

# Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt

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Edited by William H. Schlesinger, Cary Institute of Ecosystem Studies, Millbrook, NY, and approved August 19, 2015 (received for review May 20, 2015)

**Global climate change is driving species poleward and upward in high-latitude regions, but the extent to which the biodiverse tropics are similarly affected is poorly known due to a scarcity of historical records. In 1802, Alexander von Humboldt ascended the Chimborazo volcano in Ecuador. He recorded the distribution of plant species and vegetation zones along its slopes and in surrounding parts of the Andes. We revisited Chimborazo in 2012, precisely 210 y after Humboldt's expedition. We documented upward shifts in the distribution of vegetation zones as well as increases in maximum elevation limits of individual plant taxa of >500 m on average. These range shifts are consistent with increased temperatures and glacier retreat on Chimborazo since Humboldt's study. Our findings provide evidence that global warming is strongly reshaping tropical plant distributions, consistent with Humboldt's proposal that climate is the primary control on the altitudinal distribution of vegetation.**

Andes | climate change | land use change | range shifts | tropical biodiversity

The biological impacts of ongoing climate change (1) are already apparent in species' poleward and upslope range shifts and earlier spring events (2–9). However, most studies stem from high-latitude areas and are generally restricted to dynamics across the past few decades (10). To our knowledge, only three previous resurveys have studied range shifts of tropical plant taxa, all at <4,000 m in elevation (7, 8, 11). Modeling (12) and paleoecological studies (13) suggest that tropical montane vegetation should be highly sensitive to climate change. However, researchers strongly debate whether tropical plants are tracking warming temperatures along elevation gradients, with most (although scarce) studies indicating they are lagging behind (cf. 14, 15). Such lags could have negative effects on the distributions of species dependent on certain plant taxa, e.g., as a food source (16). The question is particularly urgent given the growing evidence of systematically stronger warming rates in high-mountain environments (17).

The legacy and works of Alexander von Humboldt (1769–1859) not only constitute the foundation of biogeography, but also what is likely the oldest dataset on altitudinal ranges of plant species. The observations recorded by Humboldt and Aimé Bonpland (1773–1858) during their travels in Central and South America, and synthesized in a Tableau of Mt. Chimborazo (summit 6,268 m above sea level) and accompanying essay (18), provide a unique opportunity to study tropical vegetation changes over a period of 210 y. To our knowledge, this period is more than twice as long as any previous resurvey study based on historical biodiversity records (11, 19). We revisited the upper slopes of the Chimborazo volcano in June 2012. Our aim was to record the current elevational distribution of plants and test for upward shifts since Humboldt's expedition, as a response to anthropogenic global warming. We sampled plant species presence and abundance along transects every 100 m of elevation between 3,800 and 5,200 m. Three main findings, comparing our surveys to Humboldt's data, support strong upward shifts of plant distributions: a higher upper limit for

plant growth, increased elevation of vegetation zones, and upward shifts in the upper range limits of most individual taxa.

## Results and Discussion

The ultimate upper limit of vegetation on Chimborazo has shifted strongly upward, as expected from the warming climate. We observed seed plants growing up to an elevation of 5,185 m, constituting an upward shift of the upper vegetation limit of >500 m since 1802. According to Humboldt, the upper limit for the growth of seed plants was at 4,600 m, above which only lichens could be found (18). Our highest-elevation observations were sterile individuals of *Draba aretioides* Humb. & Bonpl. ex DC. and flowering individuals of *Pentacalia hillii* (Greenm.) Cuatrec, both found at 5,185 m.

The altitudinal distribution of vegetation zones on Chimborazo has also experienced marked shifts since Humboldt's expedition (Fig. 1). Along Chimborazo's elevational gradient, Humboldt recognized vegetation zones characterized by distinct species groups. Notably, he described a “Chuquiraga-gentianes-frailejón” zone with *Chuquiraga*, *Gentianella*, *Gentiana*, and *Espeletia* occurring between 2,000 and 4,100 m in 1802. At 4,100–4,600 m, he found grass-dominated “Pajonal.” We instead found the highest abundance of the *Chuquiraga* and gentian species in a zone between 4,200 and 4,600 m. We also found high grass abundance from 3,800–4,600 m, but with presences in plots up to 5,000 m and outside-plot observations to 5,070 m. Thus, our resurvey demonstrates an upward shift of both vegetation zones, as well as a general expansion of the Pajonal-type vegetation also at lower elevations relative to Humboldt's observations.

