.4. Absolute error estimates

The average, median and range of the errors in absolute values for each model for the thirty sites are listed in Table 3. The average of the errors is smaller than the reported SE for SLR Eq. 2. SLR Eq. 3 has the smallest average error at 2.7°C, and the lowest median error, 1.7°C. MLR Eq. 9 has the largest average error, 7.3°C and highest median error, 6.9°C. The range of error (Table 3) indicates that every model can predict MAT of at least one site to within 0.8°C of its observed MAT. However, each model also produces a predicted MAT with an error of at least 8.9°C and as much as 15.1°C. The most restricted range of errors, 0.7–9.0°C, results from NN3B, while Eq. 9 has the widest range of errors, 0.0–15.1°C. The floras with the best and worst predicted MAT are not consistent from one model to the next (Table 2).

3.5. Error for high- and low-elevation sites

Because all models overestimate the MAT of seven low-temperature sites, (Baeza, Laguna de Cocos, Loja-non-ridge, Loja-ridge, La Montaña, Pasochoa, and Rio Grande), these sites were removed and evaluated separately. The percentage of modern floras that have a predicted MAT

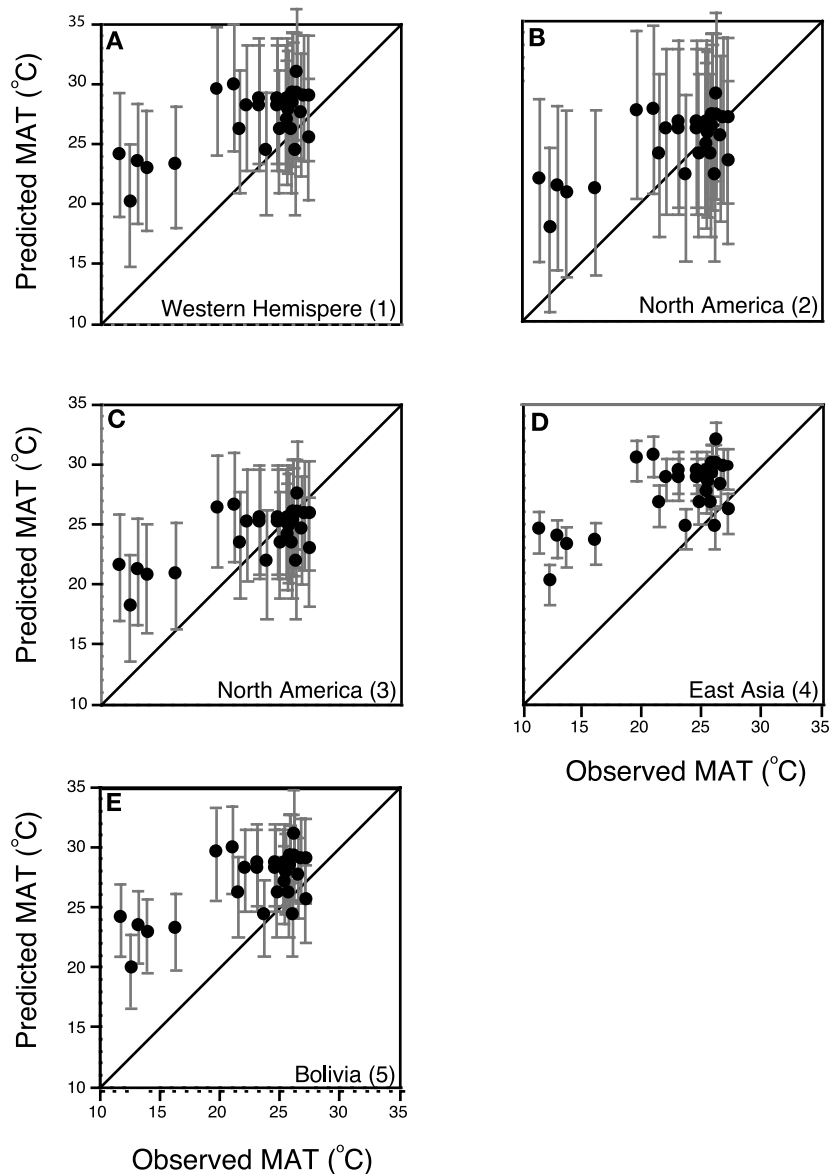


Fig. 5. Results of SLR equations. Results are plotted as predicted MAT vs. observed MAT. The diagonal line in each graph is the line of unity of predicted MAT with observed MAT. Error bars indicate the 95% predictive confidence interval. Predicted MAT values result from the use of the following models: (A) Eq. 1 (Wilf, 1997); (B) Eq. 2 (Wilf, 1997); (C) Eq. 3 (Wilf, 1997); (D) Eq. 4 (Wolfe, 1979); (E) Eq. 5 (Gregory-Wodzicki, 2000).

within the reported SE of the given model, range, median and average error were recalculated for the combined low- and combined high-temperature sites (Table 4).

For warm sites ($>21^{\circ}\text{C}$), four regression equations based on the CLAMP database, Eqs. 2, 3, 6

and 7, have the lowest average error and are the only equations with an average error within 2.0°C . These four equations estimate MAT within the SE of the equation for more than 50% of the sites tested, and have a median error of less than 2.0°C . Eq. 2 has the smallest range of errors, 0.1–

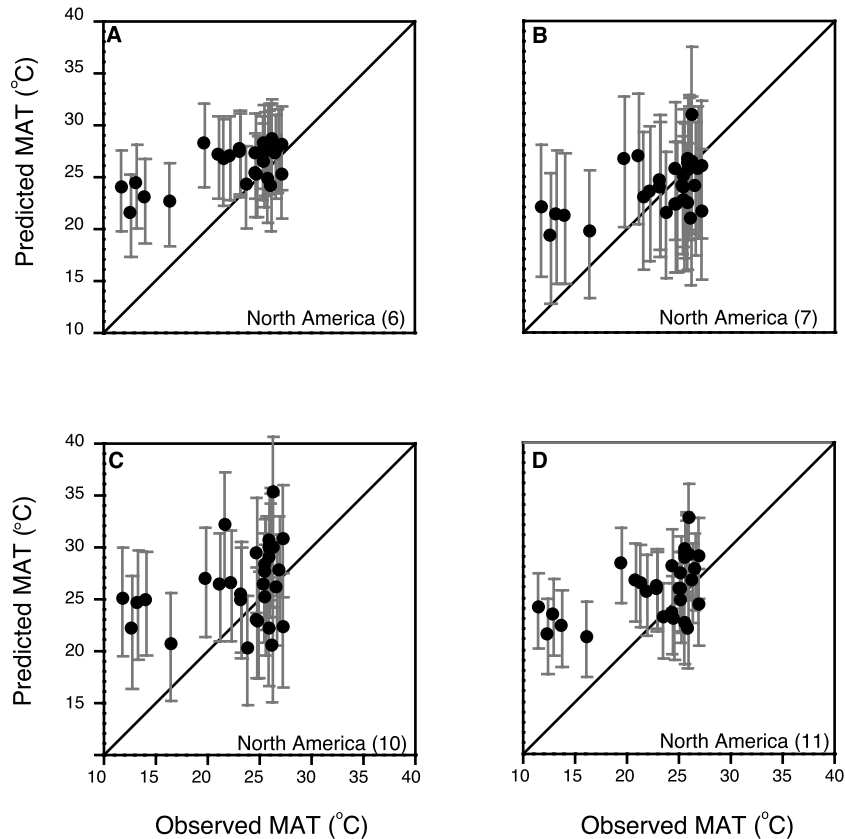


Fig. 6. Results of four MLR equations. Results are plotted as in Fig. 5. (A) Eq. 6 (Wiemann et al., 1998); (B) Eq. 7 (Wing and Greenwood, 1993); (C). Eq. 10 (Gregory and McIntosh, 1996); (D). Eq. 11 (Gregory and McIntosh, 1996).

