

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

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

<sup>a</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; <sup>c</sup>Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; <sup>d</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; <sup>e</sup>Department of Biology and Honors Chemistry, Tucson High Magnet School, Tucson, AZ 85705; and <sup>f</sup>Department of Biology, Stanford University, Stanford, CA 94305

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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.**

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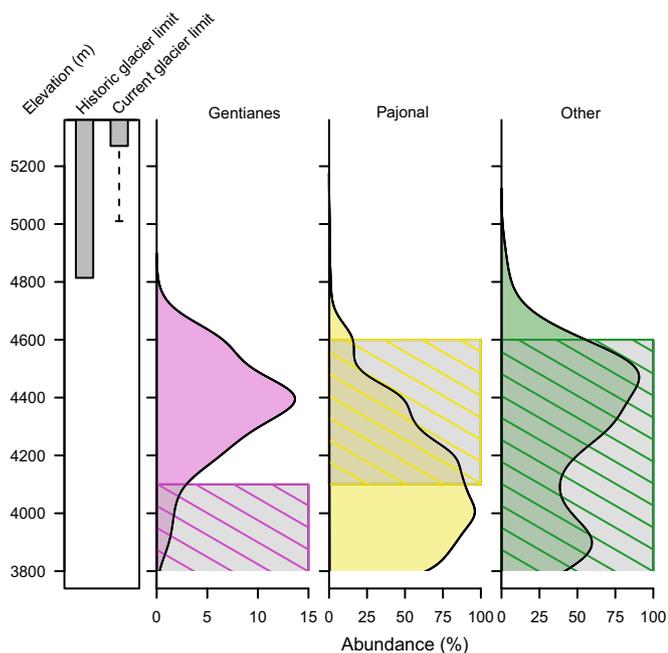
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<sup>1</sup>To whom correspondence should be addressed. Email: morueta-holme@berkeley.edu.

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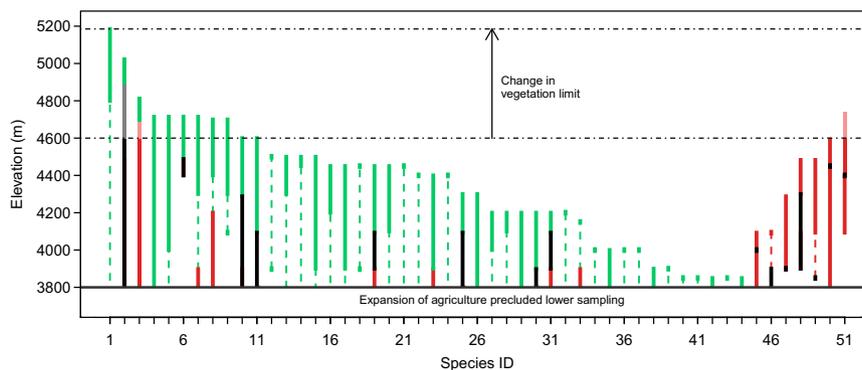
**Fig. 1.** Elevation changes of glacier limit and vegetation zones defined by Humboldt on Chimborazo. Current 2012 glacier limit is shown as mean  $\pm$  SD. Shaded areas mark the 1802 distribution of each vegetation zone dominated by *Gentianella*, *Gentiana*, and *Chuquiraga* species (Gentianes); 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  $5,270 \pm 260$  m (mean  $\pm$  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](http://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](http://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  $1.46 \pm 0.31$  °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



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*, *Mantocalia*, *Senecio*, and *Xenophyllum* (see detailed notes in [Datasets S2](#) and [S3](#)).

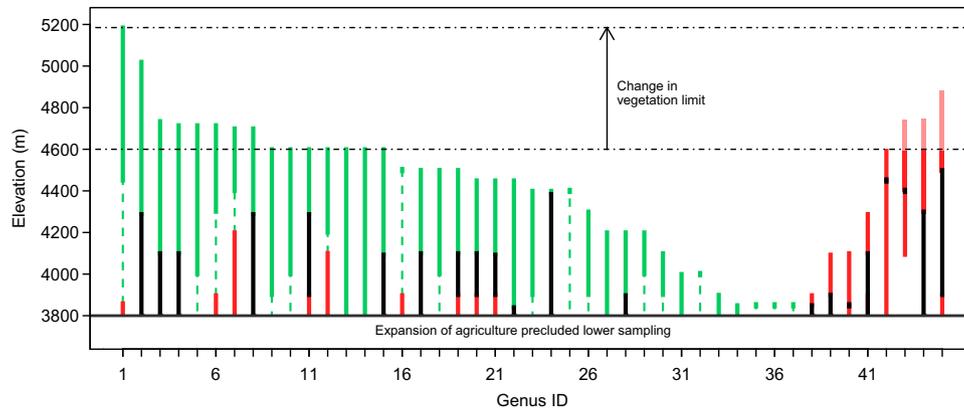
Ferns and lycophytes were excluded from the analyses, because Humboldt only noted vegetation limits for vascular plants (18).