## Significance

**Tropical regions harbor the majority of the world's biodiversity, but there is debate about whether montane species here are able to track global warming at the same rate as in temperate regions. By following in Humboldt's footsteps and revisiting his pioneering documentation of vegetation elevation ranges, we show that the limit of plant growth has already been strongly pushed upslope. Although the rate of plant range shifts matches that found in other studies, the total magnitude of change in vegetation and glacier coverage on Chimborazo is larger than expected from warming temperatures alone.**

Author contributions: N.M.-H., K.E., and J.-C.S. designed research; N.M.-H., K.E., P.S.-A., and J.D.J. performed research; R.M.S. contributed new reagents/analytic tools; N.M.-H. and K.E. 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.

This article is a PNAS Direct Submission.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1509938112/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1509938112/-DCSupplemental).



deposition or other nutrients could also potentially have contributed to the observed changes in species composition and range shifts (27). However, the extent to which nitrogen deposition is driving upward range shifts in plant species is unclear, even in high-deposition regions like Europe. The increased abundance of grasses on Chimborazo could potentially be driven in part by nitrogen (28), but could also result solely from land use changes.

The general upward shift of vegetation and individual plant taxa is broadly consistent with plant species shifting their ranges to track the changing climatic conditions. National temperature records for Ecuador between 1866 and June 2012 indicate an increase in mean annual temperature of  $1.46 \pm 0.31$  °C ([berkeleyearth.org](http://berkeleyearth.org)) (estimate  $\pm$  SE). This increase translates into an expected upshift in elevation of  $243 \pm 51$  m, assuming a lapse rate of  $\sim 6$  °C for every 1,000 m in elevation (4, 19). Temperature measurements for Ecuador from the time of Humboldt's expedition are not available, but the global average changed by  $0.26 \pm 0.45$  °C between 1802 and 1866 ([berkeleyearth.org](http://berkeleyearth.org)). Thus, following regional and global averages, the maximum expected upslope shifts would be  $\sim 410$  m since Humboldt's study. The observed glacier retreat and vegetation responses are apparently larger than expected from regional temperature increases alone, with an observed/expected shift rate ratio of  $\sim 1.6$  for vegetation overall. The high observed shift rate likely reflects changes in precipitation regime and ash deposition from Tungurahua, as well as the impacts on vegetation from the intensified land use at lower sites (Fig. 3). Our results are thus counter to the generally lagged responses of tropical trees to climate change in shorter-term studies reporting shift rates of 0.3–0.6 (7, 14). Still, a nonnegligible proportion of our study taxa exhibited upwards shifts  $<410$  m (Fig. 2), indicating lags. Although the upward shift we found here of 32 m per decade at the species level is faster than the reported median of 11 m across plant and animal species worldwide (29), it is similar to the 36 m per decade found for tropical plants in a recent study in Taiwan (11). Our findings of human-dispersed species shifting upward from elevations  $<3,800$  m also strengthen concerns that the immigration of widespread generalist species may come at the cost of high-elevation endemic species and increased biotic homogenization (11).

The substantial upward changes in the overall limit to plant growth, distribution of major vegetation zones, and upper boundaries of many species ranges show that plants are strongly responding to global warming, even within the tropics (7, 8, 16). Comparison of Humboldt's pioneering Chimborazo vegetation survey with our resurvey thus corroborates evidence for the sensitivity of tropical montane vegetation to climate change from modeling (12) and paleoecological studies (13), highlighting that dramatic shifts can occur at relatively short, contemporary time scales. The tropical Andes constitutes a major biodiversity hotspot in terms of endemic species (30), and the high-elevation ecosystems support the livelihoods of millions of people through hydrologic control and carbon storage (31). The much-stronger climate change forecasted for the near-future (1) is therefore likely to lead to dramatic vegetation changes in tropical mountainous areas, with strong effects on the rich diversity of dependent species (16) and ecosystem services (31).

