# Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest[1]

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Leaf margin characters are strong predictors of mean annual temperature (MAT) in modern plant communities and widely used tools for reconstructing paleoclimates from fossil floras. However, the frequency of nonentire-margined species may vary dramatically between different habitats of the same forest. In this paper we explore the potential for this habitat variation to introduce error into temperature reconstructions, based on field data from a modern lowland forest in Amazonian Ecuador.

The data show that the provenance of leaves can influence temperature estimates to an important degree and in a consistent direction. Woody plants growing along lakes and rivers underestimated MAT by 2.5°–5°C, while those in closed-canopy forest provided very accurate predictions. The high proportion of liana species with toothed leaves in lakeside and riverside samples appears to be responsible for a large part of the bias. Samples from closed-canopy forest that included both lianas and trees, however, were more accurate than tree-only or liana-only samples.

We conclude that paleotemperature reconstructions based on leaf margin characters will be misleading to the extent that fossilization provides a better record of certain habitats than others. The preponderance of lake and river deposits in the angiosperm fossil record suggests that underestimation of mean annual paleotemperature may be common.

**Key words:** Amazonian Ecuador; leaf margin analysis; paleoclimate; paleoenvironment; paleotemperature; Río Tiputini; tropical forests; Yasuní National Park.

What information from the paleontological record could be more useful to a wide variety of scientists than accurate reconstruction of climate? For >85 yr, paleobotanists have used leaf margins, or other aspects of leaf morphology, to estimate the mean annual paleotemperature of sites throughout the world (Bailey and Sinnott, 1915, 1916; Chaney, 1947; MacGinitie, 1953; Wolfe, 1971, 1979; Wing and Greenwood, 1993; Wilf, 1997). A strong linear correlation exists in living forests between the proportion of woody dicotyledonous species with entire-margined leaves in a flora and the mean annual temperature of the site (Wolfe, 1979, 1993; Wilf, 1997). Mesic floras living in areas with cool mean annual temperatures include smaller proportions of entire-margined species than those living in areas of warmer mean annual temperature. A single adaptive explanation has not yet surfaced to explain the strength of the correlation (Baker-Brosh and Peet, 1997; Wilf, 1997; Wing, Bao, and Koch, 2000). The correlation has been shown to be more robust if the floras analyzed include large numbers of species (≥30) of dicotyledonous angiosperms (Wolfe, 1971, 1993; Wilf, 1997). Therefore, to estimate paleo-

temperature, the simplest technique is to apply a regression equation derived from modern vegetation and climate to a sample of species that have been scored for their leaf margin state: entire or toothed. Recently the methodology has been refined, including a large number of morphological characters from leaves and employing multivariate statistical models (Wing and Greenwood, 1993; Wolfe, 1993; Gregory and MacIntosh, 1996; Gregory-Wodzicki, 2000). In spite of these modifications to the broad climate models, the variable most highly correlated with mean annual temperature remains the proportion of species that bear entire-margined leaves and therefore is likely to remain the most important estimator of paleotemperature. Most published methods have the ability to provide an estimate of the error for paleotemperature estimates. The error estimates are compounded, however, when the leaf–temperature relationship is used to reconstruct paleoelevation, paleogeography, or paleocirculation (Gregory and Chase, 1992; Meyer, 1992; Gregory-Wodzicki, McIntosh, and Velasquez, 1998; Kowalski, 1999).

The advantage of such a simple method is clear. It requires very little taxonomic background to count the number of species of plants with teeth. With some experience, most investigators can recognize the difference between the species growing in a single area, such that recognition of morphospecies is all that is necessary for the method to proceed (Leaf Architecture Working Group, 1999). Compare this type of paleoclimate reconstruction to a systematic method used widely by palynologists and paleobotanists, the "nearest-living-relative" (NLR) method. A palynologist must first recognize the pollen grain taxonomically, usually possible only to genus, then plot the range of mean annual temperatures under which each recognized genus currently occurs, and finally put to-