**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).

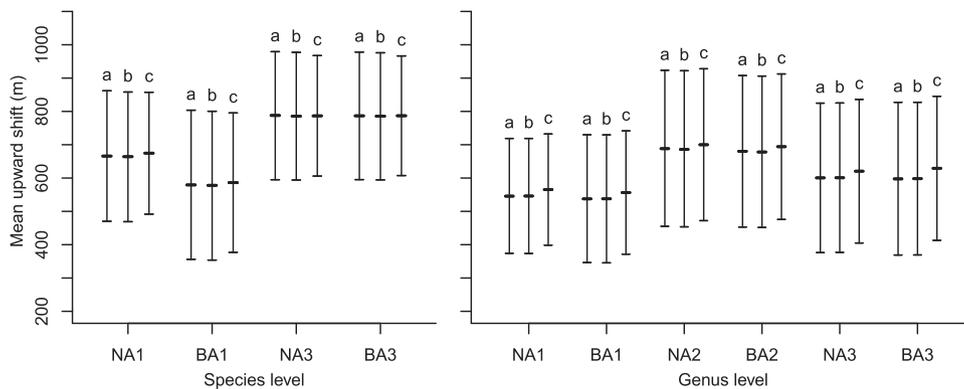
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# Supporting Information

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**Fig. S1.** Genus-level comparison of historical and observed elevation ranges for 45 genera. Color scheme is as in Fig. 2. Historical ranges >4,600 m for genera 43–45 are shown in faded colors because they are due to the visual estimation method. No plant taxa are mentioned at >4,600 m in Humboldt’s texts.



**Fig. S2.** Testing sensitivity of results to collection effort. The 2012 data were subsampled to include only one or two of three plots per transect and 1/3 or 2/3 of observations (a and b, respectively). For each subsample, a paired *t* test was used to calculate the mean upward shift since 1802 and confidence intervals. Thick lines indicate median of mean upward shift across 1,000 randomizations of data subsampling. Whiskers show median of confidence intervals. c, mean upward shift and confidence intervals based on the full dataset. Results are shown for species and genus-level comparisons based on each of the comparison methods (NA1, BA1, etc.) described in *Materials and Methods*. The sensitivity analysis shows that main results are robust to collection effort and are not driven by a more intense effort in 2012 relative to Humboldt’s, which could have led to the finding of more rare or inconspicuous species.