3.9°C, while Eq. 9 has the largest range, 0.0–15.1°C.

For cold sites ($\leq 21^\circ\text{C}$), NN3B has the lowest average error (Table 4), and predicted the MAT of cold sites more accurately than that of warm sites. NN3B has the lowest median error, and Eq. 9 has the smallest range of errors. Both CCA and NN predicted MAT of the low-temperature sites more accurately than the regression equations. Eq. 9 has the highest median and average error for cold sites at 12.2 and 11.9°C, respectively.

4. Discussion

Four of the existing models relating MAT to leaf morphology adequately predict MAT of high-temperature sites ($> 21^\circ\text{C}$), but are inad-

equately for predicting MAT in low-temperature sites ($\leq 21^\circ\text{C}$) in tropical South America. The other eleven published equations, of which ten are reported, are inadequate at predicting MAT at the majority of neotropical sites. The relationship between MAT and leaf morphology exhibits behavior in these 30 tropical South American sites different from that in sites from elsewhere. The reasons for the inadequacy of most current models to predict tropical South American MAT, especially at low-temperature sites, are probably many and not fully known.

4.1. Leaf margin percentages

One major difference between the South American neotropical sites and those used for most existing databases is the relative abundance of

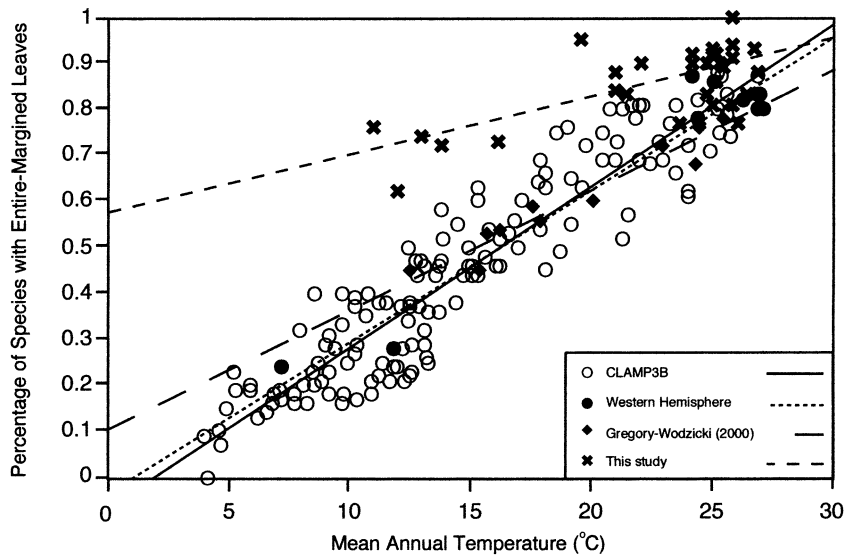


Fig. 7. Relationship between MAT and percentage of species with entire margins for four different modern datasets: (1) 144-site CLAMP 3B database (Wolfe, 1995); (2) Western Hemisphere database (Wilf, 1997); (3) Bolivian database (Gregory-Wodzicki, 2000); and (4) the thirty neotropical test sites. SLR equations are not given in the text for the CLAMP 3B or the 30 neotropical test databases but are listed here: (1) CLAMP 3B: $\text{MAT} = 24.88E + 3.53$, $R^2 = 0.87$, $\text{SE} = 2.18^\circ\text{C}$, and (2) 30 neotropical sites: $\text{MAT} = 38.54E - 10.24$, $R^2 = 0.47$, $\text{SE} = 3.39^\circ\text{C}$.

entire-margined species in tropical regions (Bailey and Sinnott, 1915; Wolfe, 1979, 1993). Fig. 7 shows MAT vs. the percentage of species with entire-margined leaves for the CLAMP 3B database and the thirty neotropical test sites. The restriction of the test sites to tropical South America eliminates floras with a low percentage of species with entire margins, but not floras with moderately low MAT, such that the resulting linear regression has a shallow slope and a high y -intercept. The SLR equation that results from the CLAMP 3B data set, as well as those from the other databases used in this paper, have a slope that is steeper and a low or negative y -intercept, in comparison with the slope derived from the tropical South American sites. In addition, the percentage of species with entire-margined leaves is the most dominant character in all MLR regression equations evaluated. The result of the dominance of the character 'percentage of entire-margined species' is that all of the models tested in this paper overestimate the MAT of lower-temperature neotropical sites (Tables 2 and 4). Comparing the slopes in Fig. 7 of the CLAMP 3B database and the South American sites tested

here using a slope equality F-test (Sokal and Rohlf, 1995) indicates that the slopes of these equations are significantly different ($p < 0.001$). Removing the sites with $< 60\%$ entire-margined species to constrain the CLAMP data set will improve the estimates of the low-temperature sites, because the slope of the regression equation that results from this culled set is similar to that of the test sites (Fig. 8), though still statistically different ($p < 0.05$). Lower MAT sites from Australia also have higher percentages of entire-margined species than do sites with similar MAT in North America (D. Greenwood, pers. commun., Victoria University of Technology, Melbourne, Vic.), as do the subalpine outliers in the CLAMP 3A database (Fig. 8). Sites with MAT above 21°C plot together in all regions sampled (Fig. 7).

Cool temperature sites from Bolivia (Gregory-Wodzicki, 2000) do not have higher than expected percentages of entire-margined species, and thus do not help to predict accurately the MAT of the seven low-MAT sites. The lower percentage of entire-margined species in the Bolivian sites may be due to environmental conditions or different sampling strategy, discussed below, or may be

due to the fact that the low-MAT sites from the Bolivian database have recently been disturbed by grazing or burning (Gregory-Wodzicki, 2000) and may be composed of successional plants. Successional, secondary forests may have more species with toothed leaves than primary forest in the same area (Kappelle and Leal, 1996).

The equation based on Western Hemisphere sites (Wilf, 1997) did not estimate the MAT of 24 of the 30 neotropical sites with accuracy, even though the database includes two South American sites with high percentages of entire-margined species. The database used to derive this predictive equation contains 9 sites encompassing a broad geographic range. Seven of the sites have a MAT between 24.2 and 27.1°C, and cluster with the other high MAT sites with high percentages of entire-margined species (Fig. 7). The two low-temperature sites, which anchor the regression and thus determine the slope and y -intercept, are North American sites with low percentages of entire-margined species. The result is that the regression equation for this data set is very similar to the equations derived from pre-

dominantly Northern Hemisphere vegetation (Fig. 7). Thus, low-temperature sites are overestimated when calculated by this equation (Fig. 2A).