gether an estimate of paleotemperature using all ranges of taxa together. Similarly megafossil paleobotanists identify leaves or any macroscopic plant part to genus or species (Hickey, 1977; Axelrod, 1987; Hickey, Johnson, and Dawson, 1988; Manchester, 1994; Mosbrugger et al., 1994). The closest-living-relative is determined by comparison with species of the same genus. The range of modern climate under which the nearest living relative currently lives is plotted for each species from the fossil flora and a composite estimate of paleotemperature is reconstructed for all species from the fossil flora. Only recently has a system emerged for estimating the error in the reconstruction of temperature using this method (Mosbrugger and Utescher, 1997). The closest-living-relative method relies on correct identification of the fossil, correct choice of the nearest living relative, complete knowledge of the modern distribution, and an assumption that climatic tolerances have not changed over time between the modern relative and the fossil in question. When fossil floras are composed of fruits, seeds, and/or wood remains, the use of morphological characteristics correlated with climate may yet allow an alternative to the nearest-living-relative method, but research on those correlations has just begun (Wiemann et al., 1998; Wiemann, Manchester, and Wheeler, 1999).

Almost since the inception of the leaf margin method for estimating paleotemperatures, it was recognized that riversides are likely to include more species with toothed margins than nonriverine habitats from the same climatic zone (MacGinitie, 1953; Wolfe, 1977, 1979, 1993). This assumption was based on observations in the North American temperate zone of various species of *Alnus, Betula, Fraxinus,* and *Salix* living on riversides. This is of particular concern in paleobotany because the majority of fossil plant deposits probably represent wetlands of some type: swamps, oxbow lakes, riversides, and deltas. Although the CLAMP methodology (Wolfe, 1993) was to collect all streamside species first, this was not always possible (e.g., Barro Colorado Island, Panama), and streamsides of high precipitation areas were presumed to have more species in common with nonstreamside areas than is the case in low precipitation areas. Aside from a count by Wolfe (1977) in temperate forests that demonstrates lower percentages of entire margins in fluvial environments, we have no estimate of how important the effect of streamsides might be. Burnham (1994) analyzed subenvironments of the Eocene Puget Group and found that the paratropical leaf deposits from distinct paleoenvironments did reconstruct different paleotemperatures. Evidence for environmental variation influencing actual and potential fossil deposits has also been presented by Burnham (1989), Johnson (1989), and Greenwood (1992). However, empirical evidence specifically on leaf margins from modern tropical environments has been lacking.

We noted high proportions of toothed-margined species along the Tiputini River in equatorial Ecuador and sought to answer the question: Do samples of species growing naturally in various environments of the lowland tropical Tiputini River reflect the modern climate similarly and accurately? When we found that temperature estimates from different environments were not equal to each other nor to the actual mean annual temperature, we sought to determine the cause for the variation.

## STUDY SITE

Fieldwork was carried out in the Amazonian lowlands of eastern Ecuador in the vicinity of Yasuní National Park (∼ 1°
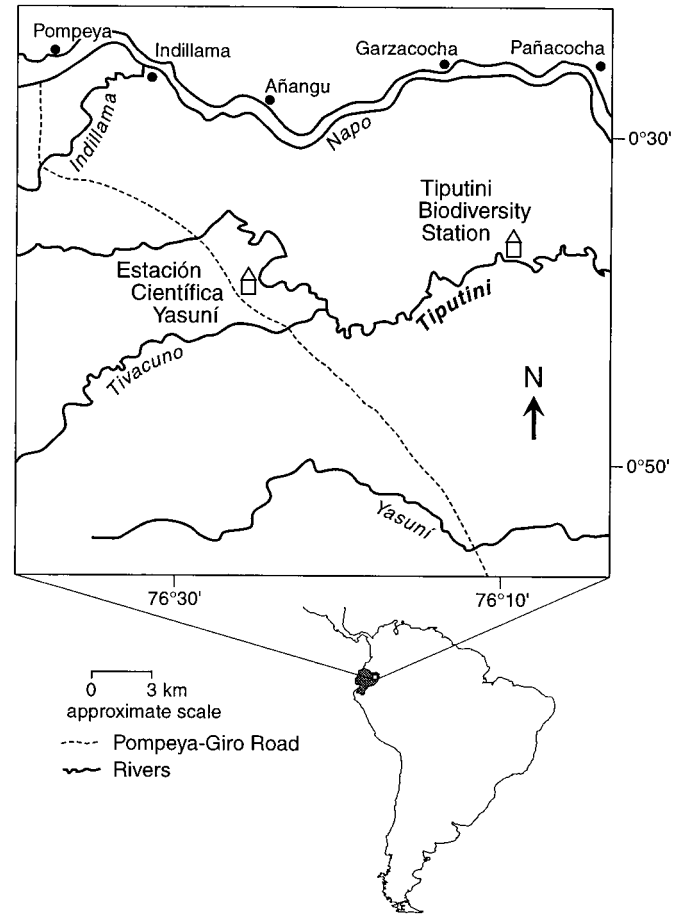


Fig. 1.   Map of the study area showing the two major sampling sites (house symbol) within Yasuní National Park, Ecuador.