**Table S1. Historical elevation ranges for species**

ID	Species accepted name	Elevation range, m					
		Narrow approach			Broad approach		
		NA1	NA2	NA3	BA1	BA2	BA3
1	<i>Draba aretioides</i> Humb. & Bonpl. ex DC.	3,508–3,508	—	3,508–3,508	3,508–3,508	—	3,508–3,508
2	<i>Senecio nivalis</i> (Kunth) Cuatrec.	4,483–4,872	—	4,483–4,561	3,898–4,872	—	3,898–4,561
3	<i>Senecio canescens</i> (Bonpl.) Cuatrec.	3,703–4,678	—	3,703–4,483	3,703–4,872	—	3,703–4,483
4	<i>Baccharis caespitosa</i> (Ruiz & Pav.) Pers.	2,339–2,924	—	2,339–2,924	1,949–2,924	—	1,949–2,924
5	<i>Hypochoeris sessiliflora</i> Kunth	2,924–2,924	—	2,924–2,924	2,924–2,924	—	2,924–2,924
6	<i>Lasiocephalus ovatus</i> Schltld.	4,483–4,483	—	4,483–4,483	4,483–4,483	—	4,483–4,483
7	<i>Xenophyllum humile</i> (Kunth) V.A.Funk	3,508–3,898	—	3,508–3,898	3,508–3,898	—	3,508–3,598
8	<i>Chuquiraga jussieui</i> J.F.Gmel.	3,313–4,200	3,500–4,200	3,313–3,547	2,000–4,200	3,600–4,200	3,313–3,547
9	<i>Valeriana alypifolia</i> Kunth	4,093–4,093	—	4,093–4,093	4,093–4,093	—	4,093–4,093
10	<i>Azorella pedunculata</i> (Spreng.) Mathias & Constance	3,898–4,288	—	3,898–4,093	3,898–4,872	—	3,898–4,093
11	<i>Werneria nubigena</i> Kunth	3,313–4,093	—	3,313–3,799	2,924–4,093	—	3,313–3,799
12	<i>Astragalus geminiflorus</i> Humb. & Bonpl.	3,898–3,898	—	3,898–3,898	3,898–3,898	—	3,898–3,898
13	<i>Gentianella cernua</i> Kunth	3,313–3,799	—	2,924–3,313	3,313–3,799	—	2,924–3,313
14	<i>Gentiana sedifolia</i> Kunth	3,118–3,508	—	3,118–3,508	3,118–3,508	—	3,118–3,508
15	<i>Plantago rigida</i> Kunth	3,313–3,703	—	3,313–3,508	2,924–3,898	—	2,924–3,898
16	<i>Castilleja fissifolia</i> L.f.	2,600–3,500	2,600–3,500	2,600–2,651	2,600–3,500	2,600–3,500	2,600–2,651
17	<i>Conyza cardaminifolia</i> Kunth	3,118–3,118	—	3,118–3,118	3,118–3,118	—	3,118–3,118
18	<i>Lupinus microphyllus</i> Desr.	3,898–3,898	—	3,898–3,898	3,898–3,898	—	3,898–3,898
19	<i>Oreomyrrhis andicola</i> (Kunth) Endl. ex Hook. f.	3,703–4,093	—	3,703–4,093	3,898–4,872	—	3,898–4,093
20	<i>Oritrophium peruvianum</i> (Lam.) Cuatrec.	3,274–3,274	—	3,274–3,274	3,274–3,274	—	3,274–3,274
21	<i>Perezia pungens</i> (Bonpl.) Less.	3,118–3,118	—	3,118–3,118	3,118–3,118	—	3,118–3,118
22	<i>Cotula mexicana</i> (DC.) Cabrera	2,202–2,202	—	2,202–2,202	2,202–2,202	—	2,202–2,202
23	<i>Eryngium humile</i> Cav.	2,631–3,898	—	2,631–3,703	2,631–3,898	—	2,631–3,703
24	<i>Plagiocheilus peduncularis</i> (Kunth) Wedd.	3,508–3,508	—	3,508–3,508	3,508–3,508	—	3,508–3,508