The high proportion of entire-margined species in many tropical South American sites may be due in part to phylogeny and the uplift history of northern South America. While some families and genera of plants do indeed show morphologic variation as MAT increases, the leaf morphology of other taxonomic groups appears to be fixed, regardless of the environment (Bongers and Popma, 1990). For example, species of *Quercus* and *Prunus* both exhibit serrate margins in temperate areas and predominantly entire margins in tropical and subtropical areas. In contrast, species in the families *Betulaceae* and *Ulmaceae* are almost always serrate (Watson and Dallwitz, 1992; Gentry, 1996), species within the genus *Eucalyptus* are, with one exception, entire-margined, as are species within the family *Magnoliaceae* (Watson and Dallwitz, 1992). The high percentage of species with entire-margined leaves in the low-temperature test floras may be due to the presence of an unusually large number of obligately en-

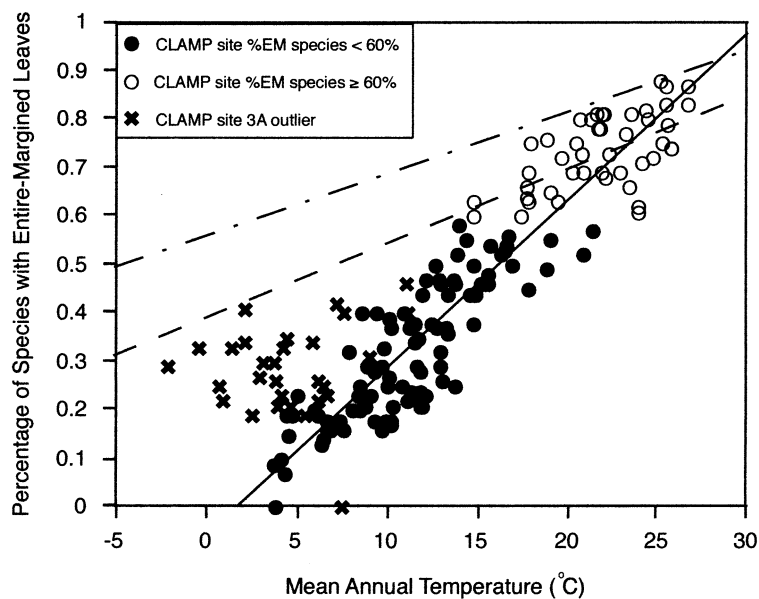


Fig. 8. MAT vs. percentage of entire-margined species for the CLAMP 3A database (Wolfe, 1995). Open circles are CLAMP 3B sites with a percentage of species with entire margins $\geq 60\%$ (dashed line); filled circles are CLAMP 3B sites with a percentage of species with an entire margin $< 60\%$ (solid line); x are CLAMP 3A outlier sites. The variably dashed line represents the slope of the entire-margin vs. MAT for the test sites.

entire-margined lineages. Further investigation is needed to ascertain if this is the case.

In addition, the uplift history of northern South America influenced the migration and evolutionary history of plants in the neotropics. Until the late Oligocene (Graham, 1995; Wijninga, 1995), a continuous lowland tropical environment existed in northern South America. During the past 25 million years, the climate changed as the Andes began to uplift, but it did not approach modern conditions until the Pliocene, approximately 4 million years ago (Wijninga, 1995). In the nearly homogeneous climate, morphologic characters suited to tropical conditions evolved, and the lack of high-elevation, low-temperature areas discouraged the migration of temperate plants. With the recent uplift of the Andes, migration of temperate elements such as *Alnus* and *Juglans* began (Burnham and Graham, 1999). Possibly, the short period of time that has elapsed since the creation of high-elevation, low-temperature sites in the neotropics has not been long enough for a significant proportion of the flora to have migrated from temperate areas or to have evolved in response to lower MAT. Six of the seven low-temperature sites with higher than expected percentages of entire-margined leaves are located above 800 m, indicating that uplift history may have influenced the plant species composition of these sites.

The distinctive leaf physiognomy of some of the high-elevation sites may also be related to environmental conditions. Five of the low-temperature sites are above 2000 m elevation and experience over 140 cm of rainfall each year (Appendix 2). These values are often associated with cloud forest, an environment usually characterized by high humidity and low temperatures. Leaves in cloud forest tend to be small, thick, and entire-margined (Leigh, 1999). The reasons for this particular leaf morphology are unknown, but explanations range from low soil nutrient levels to wind protection or low transpiration rates (Leigh, 1999). The five highest-elevation sites tested here have species that exhibit leaf morphologies similar to those of cloud-forest species, with large percentages of species with entire-margined leaves. In contrast, the high-elevation sites from the Boliv-

ian database receive <100 cm of rain and have higher percentages of toothed leaves (Gregory-Wodzicki, 2000). Large amounts of rainfall at high elevations combined with low temperature may foster the growth of a disproportionate number of species with entire-margined leaves. Thus, the plant species growing in the five high-elevation, wet sites show a different relationship between temperature and leaf-margin than plant species growing in other environments. The result of this difference in species composition may be the overestimation of MAT by most equations at high-elevation sites (Fig. 4B).

4.2. Rainfall

The inclusion of dry sites in the suite of test floras does not influence the outcome of predicted MAT for any of the tested models (Fig. 9A; Table 4). Mesic sites appear to have a continuum in the percentages of species with toothed to entire margins based on MAT, but most dry sites, ranging from frigid alpine to warm desert environments (Bailey and Sinnott, 1915; Bailey and Sinnott, 1916), have a high percentage of entire-margined species regardless of MAT. Databases of modern vegetation are sometimes restricted to mesic sites (Wolfe, 1979; Greenwood, 1992, pers. commun., Victoria University of Technology, Melbourne, Vic.) to reduce the chance that the presence of entire-margined species in the flora is due to the amount or seasonality of rainfall. In tropical Africa, Jacobs (1999) found that leaf margin correlates significantly with annual and seasonal rainfall. However, rainfall amount does not seem to influence the ability to predict MAT in the South American test sites. The average of the errors in predicted MAT for the three driest test sites, El Pechiche, Laguna de Cocos and Cerro Mutiles, ranges from 2.9 to 6.1°C (Table 2) and is consistent with the predicted MAT of the more mesic test sites (Fig. 9A).

