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

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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.
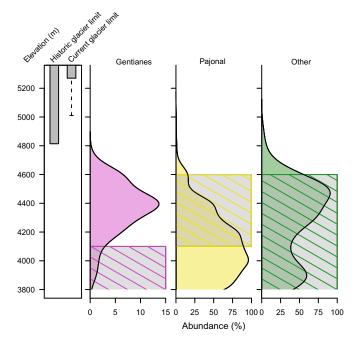
Fig. 1. Elevation changes of glacier limit and vegetation zones defined by Humboldt on Chimborazo. Current 2012 glacier limit is shown as mean ± SD. Shaded areas mark the 1802 distribution of each vegetation zone dominated by *Gentianella*, *Gentiana*, and *Chuquiraga* species (Gentianes); grasses (Pajonal); and vegetation in general. Curves show 2012 mean percent abundance of each vegetation zone along the elevation gradient. Abundance of all other species is shown for comparison. Overall, vegetation grows substantially above the 4,600-m limit reported by Humboldt. Although Pajonal abundance decreases drastically at >4,600 m, Gentianes species are found in abundance well above the 4,100-m historical elevation.

We also found pronounced upward range shifts in most individual taxa (Fig. 2). We found an average upward shift of 675 m at the species level (paired t test, $t = 7.41$; df = 50; $P < 10^{-8}$), and 565 m at the genus level ($t = 6.83$; df = 44; $P < 10^{-7}$), corresponding to an average shift per decade of 32 and 27 m, respectively. These patterns emerged consistently across multiple approaches for assembling the historical data sources, although the precise estimates of range limits varied, ranging from 586 to 787 m for species and from 557 to 700 m for genera (Fig. S1 and

Tables S1–S3). Although most species shifted upward, the magnitude and direction of the changes varied widely (Fig. 2 and Fig. S1), consistent with previous studies of changes in species' elevational ranges in other regions (4, 7, 19, 20). We found some discrepancies in the accuracy of Humboldt's elevation measurements, but no systematic bias that could explain our findings (Table S4). The results were also robust to spatial randomizations of the collection effort in 2012 (Fig. S2).

The higher vegetation limit is consistent with the reported retreat of glaciers on Chimborazo (21), which has made new habitats available for plant colonization. Glacier coverage has retreated from 4,814 m measured by Humboldt (22) to 5,270 ± 260 m (mean ± SD) in 2013 for the glaciers on the south and east side of the volcano (21). This glacier retreat of >400 m in elevation is in line with worldwide glacier recessions linked to ongoing global warming (23). Still, recent glacier retreat may also be partially attributed to accelerated ice melting due to ash deposition from the neighboring Tungurahua volcano, active since 1999 (volcano.si.edu). Tungurahua was also active before Humboldt's sampling of the region (1773–1776) and possibly again between 1777 and 1781 (volcano.si.edu and ref. 24). We did not find documentation of ash emissions during the historical eruptions, but they would be expected to have had similar effects on the glaciers. Furthermore, although ash deposition may have exacerbated recent ice melting, the effects are thought to be small (21). Hence, the plant range shifts observed are most likely primarily linked to the ongoing global climate change, although not necessarily to warming alone. There is also some evidence that precipitation patterns in the area have shifted toward drier, more unpredictable regimes during the past decades, which could also contribute to glacier recession (21).

At the lower elevations studied, land-use changes likely also contribute to observed shifts (25, 26), in particular the general increase and downward expansion of grass dominance. At the lowest sites, we observed harvesting of grass tussock and signs of localized fires, both promoting Pajonal vegetation relative to Chuquiraga-gentianes-frailejón vegetation. In addition, we recorded the presence of human-dispersed nonnative species such as *Trifolium repens* L. and *Rumex acetosella* L. at 3,800–3,900 and 3,800–4,000 m elevation, respectively, which is also consistent with more intense land use in the area. Humboldt noted that there was no agriculture at >3,600 m and that it was only scattered at >3,000 m (18). In 2012, our sampling of sites at <3,800 m was hindered by strong land cover transformation to agricultural fields. Other nonclimatic anthropogenic factors such as atmospheric nitrogen
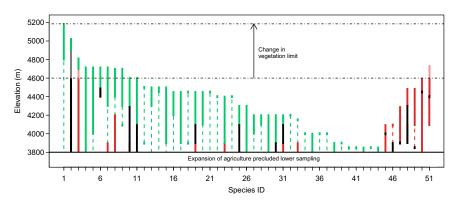

Fig. 2. Elevation range shifts for 51 plant species over 210 y. Black, overlap between observed and historical range; green, expansion of upper range limit; red, contraction of upper or lower range limit. Dashed vertical lines show discontinuities between past and present ranges. Horizontal dashed lines mark the difference between the 1802 and 2012 vegetation limits. Species names are listed in Table S1. Historical ranges >4,600 m for species 2, 3, and 51 are shown in faded colors because they are due to the visual estimation method included when reading range limits from Humboldt's illustrations. No plant taxa are mentioned >4,600 m in Humboldt's texts. Note that some of the individual range shifts are driven by changes from elevations much lower than 3,800 m, likely caused by human dispersal, and are not shown in the figure.