S 76° W, 250 m). The area is cloaked in tall, evergreen, closed-canopy forest growing on gentle hills at the base of the Andean range. Slightly >3000 species of woody plants are known from the region, and alpha diversity is among the highest in the world (Valencia, Balslev, and Paz y Mino, 1994; Jørgensen and León-Yánez, 1999). Roughly 90% of the landscape is terra firme (unflooded) forest, with small stands of swamp, riparian, and floodplain forest growing along the small rivers that drain the region.

One such river is the Tiputini, a black- and white-water hybrid (Pitman, 2000) originating in the Andean foothills and traversing the piedmont for ∼200 km before emptying into the Napo River near the Peru–Ecuador border (Fig. 1). The Tiputini is a low-gradient but moderately dynamic river, migrating laterally across a narrow floodplain dotted with oxbow lakes. The flooding dynamics of rivers in eastern Ecuador are poorly known, so our understanding of them is limited to the half-dozen flooding events witnessed by the first two authors over the last 6 yr. We estimate that the floodplains sampled in this study are inundated by the Tiputini at depths of ≤2 m once or twice per year, usually for less than a week at a time. The small amount of sediment that is deposited on them during these flooding events apparently is mixed into the soil profile by roots and soil organisms. Forests in the area are largely protected from human activity and have experienced relatively light impact from local indigenous groups.

TABLE 1. Prediction of mean annual temperatures (MAT) from leaf margin percentages.

| Sample type | $N$ species ($N$ lianas) | % entire | MAT estimate (°C) |
|---|---|---|---|
| Terra firme hectare trees | 226 | 85.0 | 27.1 ± 0.728 |
| Floodplain hectare trees | 106 | 86.8 | 27.7 ± 1.01 |
| Terra firme hectare lianas | 77 | 71.4 | 23.0 ± 1.58 |
| Floodplain hectare lianas | 55 | 76.4 | 24.5 ± 1.75 |
| Terra firme lianas + trees (all) | 302[a] (77) | 81.9 | 26.2 ± 0.684 |
| Floodplain lianas + trees (all) | 161 (55) | 83.2 | 26.6 ± 0.901 |
| River sample TBS | 58 (31) | 69.0 | 22.2 ± 1.86 |
| River sample ECY (1) | 39 (22) | 74.4 | 23.9 ± 2.14 |
| River sample ECY (2) | 48 (24) | 70.8 | 22.8 ± 2.01 |
| Lacustrine sample (Laguna Nutria) | 42 (16) | 73.8 | 23.7 ± 2.08 |
| Combined river samples | 94 (51) | 66.4 | 21.5 ± 1.49 |
| Actual mean annual temperature based on Coca record = 26.5°C | | | |

Note: Calculated errors are based on sample size, not regression error. We recommend applying errors of ±2°C for any sampling errors under 2°C (Wilf, 1997). See Fig. 2 for graphical representation. TBS = Tiputini Biodiversity Station; ECY = Estación Cientfica Yasuní.

[a] The terra firme plot includes one species (*Bauhinia brachycalyx*) that can be encountered as a tree or liana. Both life forms were encountered in the censuses; therefore, the species sum for the plot is one species less than the tree plus liana sum.

Climate in eastern Ecuador is wet, warm, and essentially aseasonal. The area receives ∼3200 mm of rain per year and exhibits remarkably stable mean temperatures throughout the year (Pitman, 2000). Our source for the mean annual temperature used in this paper (26.5°C) is a 16-yr record kept by the Department of Civil Aviation at the Coca airport, 70–80 km west of our study sites and at the same elevation. This is the closest, longest, and most reliable record available.

