



## Resurvey of Antisana supports overall conclusions of Chimborazo study

Naia Morueta-Holme<sup>a,1</sup>, Kristine Engemann<sup>b,c</sup>, Pablo Sandoval-Acuña<sup>d</sup>, Jeremy D. Jonas<sup>e</sup>, R. Max Segnitz<sup>f</sup>, and Jens-Christian Svenning<sup>b,c</sup>

Using historical data to infer temporal biotic changes is challenging (1). We are surprised that Moret et al. claim there is a "generalized misinterpretation" of Humboldt's *Tableau Physique des Andes et Pays Voisins* as representing the vegetation of Chimborazo only. The >6-km elevation span of the figure, the title, and Humboldt's descriptions, show the *Tableau* includes information from the surrounding Andes—a fact we highlighted in our publication's abstract (2). We used data from the figure with 4 other sources of historical elevation ranges, considering in detail inconsistencies and uncertainties in Humboldt's accounts. Sensitivity analyses across accounts supported the robustness of our conclusions on Chimborazo range shifts (2).

Moret et al. claim lacking preserved specimens show that Humboldt did not collect plants above 3,625 m on Chimborazo, and that he barely used the volcano in his zonation work. Specimens are indeed sparse—some possibly lost, or locality information missed in later descriptions. However, there is no reasonable doubt that Humboldt and his team collected extensive observations on plant elevational ranges on Chimborazo, visited when their knowledge of the Andean flora was at its peak. The preceding months' numerous collections would have reduced the incentive for collecting well-known species. Nevertheless, diary-based accounts of the Chimborazo ascent provide evidence of botanizing at high elevations, with plant collections and frequent elevation recordings at least up to ~4,380 m, and, beyond the last vascular plants, cryptogams up to  $\sim$ 5,500 m (3). Humboldt also paid attention to vegetation zonation, e.g., mentioning grass dominance up to  $\sim$ 4,600 m (3).

Using multiple lines of evidence (taxa, vegetation zones, growth limit), our study found strong upslope shifts in Chimborazo's vegetation (2). Recalculation of

Moret et al.'s data shows the average shift for Antisana taxa is actually 458 to 563 m, remarkably in line with our findings. Moret et al. report a 215- to 266-m shift, but only for the one species argued to indicate the overall growth limit shift on Antisana, which does not invalidate our findings. Variation in snowline and vegetation limits between mountains is not unexpected, as found across mountainsides (4, 5). On the southwest side of Chimborazo, Humboldt observed the last moss 400 toises (780 m) below the last lichen (3),  $\sim$ 4,700 m. A ~4,600-m limit for vascular plants (6) is therefore plausible for Chimborazo. We found plants higher on Chimborazo than Moret et al. on Antisana, further explaining differences in growth limit shifts between studies. The downward expansion of the grassy pajonal vegetation zone may be based on an erroneous report by Humboldt (1) but does not affect the overall upward shifts in vegetation zones (2).

Messy historical data, open to interpretation, pose difficulties for inferring precise range shifts and yet indicate trends and general estimates, complementing other evidence of biotic changes. Moret et al.'s resurvey supports our findings that plant species in the Ecuadorian Andes have shifted substantially upward over the past 2 centuries. We encourage more resurveys following in the footsteps of naturalists across the world, to increase our understanding of biotic responses to global environmental change.

## **Acknowledgments**

N.M.-H. was supported by an Individual Fellowship from Marie Skłodowska-Curie Actions (LUCCA 746334) and thanks the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate (Grant DNRF96). J.-C.S. considers this work a contribution to his VILLUM Investigator Project "Biodiversity Dynamics in a Changing World" funded by VILLUM FONDEN (Grant 16549). We thank an anonymous reviewer for comments on a previous version of this manuscript.

<sup>&</sup>lt;sup>a</sup>Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, DK-2100 Copenhagen Ø, Denmark; <sup>b</sup>Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark; <sup>c</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark; <sup>d</sup>Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, 17-01-2184 Quito, Ecuador; <sup>e</sup>Tucson High Magnet School, Tucson, AZ 85705; and <sup>f</sup>Department of Biology, Stanford University, Stanford, CA 94305

Author contributions: N.M.-H. designed research; N.M.-H. performed research; N.M.-H. analyzed data; and N.M.-H., K.E., P.S.-A., J.D.J., R.M.S., and J.-C.S. wrote the paper.

The authors declare no conflict of interest.

Published under the PNAS license.

<sup>&</sup>lt;sup>1</sup>To whom correspondence may be addressed. Email: morueta-holme@snm.ku.dk.

First published October 1, 2019.

- 1 P. Moret, P. Muriel, R. Jaramillo, O. Dangles, Humboldt's Tableau Physique revisited. Proc. Natl. Acad. Sci. U.S.A. 116, 12889–12894 (2019).
- 2 N. Morueta-Holme et al., Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. Proc. Natl. Acad. Sci. U.S.A. 112, 12741–12745 (2015).
- 3 A. von Humboldt, Notice de Deux Tentatives d'Ascension du Chimborazo (A. Pihan de la Forest, Paris, 1838).
- 4 N. Morueta-Holme et al., Reply to Sklenář: Upward vegetation shifts on Chimborazo are robust. Proc. Natl. Acad. Sci. U.S.A. 113, E409-E410 (2016).
- 5 J. La Frenierre, B. G. Mark, Detecting patterns of climate change at Volcán Chimborazo, Ecuador, by integrating instrumental data, public observations, and glacier change analysis. *Ann. Am. Assoc. Geogr.* 107, 979–997 (2017).
- 6 A. von Humboldt, A. Bonpland, "Essay on the geography of plants with a physical tableau of the equinoctial regions (1807)" in Essay on the Geography of Plants, S. T. Jackson, Ed. (The University of Chicago Press, Chicago, 2009), pp. 61–155.