## Materials and Methods

**Resurvey.** We conducted the resurvey of Mt. Chimborazo for present elevation range estimates between June 23 and July 5, 2012 on the southeastern slope of the volcano, the region originally explored by Humboldt (18). The aim was to determine the current maximum elevation of each taxon. We sampled a total of 15 transects from an elevation of 3,800 m at 100-m elevation intervals to 5,200 m, past the limit of plant growth. Each 100-m transect followed the elevation contour, and three 25-m<sup>2</sup> quadrat plots were established at the beginning, center, and end of each transect, by using plastic poles, utility cord, and tape measures. Within each plot, we determined species presence/absence and estimated abundance as percent coverage. Coverage of  $<1\%$  was set to 0.5. Additional species present along

each transect were also registered, as well as species between transects. The exact elevation of species found above the 4,700-m transect was recorded to determine the limit of vascular plant presence. Elevation and geographic position were measured by using a GPS (Trimble Juno SP,  $\pm 10$  m).

Sampled species were collected, photographed, and identified at the Herbario Nacional del Ecuador (QCN) and the Aarhus University Herbarium to supplement the identification in the field. Vouchers were deposited at QCN and the QCA herbarium of the Pontificia Universidad Católica del Ecuador. We sampled a total of 121 taxa ([Dataset S1](#)). We were unable to determine three of the seed species, and an additional two were determined only to family or order level (both in Asteraceae). Flowering individuals of Poaceae were determined to species level, but most sterile individuals could be determined only to family level. All Poaceae were therefore excluded from analyses, except for those regarding vegetation zones.

**Historical Data Sources.** We assembled historical information on plant taxa recorded by Humboldt and Bonpland from five sources: the 1807 *Essay on the Geography of Plants* (18), its accompanying *Tableau Physique* (18, 32–34), the draft to the *Tableau* published in 1826 (35), Humboldt's late 1838 description of the visit to Mt. Chimborazo (22), and the descriptions of collected species in *Nova Genera et Species Plantarum* published 1815–1825 (36).

1. *Essay on the Geography of Plants* (18) (ref. 1 in [Datasets S2](#) and [S3](#)): presents the detailed legend for the *Tableau Physique*, describing plants seen within different vegetation zones across elevations, as well as a description of the environmental variables measured (published originally in 1807).
2. *Tableau Physique* (18) (ref. 2 in [Datasets S2](#) and [S3](#)): graphic representation of the distribution of plant taxa on Chimborazo. Some of the taxa, however, are found not on Chimborazo but in other parts of Ecuador and South America, found by Humboldt during his travels. The *Tableau* was originally published in 1807. We extracted its information from the Humboldt database (32, 33) and Jackson (2009) (34).
3. Draft to the *Tableau* (ref. 3 in [Datasets S2](#) and [S3](#)): the draft includes more taxon names than the final *Tableau*. Like the final version, some taxa are from other regions than Chimborazo, but the figure summarizes the elevations at which Humboldt observed them (35).
4. Account of Chimborazo expedition (22) (ref. 4 in [Datasets S2](#) and [S3](#)): In 1838, Humboldt presented a description of the trip to Chimborazo. The description is based on his journal written at the time of the expedition (22). Additional taxa are mentioned in this text that are otherwise omitted in the *Tableau* and *Essay*.
5. *Nova Genera et Species Plantarum* (36) (ref. 5 in [Datasets S2](#) and [S3](#)): description of all of the taxa collected by Humboldt and Bonpland during their travels in the New World and brought back to Europe. For most taxa, a description is included of the elevation and collection locality.

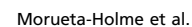
For all historical data sources, we resolved abbreviated taxon names and nomenclatural updates (including synonymies) to the current Angiosperm Phylogeny Group III system using *Nova Genera et Species Plantarum* (36) and multiple online resources (Version 1, [theplantlist.org](http://theplantlist.org); [tropicos.org](http://tropicos.org); ref. 37) ([Datasets S2](#) and [S3](#)). Historical elevations given in toises or French feet were converted to meters by using a factor of 1.949 and 3.08, respectively, following Humboldt's own conversions (22).

**Approaches to Elevation Range Comparison.** The disparate historical data sources all have advantages and disadvantages, and in some cases include inconsistent elevation estimates. Comparing the current distributions to the historical data is challenging due to the lack of a systematic design in the data collection by Humboldt. We therefore used three different approaches of data comparison to assess the sensitivity of the results to the choice of data source.