The two primary study sites used in this analysis are (1) Tiputini Biodiversity Station (00°39′ S, 76°08′ W) with samples treated in this analysis derived from within 2 km of the station and (2) Estación Cientfica Yasuní(00° 40′ S 76°25′ W) with samples derived from within 2 km of this station. Both primary sample sites are shown in Fig. 1.

## METHODS

We established a 1-ha plot in terra firme forest and a 1-ha plot in periodically inundated floodplain forest, both in the vicinity of the Tiputini Biodiversity Station. The floodplain plot was located ∼75 m from the Tiputini River, while the terra firme plot was located ∼0.5 km from the Tiputini. In both plots all trees ≥10 cm diameter at breast height (dbh) were measured for diameter, marked with a numbered aluminum tag, mapped, and vouchered or matched to trees that had been vouchered. All lianas ≥2 cm dbh in a 0.2-ha subset of each plot were similarly measured and vouchered, but not mapped or marked. Plant determinations, based primarily on sterile material, were made by comparison of materials at the following herbaria: F, MICH, MO, QCA, and QCNE.

These data were supplemented with three independent samples from the banks of the Tiputini River and one from the bank of an oxbow lake. On three separate occasions we collected all woody plant species >4 m tall encountered along a 1-km stretch of the river, once in the vicinity of the Tiputini Biodiversity Station, and twice in the vicinity of the Estación Cientfica Yasuní These sample sites differ from the floodplain plot in their constant exposure to river level fluctuations (flooded 8–10 times per year). The single lakeside sample was collected from trees on the edge of Laguna Nutria, an oxbow lake within 1.5 km of the Estación Cientfica Yasuníand within 0.25 km of the river. Sample sizes and species richness for each sample site are presented in Table 1. A combined sample composed of all three river sites was made to evaluate the importance of riverside lianas and riverside tree species on the estimates of mean annual temperature.

All taxa in all samples were sorted to species or morphospecies, and leaves of each dicotyledonous species were scored for entire or toothed margins. A toothed margin was scored for all species showing vascularized extensions of leaf margins (Wilf, 1997). No species whose leaves bore marginal spines were

encountered. Voucher specimens of most species are deposited in the National Herbarium of Ecuador (QCNE), and copies of the full data set are available as online appendices at: (http://ajbsupp.botany.org/v88/burnham.xls).

## ANALYSES

A simple linear regression reflecting the relationship between mean annual temperature and leaf margin was derived by Wing and Greenwood (1993) based on the east Asian sites initially used by Wolfe (1979). The relationship has been used widely in paleoclimate reconstructions (Wiemann et al., 1998; Wilf et al., 1998; Wilf, 2000; Wing, Bao, and Koch, 2000), The same regression equation was applied here to test the ability of the samples from a single climatic regime to reflect the correct mean annual temperature (MAT):

$$MAT = 30.6E + 1.14,$$

where $E$ = proportion of woody dicotyledonous species with entire-margined leaves (Wilf, 1997).

The application of a regression model based on data from sites in east Asia (Wolfe, 1979) to sites in South America might introduce unknown errors; however, our question was focused on the variation of climate estimates as reconstructed from a single climatic area and not on creating a new data set for the reconstruction of paleotemperatures. The point here is to demonstrate the variability in the leaf margin percentages from a restricted area within a single climatic zone, rather than to distinguish among the various climatic models derived from margin percentages. Studies to date do not indicate significant differences in the leaf margin and temperature correlation for South America vs. East Asia (Wilf, 1997; Gregory-Wodzicki, 2000).