25	<i>Ranunculus praemorsus</i> Kunth ex DC.	1,949–4,093	—	1,949–4,093	1,949–4,093	—	1,949–4,093
26	<i>Valeriana microphylla</i> Kunth	3,118–3,118	—	3,118–3,118	3,118–3,118	—	3,118–3,118
27	<i>Baccharis arbutifolia</i> (Lam.) Vahl	3,118–3,508	—	3,118–3,313	2,924–3,898	—	2,924–3,313
28	<i>Bartsia melampyroides</i> (Kunth) Benth.	2,631–3,118	—	2,631–3,118	2,631–3,118	—	2,631–3,118
29	<i>Bidens andicola</i> Kunth	3,411–3,411	—	3,411–3,411	3,411–3,411	—	3,411–3,411
30	<i>Clinopodium nubigenum</i> (Kunth) Kuntze	3,508–3,898	—	3,508–3,898	2,924–3,898	—	2,924–3,898
31	<i>Gentianella rapunculoides</i> (Willd. ex Schult.) J.S.Pringle	3,703–4,093	—	3,703–4,093	2,924–4,093	—	2,924–4,093
32	<i>Phyllactis rigida</i> (Ruiz & Pav.) Pers.	3,118–3,508	—	3,118–3,508	3,118–3,508	—	3,118–3,508
33	<i>Werneria pumila</i> Kunth	3,508–3,898	—	3,508–3,898	3,508–3,898	—	3,508–3,598
34	<i>Cerastium mollissimum</i> Poir.	2,339–2,729	—	2,339–2,729	1,949–2,924	—	1,949–2,924
35	<i>Hydrocotyle bonplandii</i> A.Rich.	2,729–2,729	—	2,729–2,729	2,729–2,729	—	2,729–2,729
36	<i>Lepidium bipinnatifidum</i> Desv.	2,631–2,631	—	2,631–2,631	2,631–2,631	—	2,631–2,631
37	<i>Nertera granadensis</i> var. <i>granadensis</i>	1,559–1,559	—	1,559–1,559	1,559–1,559	—	1,559–1,559
38	<i>Achyrocline alata</i> (Kunth) DC.	1,559–3,567	—	1,559–2,436	974–3,567	—	974–2,436
39	<i>Lobelia tenera</i> Kunth	2,339–2,924	—	2,339–2,924	1,949–2,924	—	1,949–2,924
40	<i>Acaena argentea</i> Ruiz & Pav.	2,339–3,099	—	2,339–3,099	1,949–3,099	—	1,949–3,099
41	<i>Baccharis buxifolia</i> (Lam.) Pers.	2,534–3,118	—	2,534–3,118	2,534–3,118	—	2,534–3,118
42	<i>Calceolaria ericoides</i> Juss. ex Vahl	3,313–3,703	—	3,313–3,469	2,924–3,898	—	2,924–3,469
43	<i>Gynoxys buxifolia</i> (Kunth) Cass.	3,508–3,508	—	3,508–3,508	3,508–3,508	—	3,508–3,508
44	<i>Perezia multiflora</i> (Humb. & Bonpl.) Less.	3,313–3,313	—	3,313–3,313	3,313–3,313	—	3,313–3,313
45	<i>Azorella aretioides</i> (Kunth) Willd. ex DC.	3,703–4,093	—	3,898–4,093	3,898–4,872	—	3,703–4,093
46	<i>Vicia andicola</i> Kunth	4,093–4,093	—	4,093–4,093	4,093–4,093	—	4,093–4,093
47	<i>Lupinus smithianus</i> Kunth	3,898–4,288	—	3,898–4,288	3,898–4,288	—	3,898–4,288
48	<i>Geranium humboldtii</i> Spreng.	4,093–4,483	—	3,898–4,093	3,898–4,872	—	3,898–4,093
49	<i>Arenaria serpyllifolia</i> L.	4,093–4,483	—	4,093–4,093	3,898–4,872	—	3,898–4,093
50	<i>Nototriche phyllanthos</i> (Cav.) A.W. Hill	2,000–4,592	2,000–4,100	4,093–4,592	2,000–4,872	2,000–4,100	4,093–4,592
51	<i>Eudema nubigena</i> Bonpl.	4,093–4,732	—	4,093–4,732	3,898–4,872	—	3,898–4,732

