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

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Puyasena *et al*. question our interpretation of climate-driven vegetation change on the Andean flank in western Amazonia during the middle Pleistocene and suggest that the use of *Podocarpus* spp. as a proxy of past climate change should be reassessed. We defend our assertion that vegetation change at the Erazo study site was predominantly driven by climate change due to concomitant changes recorded by multiple taxa in the fossil record.

The comment by Punyasena *et al*. (*1*) questions our interpretation of the fossil record from Erazo, Ecuador, and the inferred relationship of vegetation change with Quaternary glacial-interglacial cycles (*2*). Because of the lack of contemporaneous localities on the Amazonian flank of the Andes, Punyasena *et al*. acknowledge the importance of the Erazo study site for understanding past global glacial-interglacial cycles. The Erazo site provides the only insight into vegetation change on the Andean flank in western Amazonia during the middle Pleistocene. Given the uniqueness of these data, our interpretation is based on a series of considered assumptions, but it does not disregard the possibility of alternative interpretation. In this response we would like to (i) debate the climate-vegetation interpretation of taxa and (ii) discuss the suggested role of changing edaphic factors.

Punyasena *et al*. (*1*) challenge our inferences from specific taxa identified within the fossil wood and pollen at Erazo. The use of indicator taxa in the interpretation of fossil records is especially difficult in the tropics because many species are indistinguishable by the pollen alone and yet are able to grow in various vegetation and climate zones (*3*, *4*). Therefore, our interpretation of the drivers of vegetation change within the Erazo sediments is based on a broad consideration of the complete fossil pollen assemblage (a total of 138 pollen types identified in 29 samples). Changes across the whole assemblage were assessed using multivariate and diversity analysis [figure 3 in (*2*)] and illustrated using palynologically abundant taxa that typify the major changes (*2*), namely *Podocarpus* spp., *Ceroxylon* spp., and *Alnus* sp. We will discuss the interpretation of these individually within the context of the Erazo study site.

Punyasena *et al*. suggest that the modern altitudinal/climatic distribution of *Podocarpus* spp. on a continental scale brings our palaeoclimatic interpretation into question. However, we highlighted concomitant increases in abundance of *Podocarpus* spp., *Weinmannia* spp., *Hedyosmum* spp., *Oreopanax* spp., herbs, and grasses and interpreted the assemblage as indicative of cooler than modern climatic conditions because the taxa forming this association are generally more abundant in the tropical Andes upslope of the altitude of Erazo occupying cooler climate zones today (*5*). We also highlighted concomitant changes in abundance of the Andean palm *Ceroxylon* spp. and *Alnus* sp. This association is difficult to interpret because their modern distributions suggest differing climate signals and may have no modern analog: *Ceroxylon* spp. populations have a relatively narrow temperature range typically indicative of climate conditions similar to modern conditions at Erazo (mean annual temperature ~16° to 18°C), whereas the majority of *Alnus* sp. populations are found upslope in cooler conditions [figure 2 in (*1*)]. However, the modern distribution data for *Alnus* sp. and *Ceroxylon* spp. do not preclude co-occurrence in the past. It is possible that the concomitant rise in palms and *Alnus* sp. seen in the Erazo fossil record does not reflect changes in vegetation at the site but instead simultaneous changes occurring across an elevation gradient on the Andean flank. Palms are known to be low producers and poor dispersers of pollen such that high abundances probably indicate local presence (*3*), whereas *Alnus* sp. is a high pollen producer and effective disperser (*6*). Possible explanations for the palynological association of *Ceroxylon* spp. and *Alnus* sp. could therefore be differential dispersal of pollen types, downslope movement of *Alnus* sp. pollen along rivers, and/or changes in wind direction.