Because fossilized leaf deposits nearly always contain many fewer species than our samples did, we also explored how the dominance–diversity structure of a plant community affects its ability to reconstruct MAT. In temperate forests, Wilf (1997) demonstrated that clumped distributions of entire-margined species, within the rank-abundance order of samples, biased temperature estimates, particularly in low-diversity samples. Here we examined that bias explicitly by ranking the species found in the terra firme 1-ha plot from most abundant to least abundant, separately for lianas and trees, under the assumption that the abundance of a species would be proportional to its likelihood of appearing in a fossil sample. The two rankings
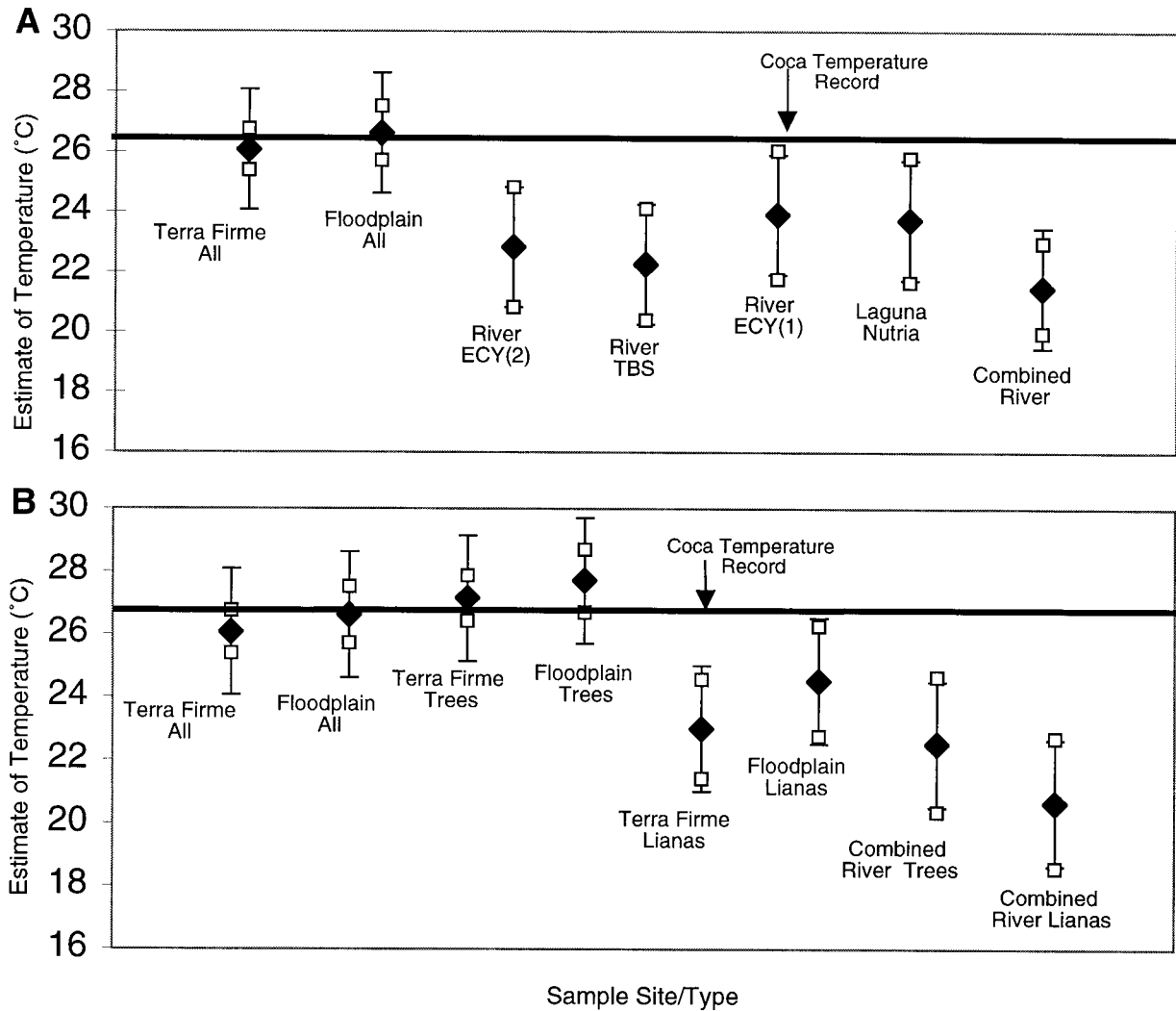
Fig. 2.   Estimates of mean annual temperature based on leaf-margin analysis of samples from YasuníNational Park, Ecuador. Actual temperature in nearby Coca = 26.5°C, shown by a horizontal line. Solid diamond represents mean annual temperature calculated using the regression equation (see text), open squares represent the calculated error estimate due only to sample size (Table 1), conservative minimum error estimate on temperature of ±2°C (Wilf, 1997) shown by vertical lines and error bars. (A) Habitat comparisons. (B) Comparisons of tree-only and liana-only samples with tree + liana samples.

were then aligned and combined, by inserting a liana species after every three tree species (lianas comprise 25% of the species for this plot). Mean annual temperature was calculated first using only the 10 most abundant species in this new ranking, then calculated using only the 11 most abundant species, and so on, until all species were included. The same procedure was carried out for the floodplain 1-ha plot with the exception that a liana was added after every two tree species in the rank order list (lianas comprise 33% of the species in this plot).