All ranges are given in meters and follow the narrow (NA) or broad (BA) approaches of historical data combinations described in *Materials and Methods*. Only taxa included in the analyses are listed. Column NA1 was used for Fig. 2. ID, species ID used in Fig. 2.

Table S2. Historical elevation ranges for genera

ID	Genus accepted name	Elevation range, m					
		Narrow approach			Broad approach		
		NA1	NA2	NA3	BA1	BA2	BA3
1	<i>Draba</i> L.	2,690–3,859	—	3,508–3,859	2,690–3,859	—	3,508–3,859
2	<i>Cerastium</i> L.	2,339–4,288	—	3,703–4,288	3,703–4,288	—	3,703–4,288
3	<i>Azorella</i> Lam.	2,100–4,100	3,500–4,100	2,100–4,093	2,000–4,100	2,000–4,100	2,100–4,093
4	<i>Baccharis</i> L.	390–4,100	3,000–4,100	390–3,898	390–4,100	2,000–4,100	390–3,898
5	<i>Hypochoeris</i> L.	2,924–2,924	—	2,924–2,924	2,924–2,924	—	2,924–2,924
6	<i>Xenophyllum</i> V.A. Funk	3,508–3,898	—	3,508–3,898	3,508–3,898	—	3,508–3,898
7	<i>Chuquiraga</i> Juss.	3,313–4,200	3,500–4,200	3,313–3,547	2,000–4,200	2,000–4,100	3,313–3,547
8	<i>Valeriana</i> L.	858–4,288	2,800–3,300	858–4,288	858–4,288	2,800–3,300	858–4,288
9	<i>Castilleja</i> Mutis ex L. f.	1,754–3,703	—	1,754–3,508	1,754–3,508	—	1,754–3,508
10	<i>Lepidium</i> L.	2,631–2,631	—	2,631–2,631	2,631–2,631	—	2,631–2,631
11	<i>Lupinus</i> L.	2,660–4,288	3,500–4,100	2,660–4,288	2,000–4,288	2,000–4,100	2,660–4,288
12	<i>Luzula</i> DC.	791–4,101	—	791–7,101	791–4,101	—	791–7,101
13	<i>Rumex</i> L.	0–31,18	—	0–3,118	0–3,118	—	0–3,118
14	<i>Vaccinium-Gaultheria</i>	700–3,313	2,800–3,300	780–3,313	780–3,313	2,000–4,100	780–3,313
15	<i>Werneria</i> Kunth	3,313–4,093	—	3,313–3,799	3,313–4,093	—	3,313–3,799
16	<i>Astragalus</i> L.	2,534–3,898	—	2,534–3,898	2,534–3,898	—	2,534–3,898
17	<i>Geranium</i> L.	2,612–4,100	3,000–4,100	2,612–4,093	2,000–4,100	2,000–4,100	2,612–4,093
18	<i>Halenia</i> Borkh.	975–3,313	—	975–3,313	975–3,313	—	975–3,313
19	<i>Plantago</i> L.	877–4,100	—	877–3,898	877–3,508	—	877–3,508
20	<i>Conyza</i> Less.	66–4,100	3,500–4,100	66–3,118	66–4,100	2,000–4,100	66–3,118
21	<i>Oreomyrrhis</i> Endl.	3,703–4,093	—	3,703–4,093	3,898–4,093	—	3,898–4,093
22	<i>Perezia</i> Lag.	3,118–3,840	—	3,318–3,840	3,118–3,840	—	3,118–3,840
23	<i>Eryngium</i> L.	780–3,703	—	780–3,703	780–3,703	—	780–3,703
24	<i>Lachemilla</i> (Focke) Rydb.	400–4,385	2,600–3,000	2,933–4,385	400–4,872	2,600–3,000	2,933–4,385
25	<i>Plagiocheilus</i> Arn. Ex DC.	2,670–3,508	—	2,670–3,508	2,670–3,508	—	2,670–3,508
26	<i>Bartsia</i> L.	2,534–3,313	—	2,534–3,313	2,534–3,313	—	2,534–3,313
27	<i>Bidens</i> L.	858–3,799	—	858–3,411	858–3,799	—	858–3,411
28	<i>Clinopodium</i> L.	390–3,898	—	390–3,898	390–3,898	—	390–3,898
29	<i>Sisyrinchium</i> L.	400–3,000	400–3,000	526–2,924	400–3,000	400–3,000	526–2,924
30	<i>Galium</i> L.	877–2,924	—	877–2,924	877–2,924	—	877–2,924
31	<i>Hydrocotyle</i> L.	0–3,000	400–3,000	0–2,729	0–3,000	400–3,000	0–2,729
32	<i>Nertera</i> Banks & Sol. ex Gaertn.	1,559–3,300	2,200–3,300	1,559–3,118	400–3,118	400–3,000	1,559–3,118
33	<i>Achyrocline</i> (Less.) DC.	2,066–3,635	—	2,066–3,635	2,066–3,635	—	2,066–3,635
34	<i>Acaena</i> Mutis ex L.	2,339–3,300	2,600–3,300	2,933–3,216	700–3,216	700–3,000	2,933–3,216
35	<i>Gynoxys</i> Cass.	2,066–3,508	—	2,066–3,508	2,066–3,508	—	2,066–3,508
36	<i>Monnina</i> Ruiz & Pav.	780–3,508	—	780–3,508	780–3,508	—	780–3,508
37	<i>Oxalis</i> L.	0–3,000	0–3,000	195–2,885	0–3,000	0–3,000	195–2,885
38	<i>Calceolaria</i> L.	2,339–3,898	2,600–3,500	3,313–3,799	2,534–3,859	2,600–3,500	3,313–3,799
39	<i>Vicia</i> L.	516–4,093	—	516–4,093	516–4,093	—	516–4,093
40	<i>Stellaria</i> L.	2,261–4,100	3,000–4,100	2,261–4,093	2,000–4,100	2,000–4,100	2,261–4,093
41	<i>Carex</i> L.	3,898–4,288	—	3,898–4,093	3,898–4,872	—	3,898–4,093
42	<i>Nototriche</i> Turcz.	97–4,592	—	97–4,592	97–4,872	—	97–4,592
43	<i>Eudema</i> Bonpl.	4,093–4,732	—	4,093–4,732	3,898–4,872	—	3,898–4,732
44	<i>Ranunculus</i> L.	1,949–4,736	—	3,898–4,288	1,949–4,736	—	3,898–4,288
45	<i>Gentianes</i>	1,364–4,873	2,000–4,100	3,313–3,799	1,364–4,873	2,000–4,100	3,313–3,799

All ranges are given in meters and follow the narrow (NA) or broad (BA) approaches of historical data combinations described in *Materials and Methods*. Only taxa included in the analyses are listed. Taxa lumped (e.g., *Gentianes* and *Vaccinium-Gaultheria*) are described in *Materials and Methods*. Column NA1 was used for Fig. S1. ID, genus ID used in Fig. S1.





**Dataset S1.** Shown are the 2012 resurvey data. Genus ID identifies taxa aggregated into each genus. Transects are coded according to their elevation (T38: 3,800 m), and plots according to elevation and 1–3 numbering (P383: plot 3 in T38). Presences (1) indicated for observations within and between transects. Abundance (percent cover) is given in each plot

[Dataset S1](#)

**Dataset S2.** Historical species-level data with original references. The file contains current and historical species name, original references, and elevation range. ID matches species ID in Fig. 2 and Table S1. Reference numbers match sources described in *Materials and Methods*. R2BA, R2NA, R3BA, and R3NA show elevation range using broad- and narrow-band visual readings, respectively

[Dataset S2](#)

**Dataset S3.** Historical genus-level data with original references. The file contains current and historical genus name, original references, and elevation range. Notes describe which species are included in the genus when taxonomy has changed over time. ID refers to genus ID in Fig. S1 and Table S2. Reference numbers are as in Dataset S2