4.3. Sampling

Sampling strategy and scoring technique may have influenced the outcome of the predicted MAT for all the models based on the CLAMP

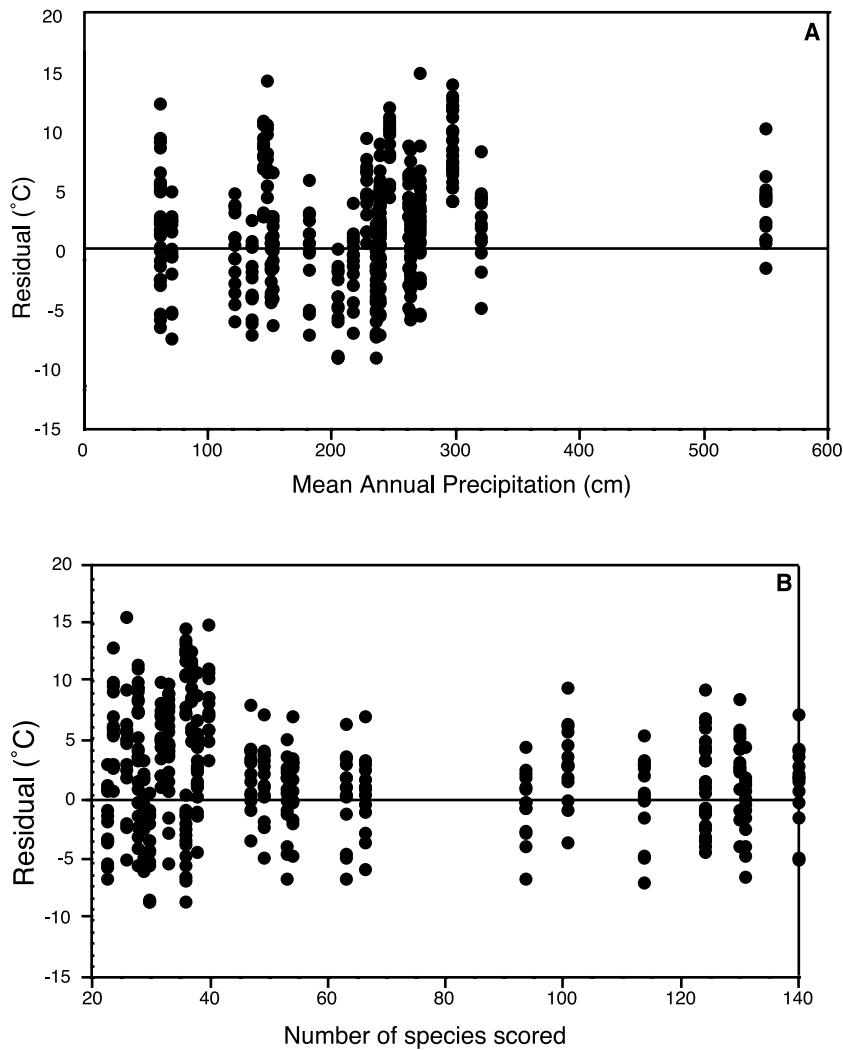


Fig. 9. Residuals of predicted MAT vs. mean annual precipitation or number of species sampled. Each point represents the residual of predicted MAT for one of the tested equations. (A) Residuals of predicted MAT for each site vs. mean annual precipitation of the site. (B) Residuals of predicted MAT for each site vs. number of species sampled in the flora.

database, as well as the model based on South American data. These two databases were assembled by collecting at least 25–30 specimens of riparian and slope taxa in a limited geographical area, usually 1–5 ha (Wolfe, 1993; Gregory-Wodzicki, 2000). All life forms of woody plants were collected, including shrubs, lianas and trees. The collection site should ideally be within 5 km of the climate station from which records are taken, though in areas with few climate stations environmental parameters are extrapolated from the

station to the site itself. For the study reported here, species lists for each of the 30 South American sites are derived from published lists, scored from herbarium specimens and are most often restricted to trees, growing within a 1-ha area. Climate stations are seldom within 5 km of the floral locality due to the paucity of climate stations in South America. This sampling strategy is similar to the one employed by Jacobs (1999) to measure the correlation between rainfall and morphology for tropical Africa.

Scoring herbarium specimens may result in different morphological character scores for each species than the expected condition because the specimens were not collected at the actual site being tested. However, leaf margin state is the most important character in all of the tested equations and does not vary significantly within species (Jordan, 1997; Kowalski, unpublished data). Therefore, margin scores should be the same regardless of collection site. In addition, in Tasmania, some leaf morphological characteristics of species have been shown to vary more due to genetic control than to environmental condition (Barnes et al., 2000), which may result in as much variation in leaf characters within a site as between sites. Therefore, scoring of herbarium specimens instead of voucher specimens should not unduly influence the outcome of the regression equations. The few sites that were scored with a majority of voucher specimens, Loja–non-ridge, Loja–ridge, Pasachoa, Baeza, Cuyabeno, and Pakitsa Plot 3, had no better estimates of MAT than the sites scored from primarily non-voucher herbarium specimens. The average error for these sites ranges from 3.3 to 10.9°C (Table 2), representing over half of the sites with an average error above 6°C.

The restriction of most sites to tree data may influence the outcome of the results, as lianas and understory trees tend to have a higher percentage of toothed margins (Givnish, 1987; Burnham et al., 2001). However, in Manu National Park, Peru, small trees are virtually absent from the litter (Burnham, 1994), and Burnham et al. (2001) have demonstrated that MAT estimates of plots composed of only trees vs. MAT estimates of plots composed of trees and lianas are similar. The average error estimate per site for the four sites that include shrubs or lianas in their floral list (Appendix 3) ranges from 2.7 to 5.8°C, well within the range of average error for all sites.

Another difference between the CLAMP and Bolivian data sets and the thirty sites tested is sampling location. The CLAMP and Bolivian sites were mostly collected from riparian settings (Wolfe, 1993; Gregory-Wodzicki, 2000), which have been shown in a tropical lowland site in

Ecuador to have a lower percentage of species with entire-margined leaves than nearby *terra firme* forest (Burnham et al., 2001). Using an equation based on riparian data to estimate temperature may result in overestimated temperatures of sites with fewer riparian species. The 30 sites tested here were collected from a variety of habitats, including riparian. However, the difference in percentage of species with entire-margined leaves due to differences in sampling location should be minimal, as the CLAMP collecting strategy also included slope taxa beyond the riverbank.

Sample size has been shown to influence the error associated with temperature prediction from leaf morphology (Burnham et al., 2001). A number of 20 species has been suggested as the minimum number of species necessary to ensure that one particular species does not over-contribute to the total (Wolfe, 1993; Povey et al., 1994), but Burnham et al. (2001) and Wilf (1997) have shown that larger sample sizes produce smaller error estimates. The sample size of the 30 test floras ranges from 24 to 140 species. However, sample size is not the most important factor in determining the magnitude of error in predicted MAT (Fig. 9B). Predicted MAT for each site has a spread of at least 10°C regardless of the number of species sampled per site.

Repeatability of scores by different researchers may be a factor in the outcome of all the tested models. Wilf (1997) and Wiemann et al. (1998) have questioned the consistency of scoring the CLAMP database among researchers. If characters are not scored in a manner consistent with the original CLAMP database, a systematic error is introduced. Predicted temperatures may reflect any error introduced by inconsistent scoring.

4.4. Low- vs. high-MAT sites

Errors derived from using CCA or NN were similar for both the low-temperature and high-temperature sites. While the median and average errors associated with these methods are still above the SE, the low overall differences in average error between low- and high-temperature sites using these methods indicate some value in using

Multivariate statistical techniques in tropical low-temperature environments. Every model tested here overestimates MAT of the five low-temperature sites. However, for CCA and NN the predicted site with the largest residual of estimated MAT is one of the high-temperature sites (Table 4). This suggests that although leaf margin state is the single character most correlated with MAT, leaf morphologic characters other than margin are important in explaining the variation in predicted MAT of tropical South America.

