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REPLY TO MORUETA-HOLME ET AL.:

Humboldt's historical data are not messy, they just need expert examination

Pierre Moret^{a,1}, Priscilla Muriel^b, Ricardo Jaramillo^b, and Olivier Dangles^{c,d}

Humboldt and Bonpland's expedition is unique in the history of biological sciences, not only for the novel theoretical concepts it gave rise to, but also for the outstanding quality of the locality data recorded for thousands of plants. The inconsistencies that distort Humboldt's *Tableau Physique* (1) should not overshadow the fact that, in most cases, the exact provenance of the collected plants can be retrieved from a cross-analysis of diaries, herbaria, and botanical publications, all now accessible online (references in ref. 1). The key question of the role of Chimborazo in the definition of vegetation zones must be addressed in this context, avoiding pointless speculations on "possibly lost" specimens (2). Let us stick to the facts. After each botanical excursion, Bonpland made a detailed report in his field notebook. Twenty vascular plants were recorded from Chimborazo, with locality information always referring to "the base of Mt Chimborazo" and elevation figures ranging from 2,885 to 3,625 m. Comparatively, 63 species came from Antisana, 46 of which $\geq 3,700$ m.

The absence of vascular plant collections above 3,625 m at Chimborazo was due to weather conditions during the ascent. According to Humboldt's diary (3), more reliable than his later published account (4), recent snow covered the ground from an elevation of 2,150 toises ($\sim 4,190$ m), not far from Lake Yanacocha where Humboldt could still observe uniform grasslands at $\sim 4,050$ m. Except for lichens and mosses collected much higher, this was his last botanical observation.

There is no mention of grass dominance at $\sim 4,600$ m, as wrongly stated (2). Hence Humboldt's surprising conclusion: "of all the Nevados we visited, it is the poorest in plants" (3).

We fully agree with Morueta-Holme et al. (2) that the *Tableau Physique* includes information from several mountains. However, Chimborazo had no part in it, as far as elevations $\geq 3,700$ m are concerned. None of the vascular plants placed there in the successive versions of the *Tableau Physique* comes from Chimborazo (ref. 1, table S2). Due to the lack of previous taxonomical work, Humboldt was unable to get precise information on the distribution of the same species among the mountains he visited. Seventy percent of his páramo plant records are limited to 1 mountain, 26% to 2, and 4% to 3. Only 3 plants were collected both on Chimborazo and on another mountain. Accordingly, his plant zonation was based on the better-studied mountains: Antisana and Pichincha.

Finally, a vascular plant upper limit at 4,600 m in 1802 (5) cannot be used to assess upslope shifts in plant distribution, for 3 reasons that Morueta-Holme et al. (2) overlook: Humboldt corrected it in his following publications (1); plants were actually collected by Bonpland at much higher elevation (1); and during the first 80 y of the 19th century, still in the last period of the Little Ice Age, vascular plants were sampled on Chimborazo far above 4,600 m (6), especially by Hall in 1831 at $\sim 5,180$ m (7) and Whympfer in 1879 at 5,060 m (8). Historical context matters.

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- 2 N. Morueta-Holme et al., Resurvey of Antisana supports overall conclusions of Chimborazo study. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.1911597116 (2019).
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- 4 A. von Humboldt, *Notice de Deux Tentatives d'Ascension du Chimborazo* (A. Pihan de la Forest, Paris, 1838).

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