REPLY TO SKLENÁŘ:

Upward vegetation shifts on Chimborazo are robust

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Working with 210-y-old botanical data is challenging. The same data quality concerns expressed by Sklenář (1) motivated the extensive sensitivity analyses reported in our study (2), all of which indicate robust results, shown in our *Supporting Information*. Although some uncertainty is unavoidable, the strength of our study lies in the broad range of evidence supporting a strong overall upward vegetation shift on Chimborazo since Humboldt's 1802 visit, consistent for the upper vegetation limit, vegetation zones, species, genera, and glacier retreats.

Importantly, Sklenář's critique (1) overlooks that we designed our resurvey to sample the same area as Humboldt, the southeastern slope of Chimborazo, key to ensuring comparability of the studies. Meyer collected *Pentacalia chimborazensis* (accepted name for *Senecio hallii*) at 5,200 m in 1903 (3), but ascended the northwestern slope, where glacier limits are much higher and the climate is "unusually favorable" (3). Hence, these localities are incomparable to Humboldt's. Hall climbed the southeastern slope (4, 5), but possible elevation overestimations (4), along with source uncertainty, make Diels' assignment of *Draba depressa* to 5,600 m questionable. Indeed, Hall describes his collection (misidentified as *D. aretioides*) at "nearly 18,000 feet" (~5,490 m) (5), and noted on his specimen labels "below snow line",* or 17,000 feet (~5,180 m).†

Sklenář questions Humboldt's vegetation zone limits (1). Our abstract states that these are based on observations from Chimborazo and surrounding Andes (2). The absence of *Espeletia* from Chimborazo does not refute the presence of codominants defining the vegetation type. Distribution mismatches between Chimborazo's vegetation zones and other areas would have been obvious to Humboldt and we see no reason

to doubt his reports. For species shifts, to be conservative, species that Humboldt observed at higher elevations outside Chimborazo were assigned their highest reported 1802 elevation in our analysis. Limiting our analysis to observations strictly reported on Chimborazo by Humboldt did not change the conclusions (2).

Species-specific shifts are the most uncertain, but are unlikely to be upwardly biased. Some will be too conservative because of overlooked individuals or exclusion of individuals with nonverified identifications. Contrary to Sklenář's claim (1), the rates reported are within previous observations (6–8). Furthermore, Sklenář uses post-Humboldt collections to compare shifts, but most were collected by Meyer and Whymper on the northwestern and western slopes (3, 9), and hence are incomparable to our study. Assuming all other collectors visited the southeastern slope, the remaining species (3) show no significant downward shift since 1870–1903.

Several expert paramo botanists confirmed our identifications, and specimens are available for revalidations (AAU, QCN, and QCA herbaria, 2). None of Sklenář's examples represent misidentifications: *Arenaria serpyllifolia* is the accepted name of *Stellaria serpyllifolia*, previously reported from Chimborazo,‡ along with *Draba aretioides* (10). We erroneously reported *Pentacalia hillii*, but not because of misidentification: the correct name is *Pentacalia chimborazensis*, recorded in the resurvey under the synonym *Senecio hallii*, leading us to *P. hillii* through misspelling. The species was unreported by Humboldt and hence excluded from the taxon-specific analyses.

Taken together, Sklenář's concerns do not affect the conclusions of our work.

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Author contributions: 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.

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*herbarium.bgbm.org/object/B100243535.

†specimens.kew.org/herbarium/K000471926.

‡www.tropicos.org/Name/6300818?tab=distribution.

- 1 Sklenář P (2016) Advance of plant species on slopes of the Chimborazo volcano (Ecuador) calculated based on unreliable data. *Proc Natl Acad Sci USA* 113:E407–E408.
- 2 Morueta-Holme N, et al. (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proc Natl Acad Sci USA* 112(41): 12741–12745.
- 3 Diels L (1937) *Beiträge zur Kenntnis der Vegetation und Flora von Ecuador* (Bibliotheca Botanica, Stuttgart).
- 4 McCosh FWJ (1984) *Boussingault: Chemist and Agriculturist* (Springer Netherlands, Dordrecht, The Netherlands).
- 5 Hall C (1835) Excursions in the neighbourhood of Quito, and towards the summit of Chimborazo, in 1830. *Companion to the Botanical Magazine*, ed Hooker WJ (Samuel Curtis, London), pp 52–65.
- 6 Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331(6015):324–327.
- 7 Uri M, et al. (2014) Inferring shifts in tree species distribution using asymmetric distribution curves: A case study in the Iberian mountains. *J Veg Sci* 25(1):147–159.
- 8 Bergamini A, Ungricht S, Hofmann H (2009) An elevational shift of cryophilous bryophytes in the last century—An effect of climate warming? *Divers Distrib* 15(5): 871–879.
- 9 Whymper E (1892) *Travels Amongst the Great Andes of the Equator* (Charles Scribner's Sons, New York).
- 10 León-Yáñez S, Pitman N (2003) *Draba aretioides*. The IUCN Red List of Threatened Species 2003: e.T43099A10771823. Available at dx.doi.org/10.2305/IUCN.UK.2003.RLTS.T43099A10771823.en. Downloaded on November 24, 2015.