Puyansena *et al*. then suggest that the changes in *Podocarpus* spp. abundance seen in the Erazo sediments could reflect changes in local edaphic

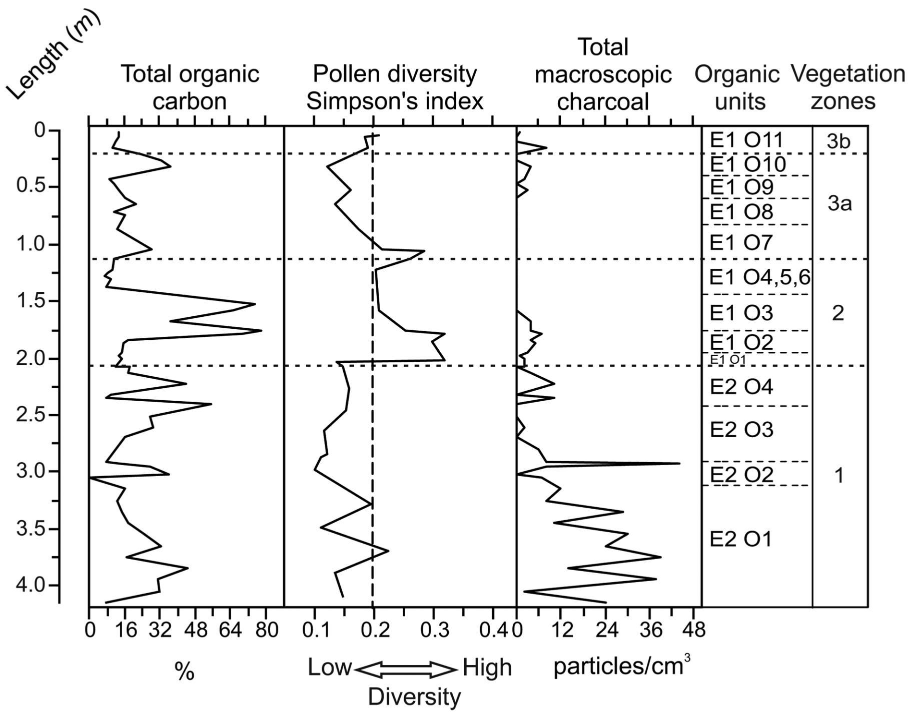

Fig. 1. Organic content, pollen diversity, and charcoal concentration from the Erazo profile. Sedimentary units and vegetation zones are as described in (*2*). The vertical dashed line, shows the modern pollen diversity level. Simpson's index is calculated from all pollen taxa (*n* = 138, comprising 118 pollen taxa identified to at least family level and 20 unidentified pollen types).

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conditions, rather than climatic change. However, the organic sedimentary units at Erazo are compositionally similar, indicating a consistency in the sedimentation across the section. This suggests that there was no change in depositional environment linked to the major vegetation changes that occurred during the period of deposition at Erazo (Fig. 1). Puyansena *et al.*'s edaphic explanation is based on an assumption that a variation in proximity of the soil surface to underlying volcanic deposits is the principal driver of vegetation composition change. Across the Erazo site, the variance in thickness of volcanic and organic deposits is similar ranging from >200 cm down to just a few cm [figure S7 in (*2*)]. Punyasena *et al.* are correct to state that the peak in *Podocarpus* spp. pollen and macrofossils does occur in an organic unit (E1O11, which is ~40 cm thick) on top of thick tephra layer (~200 cm). However, we do not consider the organic unit containing elevated *Podocarpus* to be sedimentologically atypical of the Erazo section because (i) organic units of a similar thickness are found throughout the sequence (mean organic unit thickness = 39 cm) and (ii) volcanic activity is persistent throughout and no equivalent spikes in *Podocarpus* spp. are evident in other organic units that sit atop similar ~200-cm tephra layers (E1O10, E2O2, and E2O4).

Regardless of the exact drivers of vegetation change, the Erazo fossil record testifies to a forest vegetation on the Andean flank in western Amazonia during the middle Pleistocene that was subject to change in terms of assemblage composition and diversity (*2*). After detailed reconsideration of (i) changes across the pollen assemblage [figure 3 in (*2*)], (ii) the similar nature of the observed changes with more recent climate-driven vegetation change (*7*), and (iii) independent radiometric ages [SOM 1 and figures S1 to S4 in (*2*)] that position the Erazo deposits within the known framework of Pleistocene global climate change (*8*), we are confident that the interpretation presented in our original paper, which linked observed vegetation change with marine isotope stages 9, 7, and 6, remains a plausible interpretation of the fossil record obtained from Erazo. We hope that further sites will be identified and investigated to provide a wider understanding of regional vegetation dynamism in Andean flank vegetation in western Amazonia during the middle Pleistocene.

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