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Comment on "The Response of Vegetation on the Andean Flank in Western Amazonia to Pleistocene Climate Change"

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Comment on "The Response of Vegetation on the Andean Flank in Western Amazonia to Pleistocene Climate Change"

Surangi W. Punyasena,[1]* James W. Dalling,[1,2] Carlos Jaramillo,[2] Benjamin L. Turner[2]

Cárdenas *et al*. (Reports, 25 February 2011, p. 1055) used the presence of *Podocarpus* pollen and wood to infer ≥5°C cooling of Andean forests during Quaternary glacial periods. We show that (i) *Podocarpus* has a wide elevation range in the Neotropics, and (ii) edaphic factors cannot be discounted as a factor governing its distribution. Paleoecologists should therefore reevaluate *Podocarpus* as a cool-temperature proxy.

Cárdenas *et al*. (*1*) presented a late Pleistocene tropical palynological record for Erazo, Ecuador (00°33′S, 77°52′W, 1914-m altitude) that predates the last glacial period. The relative scarcity of such records, and the effort required to develop a usable chronology for this period, make this study of particular importance in understanding the influence of glacial-interglacial cycles on Neotropical plant communities. However, we challenge the temperature reconstructions and paleoecological interpretations that form the basis of (i) the inferred paleoenvironmental changes between 324,000 and 193,000 years ago, and (ii) the correlations of the Erazo record to marine isotope stages (MIS) 9, 7, and 6. Our independent biogeographic analyses lead us to conclude that the authors' bioclimatic interpretation of three genera (*Podocarpus*, *Ceroxylon*, and *Alnus*) overemphasizes differences in altitudinal distributions and ignores potential edaphic specializations.

Cárdenas *et al*. (*1*) used the presence of *Podocarpus* pollen and macrofossils and the absence of *Ceroxylon* to identify what they believe is glacial MIS 6 and late interglacial MIS 9 cooling from the Erazo record. *Ceroxylon* is an Andean palm that includes some of the highest elevation Arecaceae species (*2*), while *Podocarpus* is a diverse genus of broadleaf conifers with a primarily southern hemispheric distribution (*3*). The authors used the dichotomy between the two genera to estimate a ≥5°C glacial cooling, based on a presumed modern upper altitudinal range of 3000 m for *Ceroxylon* and a lower limit of 2900 m for *Podocarpus*. Further, a nonanalog *Ceroxylon*-*Alnus* assemblage is assumed to reflect the warmer temperatures of interglacial MIS 7, despite the traditional characterization of *Alnus* as a high-altitude, low-temperature genus in the Neotropics (*4*).

Using herbarium records and published physiological data, we demonstrate that, although *Podocarpus* is a common taxon in high-elevation forests (*3*), it is not exclusively found at high elevations; dramatic cooling is therefore not required to generate the compositional changes observed at Erazo. We examined the elevation and bioclimatic ranges of all Neotropical *Podocarpus* species, as well as the subset for which the current distributional range encompasses either the northern Andes or western Amazonia. We conclude that an alternative hypothesis, in which compositional turnover reflects edaphic variation at relatively constant temperature and moisture, cannot be rejected.

Biogeographic data for the three genera (*Podocarpus*, *Ceroxylon*, and *Alnus*) (Fig. 1) were obtained from the Global Biodiversity Information Facility (GBIF), an online compilation of herbarium records (*5*). Bioclimatic data (Fig. 2) were derived from the WorldClim-Bioclim data set (*6*). Although not an exhaustive census, these data provide the minimum range of temperatures in which individuals are found. Because of potential reporting inaccuracies, we restricted our final analysis to specimens for which the reported site elevation was within 250 m of the estimated Bioclim altitude.

Our analysis demonstrates a significant overlap in the altitudinal and temperature ranges of *Podocarpus*, *Ceroxylon*, and *Alnus* (Fig. 2). Even *P. oleifolius* and *P. glomeratus*, the species with the highest altitudinal distributions of the genus that Cárdenas *et al*. identify as the most likely components of their *Podocarpus* record, are found at temperatures comparable to *Ceroxylon* and *Alnus* (Fig. 2). Indeed, GBIF records indicate that *P. oleifolius* is more likely to be found at warmer localities than *Alnus* or *Ceroxylon* and that *Alnus* is found at cooler sites than *P. glomeratus*. Modern biogeographic data, therefore, provide scant evidence that *Podocarpus* is a better cool-temperature indicator than either *Alnus* or *Ceroxylon*.