The seven low-temperature sites tested here can be seen as outliers from the general relationship between leaf-margin state and MAT. However, the multivariate models tested here using the full 31 leaf morphologic characters from CLAMP fared as well predicting the seven low-temperature sites as in predicting the high-temperature sites. The results presented here suggest these seven sites should not be treated as outliers, but as important sites sampling the diversity of leaf morphologic assemblages in tropical South America, and should be incorporated into equations that determine climate from leaf morphology.

5. Conclusions

I suggest that most current leaf morphology–MAT equations may not be appropriate for use in the South American tropics for low-MAT or high-elevation sites. It is important to test models of correlation between leaf morphology and climate using data from modern analogous vegetation before using that model to predict paleoclimate from fossil vegetation. Using equations generated from forests unrelated to those for which they are designed may result in poor estimates of paleo-MAT that are in error by as much as 15.4°C.

Predicting paleoclimate in tropical South America can involve uncertainty of the elevation and precipitation totals of a fossil site during its deposition, due to the continued uplift of the Andes and changing climatic patterns throughout the Cenozoic. Because elevation and precipitation totals are not always known, equations that use leaf morphology to predict paleotemperature of Late

Cenozoic neotropical sites must be able to accurately predict MAT of sites over a wide range of elevations and precipitation totals. Several of the equations tested here, Eqs. 2, 3, 6 and 7, accurately predict the majority of the high-temperature sites and might be considered for use in predicting MAT of fossil sites of known high temperature or low elevation. However, none of the models tested here consistently predicts the MAT of low-temperature or high-elevation tropical South American sites, suggesting that the MAT of these sites would be best estimated by a correlation between MAT and leaf morphology derived from the extensive data from tropical South America, not from the Northern Hemisphere or Asia.

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Appendix 1

Percent of species scored with each character state in each test flora, listed as a proportion. Characters lobed through obovate defined by Wolfe (1993) and Wolfe and Spicer (1999).

| Character | Alto Ivan | Rio Grande | Conquista | Corumbá | Belém–igapó forest | Belém–terra firme | Rio Claro | Manaus | Alto Yunda | Loja–non- ridge | Loja–ridge | Pasochoa | Baeza | Rio PalenqueEl Pechiche | |
|-----------------|-----------|------------|-----------|---------|-----------------------|----------------------|-----------|--------|------------|--------------------|------------|----------|-------|----------------------------|------|
| Lobed | 0.03 | 0.02 | 0.01 | 0.07 | 0.00 | 0.00 | 0.08 | 0.01 | 0.06 | 0.00 | 0.00 | 0.03 | 0.11 | 0.05 | 0.03 |
| No teeth | 0.93 | 0.95 | 0.77 | 0.86 | 1.00 | 0.94 | 0.83 | 0.88 | 0.83 | 0.76 | 0.62 | 0.72 | 0.73 | 0.90 | 0.83 |
| Teeth regular | 0.05 | 0.01 | 0.17 | 0.10 | 0.00 | 0.05 | 0.17 | 0.11 | 0.11 | 0.20 | 0.32 | 0.24 | 0.21 | 0.09 | 0.11 |
| Teeth close | 0.05 | 0.04 | 0.19 | 0.14 | 0.00 | 0.01 | 0.08 | 0.07 | 0.08 | 0.23 | 0.34 | 0.28 | 0.19 | 0.05 | 0.09 |
| Teeth round | 0.04 | 0.02 | 0.17 | 0.07 | 0.00 | 0.06 | 0.13 | 0.05 | 0.08 | 0.19 | 0.24 | 0.16 | 0.14 | 0.00 | 0.12 |
| Teeth acute | 0.02 | 0.02 | 0.05 | 0.07 | 0.00 | 0.00 | 0.04 | 0.07 | 0.03 | 0.05 | 0.15 | 0.11 | 0.10 | 0.10 | 0.07 |
| Teeth compound | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.03 |
| Nanophyll | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Leptophyll I | 0.00 | 0.01 | 0.02 | 0.12 | 0.04 | 0.02 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 |
| Leptophyll II | 0.00 | 0.05 | 0.02 | 0.05 | 0.00 | 0.01 | 0.06 | 0.00 | 0.00 | 0.01 | 0.02 | 0.03 | 0.00 | 0.00 | 0.03 |
| Microphyll I | 0.01 | 0.13 | 0.11 | 0.07 | 0.02 | 0.01 | 0.08 | 0.02 | 0.01 | 0.13 | 0.10 | 0.22 | 0.01 | 0.02 | 0.11 |
| Microphyll II | 0.16 | 0.29 | 0.29 | 0.33 | 0.18 | 0.21 | 0.24 | 0.17 | 0.20 | 0.39 | 0.50 | 0.31 | 0.15 | 0.11 | 0.29 |
| Microphyll III | 0.27 | 0.29 | 0.31 | 0.25 | 0.25 | 0.36 | 0.23 | 0.30 | 0.21 | 0.34 | 0.27 | 0.27 | 0.25 | 0.20 | 0.25 |
| Mesophyll I | 0.21 | 0.18 | 0.18 | 0.09 | 0.22 | 0.22 | 0.17 | 0.27 | 0.16 | 0.08 | 0.05 | 0.10 | 0.19 | 0.21 | 0.18 |
| Mesophyll II | 0.28 | 0.04 | 0.05 | 0.05 | 0.22 | 0.17 | 0.12 | 0.21 | 0.32 | 0.04 | 0.07 | 0.07 | 0.24 | 0.30 | 0.12 |
| Mesophyll III | 0.08 | 0.00 | 0.02 | 0.03 | 0.07 | 0.00 | 0.04 | 0.03 | 0.10 | 0.00 | 0.00 | 0.00 | 0.16 | 0.16 | 0.00 |
| Apex emarginate | 0.08 | 0.20 | 0.08 | 0.12 | 0.07 | 0.04 | 0.17 | 0.04 | 0.00 | 0.06 | 0.04 | 0.04 | 0.03 | 0.02 | 0.03 |
| Apex round | 0.16 | 0.27 | 0.24 | 0.22 | 0.13 | 0.07 | 0.29 | 0.08 | 0.31 | 0.25 | 0.31 | 0.21 | 0.06 | 0.04 | 0.16 |
| Apex acute | 0.69 | 0.60 | 0.72 | 0.76 | 0.81 | 0.89 | 0.69 | 0.78 | 0.60 | 0.72 | 0.63 | 0.71 | 0.70 | 0.85 | 0.71 |
| Apex attenuate | 0.15 | 0.13 | 0.04 | 0.02 | 0.06 | 0.04 | 0.02 | 0.14 | 0.09 | 0.03 | 0.06 | 0.07 | 0.24 | 0.10 | 0.13 |
| Base cordate | 0.13 | 0.02 | 0.06 | 0.12 | 0.13 | 0.05 | 0.19 | 0.08 | 0.08 | 0.05 | 0.10 | 0.11 | 0.16 | 0.18 | 0.14 |
| Base round | 0.28 | 0.24 | 0.32 | 0.22 | 0.39 | 0.23 | 0.31 | 0.19 | 0.14 | 0.35 | 0.28 | 0.39 | 0.35 | 0.22 | 0.33 |
| Base acute | 0.59 | 0.73 | 0.63 | 0.66 | 0.48 | 0.72 | 0.50 | 0.73 | 0.78 | 0.59 | 0.62 | 0.50 | 0.48 | 0.60 | 0.53 |
| L:W < 1:1 | 0.01 | 0.01 | 0.01 | 0.07 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.02 | 0.02 |
| L:W 1–2:1 | 0.23 | 0.22 | 0.24 | 0.43 | 0.22 | 0.15 | 0.44 | 0.20 | 0.40 | 0.34 | 0.38 | 0.39 | 0.30 | 0.34 | 0.34 |
| L:W 2–3:1 | 0.60 | 0.54 | 0.52 | 0.28 | 0.56 | 0.65 | 0.35 | 0.58 | 0.44 | 0.54 | 0.47 | 0.42 | 0.59 | 0.47 | 0.55 |
| L:W 3–4:1 | 0.13 | 0.20 | 0.18 | 0.16 | 0.15 | 0.17 | 0.08 | 0.20 | 0.12 | 0.09 | 0.12 | 0.10 | 0.08 | 0.14 | 0.09 |
| L:W > 4:1 | 0.03 | 0.03 | 0.05 | 0.07 | 0.07 | 0.02 | 0.08 | 0.01 | 0.03 | 0.03 | 0.03 | 0.09 | 0.00 | 0.03 | 0.00 |
| Obovate | 0.08 | 0.10 | 0.13 | 0.07 | 0.07 | 0.12 | 0.13 | 0.10 | 0.04 | 0.05 | 0.04 | 0.09 | 0.07 | 0.08 | 0.09 |
| Elliptic | 0.77 | 0.74 | 0.72 | 0.72 | 0.74 | 0.72 | 0.58 | 0.82 | 0.82 | 0.74 | 0.74 | 0.63 | 0.54 | 0.66 | 0.59 |
| Ovate | 0.15 | 0.16 | 0.16 | 0.21 | 0.19 | 0.15 | 0.29 | 0.08 | 0.14 | 0.20 | 0.22 | 0.29 | 0.39 | 0.27 | 0.32 |