## RESULTS

Figure 2 and Table 1 summarize the mean annual temperature estimates derived from the samples. Mean annual temperatures reconstructed from lake and riparian samples were consistently and significantly lower than those reconstructed from closed-canopy (either terra firme or floodplain) forest samples (Table 1, Fig. 2a). Closed-canopy forest leaf margin percentages provided accurate estimates of the site's MAT, while lake and river samples underestimated MAT by 2.5°–5°C.

Trees species had higher percentages of entire-margined leaves than lianas from the same closed-canopy plots, with the result that tree-only plot samples predicted slightly warmer temperatures than liana-only samples (Fig. 2b). Lianas comprise a high proportion of the total species found in the river and lake samples (Table 1); however, the high concentration of liana species in the river and lake samples was not the only source of the cooler MAT estimates from those habitats. Tree species growing along the river also display a relatively high proportion of toothed margins and thus underestimate MAT by 4°C.

Smaller sample sizes than those used here are more likely to be retrieved from the fossil record and may adversely affect the estimate of MAT. An assumption we make is that fossil species would be recovered in order of decreasing stem abundance, with rare species added last. Figures 3 and 4 show the trajectory of mean annual temperature estimates made using the terra firme and floodplain samples by sequentially adding species one by one, starting with the ten most abundant species. The high degree of variability when using a small number

## Effect of Increasing Sample Size on Temperature Estimate: Terra Firme Plot
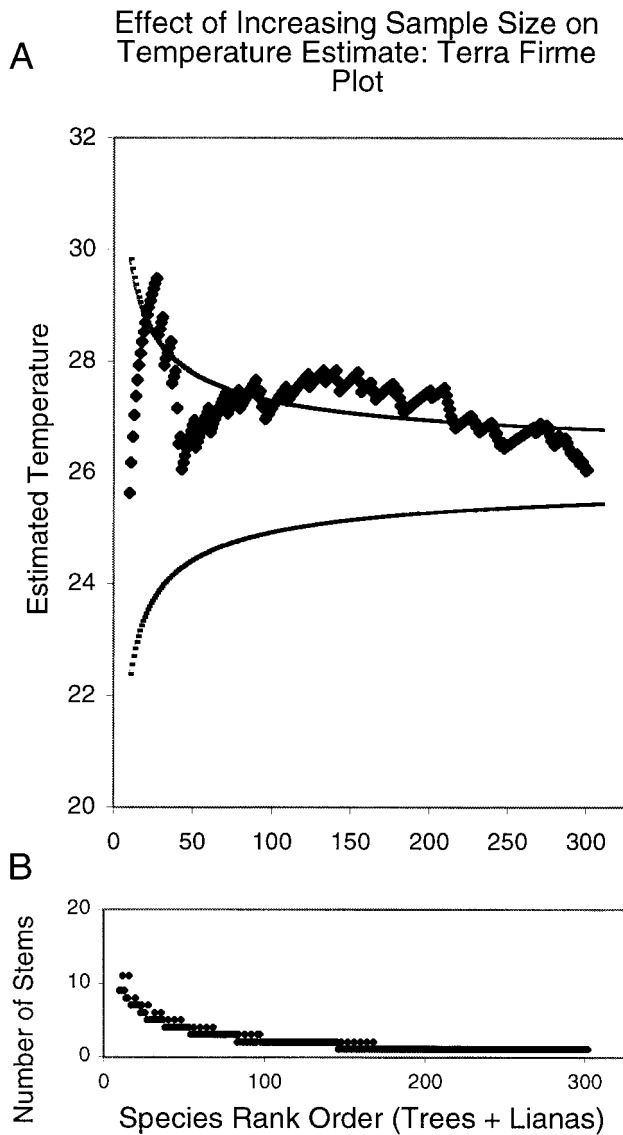
A

B

Fig. 3. Effect of increasing sample size on mean annual temperature estimate. (A) Sample from terra firme forest, including all species of dicotyledonous trees and lianas. Curves represent error due to number of species sampled (Wilf, 1997: equation 4). Within equal abundance groups, species are listed alphabetically by family and genus, thus a slight phylogenetic effect is shown within equal abundance groups (see B for stem abundance). (B) Species rank-order abundance in the terra firme plot, with species ranked based on stem abundance. Note that trees and lianas are ranked separately, then combined, thus the curve appears to show two overlapping rank abundance curves.