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 ± 0.31 °C (berkeleyearth.org) (estimate ± SE). This increase translates into an expected upshift in elevation of 243 ± 51 m, assuming a lapse rate of ~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 ± 0.45 °C between 1802 and 1866 (berkeleyearth.org). Thus, following regional and global averages, the maximum expected upslope shifts would be ~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 ~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-m² quadratic 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, ±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; 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
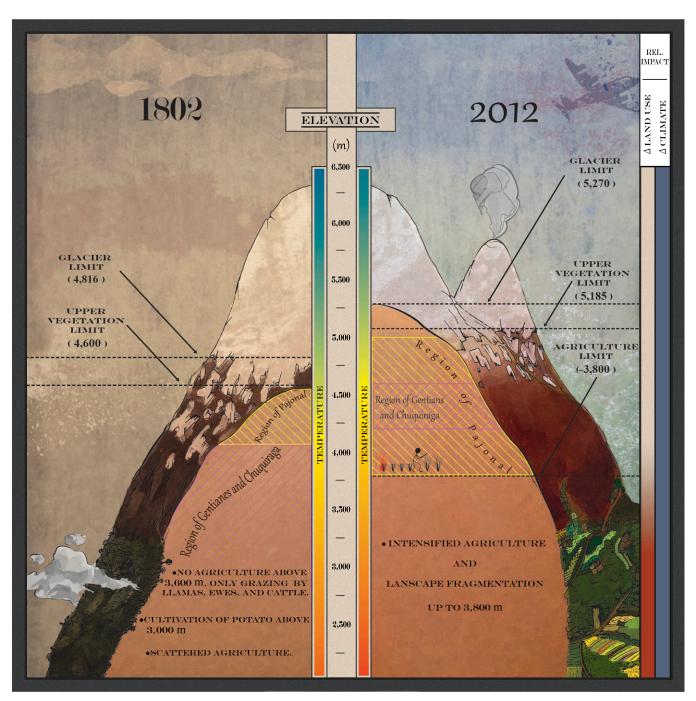
Fig. 3. An update of Humboldt's *Tableau*. Shown is a summary of major changes in overall vegetation limit, average glacier limit, and shifts in topmost vegetation regions on Chimborazo from 1802 to 2012. The major drivers of change, climate, and land use change are represented by the bars to the right: a constant impact of climate change—in particular, increased temperature—the stronger relative impact of land use at the lower sites, mainly through intensified agriculture, and the effect of grass harvesting and local burning. Illustration of glaciers is approximate.

largest number of taxa for the analysis, although there is more subjectivity in the choice of source.

For images, we used visual estimation to extract information on elevation ranges (refs. 2 and 3 in Datasets S2 and S3). Because the method is more uncertain, we used both a broad and a narrow delimiting frame around the name of each taxon to record its altitudinal range. Each comparison approach is thus presented in two versions: NA1, NA2, and NA3 (narrow) and BA1, BA2, and BA3 (broad). This method allowed us to further assess the robustness of the results to the methodology.

Taxon-Level Range Shift Analysis. We used paired *t* tests to compare the historical and current maximum range limit of individual plant taxa. Taxonomic

resolution of the data varied, and we therefore made two comparisons for each approach: one at the species level and one at the genus level (Table S3).

For all approaches at the genus level, species were lumped to the classification used by Humboldt. Thus, *Gentiana* and *Gentianella* were lumped to "Gentianes," *Arenaria* was classified as *Stellaria*, *Phyllactis rigida* was included in *Valeriana*, and *Blumea viscosa* was included in *Conyza*. *Vaccinium* and *Gaultheria* were also lumped ("*Vaccinium-Gaultheria*"), because we were unable to identify sterile individuals to the correct genus in the field. All grasses (Poaceae) were excluded from taxon-level analyses due to the difficulties in identifying sterile individuals.

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, Garcia Moreno, Boussignault, Nicolas Martin, Carlos Pinto, and Humboldt), the limit of clean ice was 5,270 ± 260 m (mean ± SD). The minimum elevation of clean ice for Chimborazo as a whole was 5,320 ± 290 m.

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