Appendix 1 (Continued).

| Character | Cuyabeno | Añanagu– floodplain | Añanagu– unflooded | Jauneche | Cerro Mutiles | Guyana– mora | Guyana– mixed forest | Guyana– Morabukea | Pakitsa, Manu NP 1 | Pakitsa, Manu NP 3 | La Montaña | Laguna de Cocos | Corozal– woody savanna | Corozal– Guiana Shield | Delgadito Creek |
|-----------------|----------|------------------------|-----------------------|----------|------------------|-----------------|-------------------------|----------------------|--------------------------|--------------------------|---------------|--------------------|------------------------------|------------------------------|--------------------|
| Lobed | 0.03 | 0.04 | 0.01 | 0.02 | 0.04 | 0.00 | 0.00 | 0.00 | 0.04 | 0.03 | 0.00 | 0.00 | 0.03 | 0.02 | 0.10 |
| No teeth | 0.92 | 0.86 | 0.92 | 0.90 | 0.89 | 0.94 | 0.94 | 0.91 | 0.90 | 0.92 | 0.74 | 0.96 | 0.81 | 0.93 | 0.77 |
| Teeth regular | 0.08 | 0.14 | 0.07 | 0.09 | 0.10 | 0.06 | 0.06 | 0.09 | 0.10 | 0.08 | 0.24 | 0.04 | 0.19 | 0.06 | 0.20 |
| Teeth close | 0.04 | 0.09 | 0.05 | 0.08 | 0.07 | 0.06 | 0.04 | 0.07 | 0.09 | 0.08 | 0.22 | 0.04 | 0.16 | 0.07 | 0.19 |
| Teeth round | 0.08 | 0.07 | 0.05 | 0.02 | 0.02 | 0.06 | 0.04 | 0.07 | 0.05 | 0.06 | 0.11 | 0.00 | 0.11 | 0.04 | 0.03 |
| Teeth acute | 0.00 | 0.06 | 0.03 | 0.08 | 0.09 | 0.00 | 0.02 | 0.02 | 0.04 | 0.02 | 0.14 | 0.04 | 0.08 | 0.04 | 0.19 |
| Teeth compound | 0.01 | 0.02 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.03 |
| Nanophyll | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Leptophyll I | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.03 | 0.02 | 0.02 | 0.02 | 0.03 | 0.01 | 0.08 | 0.05 | 0.02 | 0.03 |
| Leptophyll II | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.01 | 0.02 | 0.04 | 0.10 | 0.00 | 0.00 | 0.03 |
| Microphyll I | 0.03 | 0.01 | 0.04 | 0.03 | 0.03 | 0.01 | 0.01 | 0.03 | 0.01 | 0.03 | 0.11 | 0.15 | 0.07 | 0.05 | 0.08 |
| Microphyll II | 0.06 | 0.12 | 0.12 | 0.19 | 0.18 | 0.07 | 0.13 | 0.11 | 0.14 | 0.14 | 0.25 | 0.37 | 0.31 | 0.32 | 0.34 |
| Microphyll III | 0.20 | 0.22 | 0.21 | 0.27 | 0.28 | 0.32 | 0.31 | 0.29 | 0.28 | 0.25 | 0.27 | 0.25 | 0.28 | 0.33 | 0.24 |
| Mesophyll I | 0.27 | 0.23 | 0.22 | 0.23 | 0.21 | 0.29 | 0.25 | 0.25 | 0.22 | 0.23 | 0.17 | 0.04 | 0.16 | 0.16 | 0.11 |
| Mesophyll II | 0.32 | 0.32 | 0.30 | 0.20 | 0.17 | 0.24 | 0.16 | 0.22 | 0.23 | 0.23 | 0.13 | 0.02 | 0.12 | 0.08 | 0.11 |
| Mesophyll III | 0.12 | 0.10 | 0.10 | 0.08 | 0.11 | 0.03 | 0.11 | 0.08 | 0.10 | 0.08 | 0.02 | 0.00 | 0.00 | 0.04 | 0.06 |
| Apex emarginate | 0.03 | 0.01 | 0.01 | 0.05 | 0.02 | 0.06 | 0.03 | 0.06 | 0.03 | 0.05 | 0.03 | 0.24 | 0.04 | 0.04 | 0.15 |
| Apex round | 0.11 | 0.10 | 0.08 | 0.08 | 0.08 | 0.03 | 0.39 | 0.12 | 0.07 | 0.09 | 0.21 | 0.60 | 0.11 | 0.09 | 0.18 |
| Apex acute | 0.62 | 0.77 | 0.80 | 0.78 | 0.79 | 0.88 | 0.55 | 0.85 | 0.83 | 0.79 | 0.71 | 0.40 | 0.82 | 0.79 | 0.77 |
| Apex attenuate | 0.28 | 0.13 | 0.12 | 0.14 | 0.13 | 0.09 | 0.06 | 0.04 | 0.10 | 0.12 | 0.08 | 0.00 | 0.07 | 0.12 | 0.05 |
| Base cordate | 0.09 | 0.14 | 0.13 | 0.20 | 0.15 | 0.06 | 0.05 | 0.04 | 0.15 | 0.16 | 0.09 | 0.04 | 0.05 | 0.07 | 0.23 |
| Base round | 0.36 | 0.22 | 0.18 | 0.25 | 0.18 | 0.25 | 0.26 | 0.25 | 0.20 | 0.22 | 0.20 | 0.44 | 0.22 | 0.23 | 0.22 |
| Base acute | 0.55 | 0.64 | 0.70 | 0.55 | 0.68 | 0.69 | 0.69 | 0.71 | 0.65 | 0.63 | 0.71 | 0.52 | 0.73 | 0.71 | 0.55 |
| L:W < 1:1 | 0.00 | 0.02 | 0.00 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | 0.02 | 0.02 | 0.00 | 0.02 | 0.03 | 0.00 | 0.05 |
| L:W 1–2:1 | 0.14 | 0.30 | 0.21 | 0.37 | 0.40 | 0.16 | 0.14 | 0.15 | 0.22 | 0.17 | 0.34 | 0.50 | 0.22 | 0.16 | 0.35 |
| L:W 2–3:1 | 0.53 | 0.56 | 0.59 | 0.47 | 0.43 | 0.58 | 0.65 | 0.60 | 0.57 | 0.58 | 0.47 | 0.44 | 0.57 | 0.62 | 0.43 |
| L:W 3–4:1 | 0.23 | 0.10 | 0.18 | 0.10 | 0.12 | 0.17 | 0.18 | 0.20 | 0.18 | 0.19 | 0.14 | 0.04 | 0.15 | 0.20 | 0.14 |
| L:W > 4:1 | 0.10 | 0.02 | 0.02 | 0.05 | 0.04 | 0.08 | 0.03 | 0.06 | 0.02 | 0.04 | 0.04 | 0.00 | 0.04 | 0.02 | 0.04 |
| Obovate | 0.10 | 0.10 | 0.10 | 0.06 | 0.07 | 0.06 | 0.13 | 0.19 | 0.06 | 0.06 | 0.04 | 0.20 | 0.03 | 0.11 | 0.06 |
| Elliptic | 0.79 | 0.72 | 0.80 | 0.67 | 0.62 | 0.90 | 0.68 | 0.71 | 0.78 | 0.82 | 0.72 | 0.58 | 0.88 | 0.77 | 0.68 |
| Ovate | 0.10 | 0.18 | 0.11 | 0.27 | 0.31 | 0.04 | 0.18 | 0.11 | 0.15 | 0.12 | 0.24 | 0.22 | 0.09 | 0.12 | 0.26 |

