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

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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. Paleoclimatologists should therefore reevaluate Podocarpus as a cool-temperature proxy.

Using herbarium records and published palynological 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 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. parafragans, 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.

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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 CO₂ 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 (9). Thus, tropical conifers have been able to persist in 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 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. leuzechis, 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.

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.

**References**