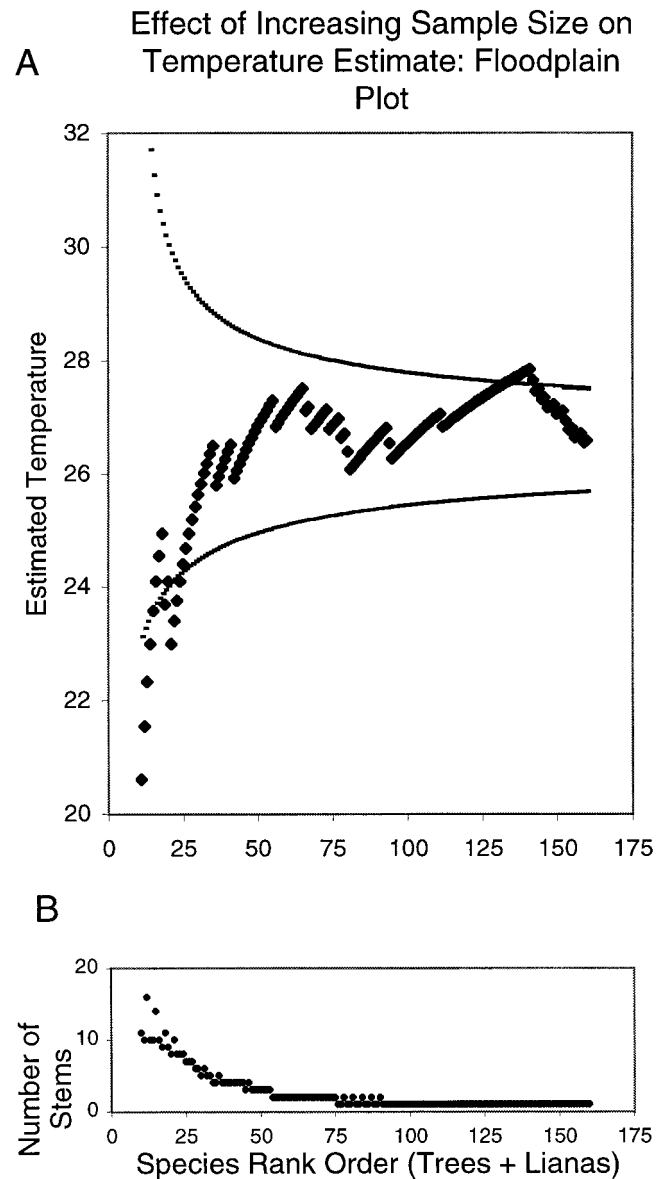## Effect of Increasing Sample Size on Temperature Estimate: Floodplain Plot

A

B

Fig. 4. Effect of increasing sample size on mean annual temperature estimate. (A) Sample from floodplain forest, including all species of dicotyledonous trees and lianas. Curves represent error due to species sampled (Wilf, 1997: equation 4). Within equal abundance groups, species are listed alphabetically by family and genus, thus a slight phylogenetic effect is shown within equal abundance groups (see B for stem abundance). (B) Species rank-order abundance in the floodplain plot, with species ranked based on stem abundance. Note that trees and lianas are ranked separately, then combined, thus the curve appears to show two overlapping rank abundance curves.

of species (10–20 species) indicates the degree of error that might be expected when using small samples, given the dominance–diversity pattern of these forests. For floodplain and terra firme samples, sample sizes of 29 and 36 species, respectively, are required to constrain the error to within ±2°C of the temperature reflected by the complete sample. Samples including <30 species are highly variable, with predicted mean annual temperature ranging from 20° to 29°C. The relative effect of a continued series of one margin type or the other on the temperature estimates decreases as more species are added, and such a series has a lower proportional effect on the cumulative entire-margin percentage. The variation in

temperature estimates seen in Figs. 3 and 4 at the point where singleton species (n = 1 for a species) are added is due to listing species alphabetically by family within equal abundance values (e.g., Sapindaceae especially frequently bear leaves with toothed margins).