Appendix 2

Location, elevation and climatic data for the 30 modern tropical South American sites studied in this paper. Dry months are those with less than 10 cm of rain. Sites with a MAT of $\leq 21^\circ\text{C}$ are in bold type. Citations listed below. Length of MAT record is in years. Abbreviations: mean annual precipitation (MAP).

| Country and site | Latitude | Longitude | Elevation (m) | MAT ($^\circ\text{C}$) | MAP (cm) | Dry months | Length MAT record |
|---------------------------------------|----------|-----------|------------------|-----------------------------|------------------|---------------|----------------------|
| <i>Bolivia</i> | | | | | | | |
| ¹ Alto Ivan | 11°45'S | 66°02'W | 200 | 26.8 | 157 | 7 | 18 |
| <i>Brazil</i> | | | | | | | |
| ² Rio Grande | 21°10'S | 44°54'W | 825 | 19.6 | 152 | 5 | 32 |
| ³ Conquista | 19°59'S | 47°36'W | 510–530 | 23.7 | 155 | 6 | 26 |
| ⁴ Corumbá | 19°01'S | 57°39'W | 90 | 24.6 ^a | 125 | 6 | 10 |
| ⁵ Belém–igapó forest | 1°54'S | 48°29'W | 25 | 26.2 ^b | 274 ^a | 0 | 26 |
| ⁵ Belém–terra firme | 1°54'S | 48°29'W | 25 | 26.2 ^b | 274 ^a | 0 | 26 |
| ⁴ Rio Claro | 16°16'S | 56°38'W | 75–150 | 25.8 ^b | 139 | 6 | 88 |
| ⁶ Manaus | 3°08'S | 60°01'W | 75 | 26.6 ^b | 221 ^a | 2 | 76 |
| <i>Colombia</i> | | | | | | | |
| ⁷ Alto Yunda | 3°32'N | 76°48'W | 1050 | 21.5 | 553 | 0 | 10 |
| <i>Ecuador</i> | | | | | | | |
| ⁸ Loja–non-ridge | 4°05'S | 79°10'W | 2900 | 11.5 ^a | 300 | 0–1 | 10 |
| ⁸ Loja–ridge | 4°28'S | 79°09'W | 2700 | 12.4 ^a | 300 | 0–1 | 10 |
| ⁹ Pasocha | 0°29'S | 78° 41'W | 3260–3310 | 13.8 | 149 | 0–1 | 10 |
| ¹⁰ Baeza | 0°28'S | 77° 54'W | 2000 | 16.2 | 232 | 0 | 8 |
| ¹¹ Rio Palenque | 0°33'S | 79°18'W | 150–220 | 22.1 ^a | 265 | 6 | 10 |
| ¹² El Pechiche | 1°26'S | 80°41'W | 320–365 | 24.8 ^a | 65 | 8 | 10 |
| ¹³ Cuyabeno | 0°0'S | 76°12'W | 265 | 24.6 ^a | 324 | 0 | 10 |
| ¹⁴ Añanagu–floodplain | 0°32'S | 76°26'W | 285 | 25.4 ^a | 248 | 0 | 10 |
| ¹⁴ Añanagu–unflooded | 0°32'S | 76°26'W | 285–365 | 25.4 ^a | 248 | 0 | 10 |
| ¹⁵ Jauneche | 1°20'S | 79°35'W | 70 | 25.3 ^a | 185 | 8 | 10 |
| ¹⁶ Cerro Mutiles | 0°54'N | 79°37'W | 200–300 | 25.5 ^a | 75 ^a | 5–6 | 10 |
| <i>Guyana</i> | | | | | | | |
| ¹⁷ Mora consociation | 6°11'N | 58°37'W | 50–100 | 25.9 | 267 | 0 | 10 |
| ¹⁷ Mixed forest | 6°11'N | 58°37'W | 50–100 | 25.9 | 267 | 0 | 10 |
| ¹⁷ Morabukea consociation | 6°11'N | 58°37'W | 50–100 | 25.9 | 267 | 0 | 10 |
| <i>Peru</i> | | | | | | | |
| ¹⁸ Pakitsa, Manu NP Plot 1 | 11°56'S | 71°15'W | ~ 340 | 23.1 | 243 | 0–1 | 4 |
| ¹⁸ Pakitsa, Manu NP Plot 3 | 11°56'S | 71°15'W | ~ 360 | 23.1 | 243 | 0–1 | 4 |
| <i>Venezuela</i> | | | | | | | |
| ¹⁹ La Montaña | 8°35'N | 71°07'W | 2550–2650 | 13.0 | 250 | 2 | 5 |
| ²⁰ Laguna de Cocos | 10°30'N | 63°45'W | ~ 200 | 21.0 ^a | ~ 65 | 5 | 10 |
| ²¹ Corozal–woody savanna | 6°55'N | 66°30'W | 90–100 | 27.2 ^c | 240 | 6 | 13 |
| ²¹ Corozal–Guiana Shield | 6°55'N | 66°30'W | 100–500 | 27.2 ^c | 240 | 6 | 13 |
| ²² Delgadito Creek | 8°49'N | 69°29'W | ~ 150 | 26.1 | 209 | 5 | 6 |