[Dataset S3](#)

# Downward shift of montane grasslands exemplifies the dual threat of human disturbances to cloud forest biodiversity

The study by Morueta-Holme et al. (1) provides unique and invaluable insight into how tropical montane ecosystems have responded to climate change and other anthropogenic disturbances over the past two-plus centuries. Clearly, one of the most important findings of their study is that many species and ecosystems have shifted their distributions upslope to higher elevations, in accord with rising global mean temperatures (1). Another extremely important finding of the study that is deserving of extra attention is that the high-elevation grasslands of Chimborazo (i.e., the Pajonal) have expanded their distributions not only upslope but also downslope by several hundreds of meters. The upslope expansion of the Pajanal fits with the predictions of species migrations driven by rising temperatures; on the other hand, the downslope expansion of the Pajanal is likely driven by the increasing impacts of human activities, such as forest clearing for agricultural expansion, cattle grazing, and the setting of fires to improve fodder (1). The downslope expansion of Pajonals is not limited to Chimborazo; previous studies have similarly observed that the treeline (the ecotone transition between high-elevation montane grasslands and the underlying cloud forest) is stable or moving downslope throughout many parts of the tropics (2). At the same time, a growing number of studies show that many of the tropical montane plant and animal species that occur below the current treeline are shifting their distributions upslope in response to

global warming [at rates similar to those observed by Morueta-Holme et al. (1) for alpine plant species] (3, 4). In order for these cloud forest species to continue migrating upslope, they will eventually need to expand their ranges past the current treeline into the areas occupied by the Pajonal or other montane grasslands. If the lower distributional limit of the grasslands is stable, or even worse if the grasslands are expanding into lower elevations as was observed at Chimborazo, then cloud forest species will be prevented from shifting the leading edges of their ranges upslope (2). This will result in reduced population sizes and increased risks of extinction for many species, as the lower elevation portions of their ranges become intolerably hot but the species are prevented from migrating into higher cooler elevations (5). This process is analogous to the “mountaintop extinctions” predicted for many species of various alpine systems, but in this case the extinctions will be driven not by the physical absence of land at higher elevations but instead by the fact that any lands at higher elevations are made “unavailable” to forest species by human activities that favor grasses over trees. In other words, our activities are simultaneously forcing many cloud forest species to migrate upslope but at the same time we are preventing them from doing so. Given the incredibly high biodiversity of tropical montane cloud forests and the many important ecosystem services that they

provide, we must find ways to slow or reverse the downslope expansion of human-dominated grasslands, and thereby allow forest species to respond to climate change through upward migrations.

**Kenneth J. Feeley<sup>a,b,1</sup> and Evan M. Rehm<sup>c</sup>**  
<sup>a</sup>Department of Biological Sciences, International Center for Tropical Botany, Florida International University, Miami, FL 33199; <sup>b</sup>Fairchild Tropical Botanic Garden, Coral Gables, FL 33156; and <sup>c</sup>Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523

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<sup>1</sup>To whom correspondence should be addressed. Email: kfeeley@gmail.com.



# Reply to Feeley and Rehm: Land-use intensification increases risk of species losses from climate change

A growing body of evidence challenges the view that species' ranges are shifting unidirectionally in response to anthropogenic climate change (1). As Feeley and Rehm (2) point out, our resurvey of Chimborazo's vegetation (3) presents yet another example of the complex dynamics of ongoing range shifts. Although we do find a strong average upslope trend, we also note that several species are lagging behind. We agree with Feeley and Rehm (2) that the observed downward expansion of the grass-dominated Pajonal vegetation into lower elevations is likely the result of land-use changes, as illustrated in our updated version of Humboldt's *Tableau Physique* (3).

The idea that land-use activities may limit climate-driven range shifts is not new (4). The direct land-use effects mentioned by Feeley and Rehm (2) promote the expansion of Pajonal vegetation, which hinders tree establishment and thus the potential upward range shift of cloud forests from lower elevations. Indeed, we can expect strong disequilibrium dynamics in the leading edge of cloud forests because of the barriers that habitat loss and fragmentation of source populations pose to low-elevation species (1).

Water availability may also limit the upward migration of cloud forests. The pollen record provides examples in which reduced precipitation—rather than human activities—possibly hindered the expansion of cloud forests to higher elevations in times of warming (5). If the current climate is shifting toward drier conditions in tropical mountain regions,

as suggested for Chimborazo (3) and predicted under most future climate-change scenarios for the tropical Andes (6), more research should be directed toward the effects of this aspect of human-driven climate change on the ability of species to respond to the warming climate.