### DISCUSSION

Botanists reconstructing the climate of eastern Ecuadorian forests based on leaf margin characters will reach very different conclusions depending on which part of the landscape they

choose to sample. Plant communities growing along the margins of rivers and lakes indicate a cooler MAT than that actually recorded, to the extent that a researcher whose only information about the site was a sample of its streamside plant community might guess that it was as much as 10° of latitude distant from its actual location or several hundred metres higher in elevation.

Both closed-forest samples, floodplain and terra firme, correctly reconstruct the mean annual temperature, and yet it is clear that none of the lake or river samples, nor the liana-only samples, reconstruct mean annual temperature accurately. A fossil assemblage composed solely of liana leaves is highly unlikely, and we present those data to demonstrate that lianas show a small but significant bias in their leaf margin characteristics. River and lake samples, however, are a much more troubling phenomenon and reflect long-standing concerns of paleobotanists: that river samples tend to underestimate paleotemperature because of their higher proportion of nonentire leaves (MacGinitie, 1953; Wolfe, 1977).

A large part of the deviation from actual mean annual temperature in the river and lake estimates is due to a high proportion of lianas in those samples (~50%; see Table 1). However, if the lake and river samples were composed of 100% lianas, they would rarely reconstruct a temperature as low as the TBS River sample. When the three river samples are combined to evaluate the importance of lianas on the estimates of temperature, it is clear that trees along the river also are disproportionately low in entire-margined species. The tree species in the combined river sample include 69.8% entire-margined species, substantially fewer than characterizes the two tree-only 1-ha samples (Table 1). This indicates that although the riverside lianas contribute to the low temperature estimates derived from riverine samples, the low estimates are not purely a liana phenomenon.

Kappelle and Leal (1996) document a successional trend in percentages of entire leaf margins in montane forests in Costa Rica: higher percentages are found in primary forest than in secondary forests. Although they do not propose an explanation for the phenomenon, such a trend is important in interpreting fossil floras from basins with high sedimentation rates (and thus potentially high rates of disturbance). We propose that the river and lakeside samples have low proportions of nonentire leaves, in part because there is an advantage to fast growth in these open habitats. Overgrowing neighbors along the river banks is of prime importance in gaining access to sunlight. The advantage of teeth as agents of rapid water loss (and thus rapid water movement), early in the leaf lifetime (Canny, 1990), may be strong in the presumably highly competitive environment along the Tiputini River and Laguna Nutria. In seasonal temperate environments rapid leaf expansion and growth would confer a competitive advantage to rapid expansion because of the short growing season and would similarly cause a bias toward toothed margins, as proposed by Baker-Brosh and Peet (1997).

The impact of this research on paleobotanical reconstruction of paleoclimate is to underscore the importance of determining the type of paleoenvironments represented by the sedimentary sequence from which the fossils are derived. Burnham (1994) cautioned that fossil species from channel margin facies severely underrepresented apparent paleotemperature and emphasized the importance of identifying such deposits in fossil suites. At the same time, it was noted that stable forested habitats were the best single environment for climate reconstruc-

tion and, of any single paleoenvironment, would be most likely to reconstruct the prevailing climatic conditions. Because the great majority of fossil deposits are derived from sites that have high rates of sedimentation, or low rates of decomposition, the application of temperature-margin regressions based on nonriparian habitats increases the error involved in temperature reconstruction. This research documents that terra firme and floodplain forests in this tropical lowland setting adequately reconstruct mean annual temperatures, but riverine and lacustrine habitats from the same local area substantially underestimate the mean annual temperature. We strongly recommend that environmentally constrained samples in adjacent habitats from a variety of modern climatic zones should be analyzed to determine the generality of our observations.

We propose that all compilations of modern floras for predicting paleotemperatures include lianas from each site, along with trees. Because life form is not obvious from fossil leaves preserved and subsequently used for paleotemperature analysis, a combined regression data set will allow for differences that are life-form specific. Liana species comprise from 5 to 43% of species lists from modern tropical and temperate forests (Gentry, 1991; R. Burnham, unpublished data) and are likely to contribute similarly to angiosperm-dominated fossil deposits.

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