Sources: ¹Boom, 1986; ²Oliveira-Filho et al., 1994; ³Oliveira-Filho et al., 1997; ⁴Ratter et al., 1988; ⁵Black et al., 1950; ⁶Prance et al., 1976; ⁷Hilty, 1980; ⁸Madsen and Øllgaard, 1994; ⁹Valencia and Jørgensen, 1992; ¹⁰Valencia, 1995; ¹¹Dodson and Gentry, 1978; ¹²Josse and Balslev, 1994; ¹³Korning and Balslev, 1994; ¹⁴Balslev et al., 1987; ¹⁵Dodson, 1985; ¹⁶Parker and Carr, 1992; ¹⁷Davis and Richards, 1933, 1934; ¹⁸Pitman, 2000, pers. commun.; ¹⁹Kelly et al., 1994; ²⁰Guevarade de Lampe et al., 1992; ²¹Boom, 1990; ²²Stergios et al., 1998; ^aFAO, 1985; ^bGlobal Historical Climatology Network, 1999; ^cCODESUR, 1979.

Appendix 3

Number of species sampled, sampling area and strategy and forest type for the 30 modern South American sites used in this study. Citations as in Appendix 2. The heading ‘number of species’ refers to the number of species reported in the literature; ‘number scored’ is the number of species in the flora that were available at the herbaria visited. The mention ‘woody plants’ refers to all woody plants including trees, lianas and shrubs. Sites with MAT $\leq 21^{\circ}\text{C}$ are in bold type. Abbreviations: diameter at breast height (dbh); diameter at base of trunk (dbt); circumference at base of stem (cbs).

| Country and site | No. spp. | No. scored | Area | Type of individual sampled | Forest type |
|---|----------|------------|---------------|-------------------------------|------------------------------|
| <i>Bolivia</i> | | | | | |
| ¹ Alto Ivan | 76 | 67 | 1 ha | trees ≥ 10 cm dbh | Premontane, moist |
| <i>Brazil</i> | | | | | |
| ² Rio Grande | 46 | 41 | 0.54 ha | trees ≥ 5 cm dbt | Montane, semideciduous |
| ³ Conquista | 136 | 124 | 1.13 ha | trees ≥ 15.7 cm cbs | Submontane, semideciduous |
| ⁴ Corumbá | 35 | 29 | ~ 1.0 ha | trees ≥ 10 cm dbh | Deciduous, savanna |
| ⁵ Belém– <i>igapó</i> forest | 27 | 27 | 1.0 ha | trees ≥ 10 cm dbh | Lowland tropical |
| ⁵ Belém– <i>terra firme</i> | 56 | 50 | 1.0 ha | trees ≥ 10 cm dbh | Lowland tropical |
| ⁴ Rio Claro | 25 | 24 | ~ 1.0 ha | trees ≥ 10 cm dbh | Savanna, seasonal floods |
| ⁶ Manaus | 150 | 131 | 1.0 ha | trees ≥ 5 cm dbh | <i>Terra firme</i> |
| <i>Colombia</i> | | | | | |
| ⁷ Alto Yunda | 50 | 39 | 0.6 ha | trees $\geq 3\text{m}$ height | Premontane rainforest |
| <i>Ecuador</i> | | | | | |
| ⁸ Loja–non-ridge | 43 | 37 | 1.0 ha | trees ≥ 5 cm dbh | Upper montane rainforest |
| ⁸ Loja–ridge | 46 | 34 | 1.0 ha | trees ≥ 5 cm dbh | Upper montane rainforest/C > |
| ⁹ Pasocha | 29 | 29 | 1.0 ha | trees ≥ 5 cm dbh | Humid montane |
| ¹⁰ Baeza | 33 | 33 | 1.0 ha | trees ≥ 5 cm dbh | Montane |
| ¹¹ Río Palenque | 163 | 124 | 87 ha | common trees, shrubs | Wet tropical |
| ¹² El Pechiche | 30 | 30 | 1.0 ha | trees ≥ 5 cm dbh | Dry, semideciduous |
| ¹³ Cuyabeno | 39 | 39 | 1.0 ha | trees ≥ 10 cm dbh, > 1% | Moist tropical |
| ¹⁴ Añanagu–floodplain | 97 | 94 | ~ 1.0 ha | trees ≥ 10 cm dbh | Moist tropical |
| ¹⁴ Añanagu–unflooded | 151 | 140 | ~ 1.0 ha | trees ≥ 10 cm dbh | Moist tropical |
| ¹⁵ Jauneche | 70 | 64 | 130 ha | common woody plants | Moist tropical |
| ¹⁶ Cerro Mutiles | 119 | 114 | ~ 20 ha | common woody plants | Semi-deciduous, moist |
| <i>Guyana</i> | | | | | |
| ¹⁷ Mora consociation | 37 | 34 | 1.5 ha | trees ≥ 10 cm dbh | Lowland tropical |
| ¹⁷ Mixed forest | 57 | 48 | 1.5 ha | trees ≥ 10 cm dbh | Lowland tropical |
| ¹⁷ Morabukea consociation | 64 | 55 | 1.5 ha | trees ≥ 10 cm dbh | Lowland tropical |
| <i>Peru</i> | | | | | |
| ¹⁸ Pakitsa, Manu NP Plot 1 | 133 | 130 | 1.0 ha | trees ≥ 10 cm dbh | Lowland tropical |
| ¹⁸ Pakitsa, Manu NP Plot 3 | 107 | 101 | 1.0 ha | trees ≥ 10 cm dbh | Lowland tropical |
| <i>Venezuela</i> | | | | | |
| ¹⁹ La Montaña | 50 | 38 | 1.5 ha | species ≥ 3.2 cm dbh | Lower montane, wet forest |
| ²⁰ Laguna de Cocos | 29 | 25 | 0.06 ha | all trees, tall shrubs | Thorn woodland |
| ²¹ Corozal–woody savanna | 39 | 37 | 0.5 ha | trees ≥ 10 cm dbh | Tall woody savanna |
| ²¹ Corozal–Guiana Shield | 59 | 54 | 0.5 ha | trees ≥ 10 cm dbh | Tropical moist forest |
| ²² Delgadito Creek | 35 | 31 | 1.0 ha | trees ≥ 10 cm dbh | Semideciduous, gallery |

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