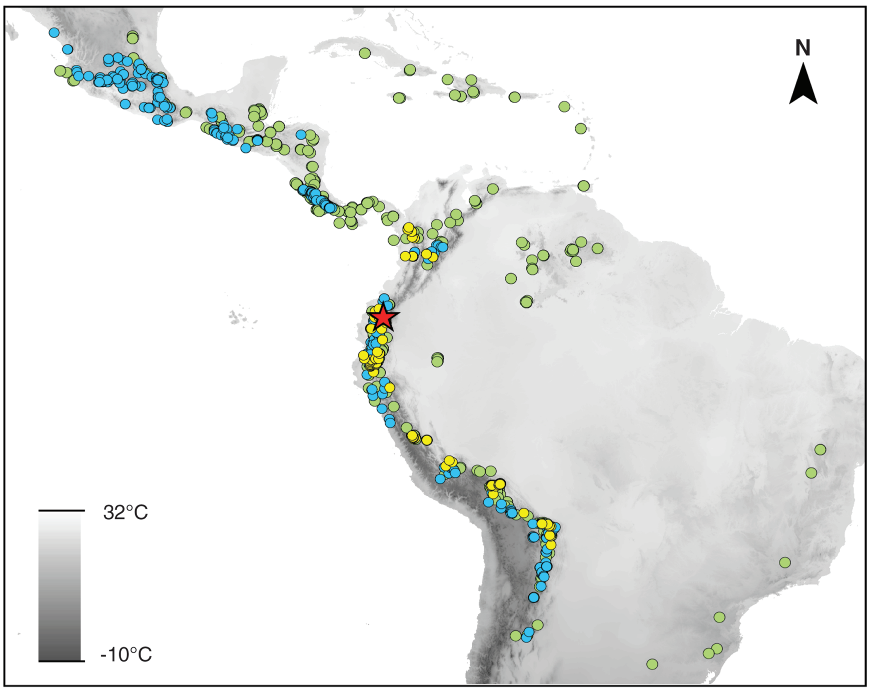

Fig. 1. Map of the collecting localities for specimens included in the analysis. *Alnus* (in blue, n = 390 specimens) is represented by one Neotropical species (*A. acuminata*). *Ceroxylon* (in yellow, n = 199) is represented by multiple species (*C. alpinum*, *C. amazonicum*, *C. ceriferum*, *C. echinulatum*, *C. flexuosum*, *C. floccosum*, *C. interruptum*, *C. mooreanum*, *C. parvifrons*, *C. parvum*, and *C. quindiuense*), as well as multiple individuals identified only to the genus. *Podocarpus* (in green, n = 685) is represented by the species identified in Fig. 2. Specimens are mapped against mean annual temperatures for central and northern South America. Data are from (*5*, *6*). The red star marks the location of the Erazo core.

[1]Department of Plant Biology, University of Illinois, 505 South Goodwin Avenue, Urbana, IL 61801–3750, USA. [2]Smithsonian Tropical Research Institute, Apartado 0843–03092, Ancon, Republic of Panama.