It is clear that species' range shift dynamics in response to the ongoing climate changes are not a simple matter (1), and we can only encourage further research, in particular for the understudied case of plants in the biodiverse tropics (1). The fact that increasing land-use intensity may strongly modulate climate-change impacts on species' distributions—often facilitating range adjustments of human-dispersed plants (frequently invasive exotics), but limiting expansions of many other species—is worrisome. Although climate-change mitigation requires global-scale efforts, the impacts of land use can be mitigated through local and regional conservation planning. Socioeconomic considerations need to be integrated in such actions, but ecological research toward quantifying and understanding past changes and improving predictive modeling of future ones is a first step toward reducing the risks.

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

<sup>a</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University,

DK-8000 Aarhus C, Denmark; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; <sup>c</sup>Laboratorio de Ecología de Plantas, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Aptado 17-01-2184, Quito, Ecuador; <sup>d</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; <sup>e</sup>Department of Biology and Honors Chemistry, Tucson High Magnet School, Tucson, AZ 85705; and <sup>f</sup>Department of Biology, Stanford University, Stanford, CA 94305

**1** Lenoir J, Svenning J-C (2015) Climate-related range shifts—A global multidimensional synthesis and new research directions. *Ecography* 38(1):15–28.

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<sup>1</sup>To whom correspondence should be addressed. Email: morueta-holme@berkeley.edu.

# Advance of plant species on slopes of the Chimborazo volcano (Ecuador) calculated based on unreliable data

Petr Sklenář<sup>a,1</sup>

Morueta-Holme et al. (1) report an average upper range limit shift of 675 m for 51 species of vascular plants on Chimborazo since Humboldt's 1802 ascent. About 86% of the species advanced (as much as >2,000 m), whereas 14% retreated (as much as >500 m). No explanation is provided for such varied species-specific responses to environmental change or for a migration rate on Chimborazo about 2.6-times faster than plants and animals elsewhere.

Plants have moved upwards in the equatorial Andes, but in the study at issue (1), quantification of that process is flawed. Because Humboldt mentioned no species above 4,600 m (2), that elevation was considered the upper limit of the 1802 Chimborazo phanerogam occurrence. However, that assumption may be invalid, because *Draba depressa* was collected there at 5,600 m in 1831–1832 and *Senecio hallii* was collected there at 4,900 m in 1872 (3). Additionally, Humboldt's account apparently was not limited to Chimborazo, because he referred to *Espeletia* (never observed on Chimborazo) in his "Région des Chuquiraga des Gentianes et du Frailexon" vegetation belt (2). Therefore, Humboldt's account is unreliable for quantifying vegetation change on Chimborazo. The explicit use by Morueta-Holme et al. (1) of Humboldt's species elevation information from mountains other than Chimborazo makes the historical data used even less reliable.

The 2012 dataset used by Morueta-Holme et al. (1) is also problematic. For example, *Eudema nubigena* reportedly retreated by >300 m from its 1802 limit of

4,872 m, but it has recently been collected from >4,800 m on Chimborazo; similarly, *Azorella aretioides* reportedly retreated to 4,000 m, although it has recent records from up to 4,600 m. Additionally, the 2012 list included questionable species, such as *Arenaria serpyllifolia*, which has not been reported from Ecuador (4), and *Draba aretioides*, which lacks reliable records from Chimborazo (Table 1). Moreover, *Pentacalia hillii*, reported from 5,185 m, is likely misidentified, because that species is a montane-forest vine (4).

Diels (3) published upper range limits of species for Chimborazo and elsewhere in Ecuador, using herbarium collections from 1870 to 1903. Of these, the limits of 35 species from Chimborazo and 58 from Ecuador more generally can be compared with the 1802 and 2012 limits of Morueta-Holme et al. (1). This comparison indicates species advances of 851 and 724 m from 1802 to 1870–1903, followed by retreats of 202 and 136 m as of 2012, for Chimborazo and Ecuador, respectively. The resulting average upward shift of 72–85 m per decade during the 19th century would be unprecedented in its speed. Moreover, the inferred retreat during 1903–2012 contradicts observations of advancing alpine plants in response to recent climate change (5). Assuming, therefore, that these inferred movements do not reflect reality, the two possible explanations are that Diels' (3) information is incorrect or that the inferences of Morueta-Holme et al. (1) are questionable. Given the data problems with Morueta-Holme et al. (1), and Diels' (3) reliance on collected specimens, we suggest consideration of the latter.