**Approach A1.** Approach A1 had the broadest range of all sources. Here we used all five sources of information and assigned the broadest and most conservative elevation range reported in any source. Priority was given to the finest taxonomic resolution. Thus, a taxon could be assigned a maximum elevation higher than what Humboldt observed on Chimborazo, if it was described higher up at a different location. Figs. 1–3 are based on this approach.

**Approach A2.** Approach A2 was a comparison with the *Tableau* and *Essay*. In this approach, we restricted the comparison with taxa specifically mentioned in the *Essay* or depicted on the *Tableau*. The rationale behind this approach is that these two sources represent Humboldt's own final summary on Chimborazo of his observations and was validated by the botanist José Celestino Mutis (18). Most taxa were mentioned at the genus level only, so this approach could not be applied to the species level.

**Approach A3.** Approach A3 was a geographic priority choice. For this approach, we chose the "best available" data source for each taxon. In cases with data from more than one source, we chose the most specific to Mt. Chimborazo, else Ecuador, else other localities in the Andes. This approach rendered the



Genus-level historical data were assigned by using Humboldt's observations at the genus level where available, and otherwise assigning the highest

elevation observed for species in the genus. Genera with uncertainties in the taxonomic resolution were excluded (e.g., if species in the genus now are considered to be in different genera). This exclusion was the case for, e.g., *Aa*, *Achyrocline*, *Cerastium*, *Cotula*, *Hieracium*, *Lasiocephalus*, *Monticalia*, *Senecio*, and *Xenophyllum* (see detailed notes in [Datasets S2 and S3](#)).

Ferns and lycophytes were excluded from the analyses, because Humboldt only noted vegetation limits for vascular plants (18).

**Vegetation-Level Range Shift Analysis.** The two uppermost vegetation zones defined by Humboldt are the Pajonal, dominated by Poaceae (4,100–4,600 m), and the Gentianes region with *Chuquiraga*, Gentianes and *Frailejón* (3,000–4,100 m). To assess potential changes in the distribution of these vegetation zones, we used the abundance data recorded in the plots. For Pajonal, we summed the estimated coverage of all grasses and averaged across the three plots sampled at each elevation transect. Similarly, for the Gentianes vegetation zone, we summed the abundances of *Chuquiraga*, *Gentiana*, and *Gentianella*. We then plotted the mean abundances across elevation to visually assess the shifts in dominance of each vegetation zone. For comparison, we also plotted the summed abundances for all other taxa observed (Fig. 1).

**Changes in Glacier Elevation.** Because glacier data for 2012 were not available, we calculated the mean of the 2013 lower limits of glaciers on Chimborazo based on data by La Frenierre (21). We assumed that any change between 2012 and 2013 would be negligible. Looking only at the glaciers on the south and east side of the volcano (glaciers Theodoro Wolf, García Moreno, Boussignault, Nicolas Martin, Carlos Pinto, and Humboldt), the limit of clean ice was  $5,270 \pm 260$  m (mean  $\pm$  SD). The minimum elevation of clean ice for Chimborazo as a whole was  $5,320 \pm 290$  m.

**ACKNOWLEDGMENTS.** We thank B. Øllgaard, S. Lægaard, P. Sklenář, P. M. Jørgensen, B. Boyle, D. Fernández, and G. Peyre for assistance with validation of taxonomic determinations; Dirección Provincial del Ambiente de Chimborazo for working permits; K. Romoleroux and R. Valencia for logistic support; and F. Borchsenius for discussions on field sampling design and logistics. Assistance in the field was provided by C. Morales, guides from Andean Adventures, and park rangers at the Reserva de Producción Faunística Chimborazo. J. La Frenierre helped with data and discussions on glacier retreat. We also thank D. Akerly, B. Blonder, R. Field, and two anonymous reviewers for useful comments that helped improve this manuscript. This work was supported by an EliteForsk Award (to N.M.-H.) and by the Ingeniør Svend G. Fiedler og Hustrus Grant (to N.M.-H. and K.E.). J.C.S. considers this study a contribution to the Danish National Research Foundation Niels Bohr professorship project Aarhus University Research on the Anthropocene (AURA).

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