*To whom correspondence should be addressed. E-mail: punyasena@life.illinois.edu

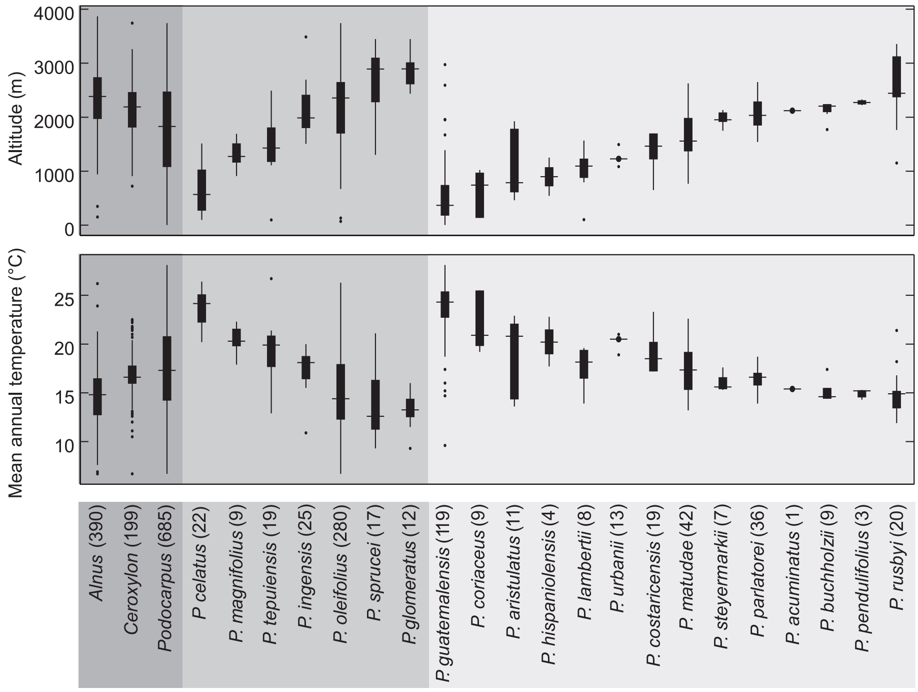

Fig. 2. Box plots of altitudinal and temperature distributions for the 1274 specimens included in the analysis. Median values are designated by horizontal bars. The edges of the box are the 25th and 75th percentiles. Whiskers represent ±2.7 SD, or 99% of the data. Outliers are plotted as single points. Summary plots of the three genera are highlighted in dark gray. Northern Andean and western Amazonian *Podocarpus* species are highlighted in mid-tone gray. Other Neotropical *Podocarpus* species are highlighted in light gray. The number of specimens included in the box plot is referenced in parentheses. Erazo is at 1914 m elevation, at the mean altitudinal range for *Podocarpus*, and below the mean altitudinal range for *Alnus* and *Ceroxylon*.

Rather than providing an index of temperature change, we suggest that the presence of *Podocarpus* at Erazo reflects changes in regional edaphic conditions. The maximum photosynthetic capacity of conifers like *Podocarpus* is limited by their lower hydraulic efficiency and lower internal CO_2 conductance relative to competing angiosperms (*7*, *8*). The resulting difference in maximal growth rates is hypothesized to have been responsible for the displacement of conifers from tropical forests by angiosperms over the past 100 million years (*9*). To the extent that tropical conifers have been able to persist in (or reinvade) tropical forests, they should be restricted to relatively infertile environments where growth is constrained by low soil nutrient availability (*10*, *11*). The thin organic sediment layers of the Erazo record, separated by multiple layers of thick volcanic ash and pyroclastic flows, indicates the presence of the infertile soils in which *Podocarpus* is most competitive. Concordantly, *Podocarpus* pollen occurs in greatest abundance in organic sediments deposited after the thickest tephra layers.

Evidence for edaphic specialization of *Podocarpus* in midelevational forests comes from the Cordillera del Cóndor, 280 km south of Erazo. There, two *Podocarpus* species, *P. sprucei* and *P. tepuiensis*, are common on infertile soils developed on Hollin formation sandstone at 1120 m and 1620 m, respectively, yet are absent from nearby nonsandstone substrates (*12*). Similarly, *P. oleifolius*, which has a median elevation of 2400 m (Fig. 1), extends to lower montane forest (1000 m) in western Panama on soils developed on extremely infertile rhyolitic tuff but is absent from more fertile neighboring soils developed on andesite and dacite with similar elevation and annual rainfall (*13*). In Colombia, *P. guatemalensis* extends to sea-level at sites with infertile ultramafic soils and high precipitation (*14*). Soils can therefore play as large a role as temperature in the distribution of *Podocarpus*.

This alternative edaphic interpretation for *Podocarpus* pollen has profound implications for our understanding of Amazonian paleoecology that extend beyond the Cárdenas *et al.* study. Although *Podocarpus* has long served as a cool-temperature indicator in Quaternary paleoecology (*15*), this interpretation has been based on a narrow view of its biogeography and autecology. It is unrealistic to describe *Podocarpus* as an exclusively high-elevation, low-temperature genus. Given our contemporary understanding of *Podocarpus* physiology and the range of environments it inhabits, Quaternary paleoecologists should revisit *Podocarpus* as an indicator of cool temperatures. For sites with clear edaphic changes, temperature will not be the only factor governing the distribution of *Podocarpus* in the paleorecord.

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