- 1 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.
- 2 Humboldt A, Bonpland A (1807) *Essai sur la Géographie des Plantes, Accompagné d'un Tableau Physique des Régions Equinoxiales* (Fr. Schoell Libraire, Paris). Available at [botanicus.org/title/b12218212](http://botanicus.org/title/b12218212). Accessed November 1, 2015.
- 3 Diels L (1937) *Beiträge zur Kenntnis der Vegetation und Flora von Ecuador* (Bibliotheca Botanica, Stuttgart), Vol. 116.
- 4 Jørgensen PM, León-Yáñez S (1999) *Catalogue of the Vascular Plants of Ecuador* (Missouri Botanical Garden Press, St. Louis).
- 5 Grytnes J-A, et al. (2014) Identifying the driving factors behind observed elevational range shifts on European mountains. *Glob Ecol Biogeogr* 23(8):876–884.

<sup>a</sup>Department of Botany, Charles University, 128 01 Prague 2, Czech Republic

Author contributions: P.S. wrote the paper.

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<sup>1</sup>Email: [petr.sklenar@natur.cuni.cz](mailto:petr.sklenar@natur.cuni.cz).

**Table 1. Herbarium voucher specimens of *Draba aretioides* Kunth listed in the TROPICOS database ([www.tropicos.org/Name/4105034?tab=specimens](http://www.tropicos.org/Name/4105034?tab=specimens); export: December 16, 2015)**

Country	Province	Elevation (m)	Latitude	Longitude	Date	Collectors	Coll. No.	Institutions
Ecuador	Azuay	4,200–4,300	02°49'S	079°15'W	May 1, 1992	Læggaard	102667	
Ecuador	Carchi	4,300–4,400	00°48'N	077°57'W	June 21, 1995	Sklenář	711	MO
Ecuador	Cotopaxi	4,100–4,180	00°53'S	078°48'W	April 4, 1992	Læggaard	102111	
Ecuador	Cotopaxi	4,100			December 29, 1983	Jaramillo	7366	MO
Ecuador	Imbabura	4,300–4,400	00°22'N	078°20'W	June 6, 1985	Læggaard	54511	MO
Ecuador	Imbabura	4,200–4,400	00°21'N	078°21'W	September 9, 1995	Sklenář & Kosteckova	1223	AAU, MO
Ecuador	Imbabura	4,100–4,320	00°22'N	078°21'W	November 9, 1983	Larsen et al.	45657	AAU
Ecuador	Imbabura	4,800			May 31, 1939	Penland & Summers	794	F
Ecuador	Imbabura	3,600	00°25'N	078°20'W	April 28, 1996	Clark et al.	2537	MO, QCNE
Ecuador	Napo	4,700	00°29'S	078°09'W	November 28, 1998	Neill et al.	11497	MO, QCNE
Ecuador	Pichincha	4,400	00°03'S	078°00'W	June 18, 1980	Holm-Nielsen	24236	AAU
Ecuador	Pichincha	4,600	00°02'S	077°59'W	June 18, 1980	Holm-Nielsen	24262	AAU
Ecuador	Pichincha	4,600			July 3, 1876	André	3846	F, GH, K, NY, PH, S, U, US
Ecuador	Pichincha	4,200–4,350	00°06'S	077°58'W	August, 30, 1995	Sklenář & Kosteckova	1355	AAU
Ecuador	Pichincha	4,500	00°01'N	078°01'W	July 2, 1995	Sklenář & Kosteckova	1896	AAU
Ecuador	Pichincha	4,500–4,400	00°11'S	078°33'W	November 18, 1990	Øllgaard	98260	AAU, MO
Ecuador	Pichincha	4,500–4,400	00°11'S	078°33'W	November 18, 1990	Øllgaard	98284	AAU
Ecuador	Pichincha	4,400–4,650	00°40'S	078°42'W	May 28, 1995	Sklenář & Kosteckova	408	AAU
Ecuador	Pichincha	4,000–4,400	00°35'S	078°31'W	March 13, 1993	Cerón et al.	21571	
Ecuador	Pichincha	4,300	00°10'N	078°34'W	May 12, 1995	Sklenář	1–7	MO
Ecuador	Pichincha	4,600	00°10'N	078°34'W	May 18, 1995	Sklenář	11–3	MO
Ecuador	Pichincha	4,500	00°10'N	078°34'W	August 12, 1995	Sklenář	892	MO
Ecuador	Pichincha	4,550–4,660	00°03'S	078°00'W	March 1, 1988	Molau & Eriksen	3229	AAU, GB, MO
Ecuador	Pichincha	4,400–4,500	00°07'S	078°34'W	March 6, 1988	Molau & Eriksen	3281	AAU, GB, MO, QCA
Ecuador	Pichincha	4,264	00°10'S	078°33'W	July 6, 2005	von Meijenfeldt	06	MO
Ecuador	Pichincha	4,500–4,700	00°01'N	078°01'W	July 2, 1995	Sklenář	727	MO
Ecuador	Pichincha	4,500–4,700	00°01'N	078°01'W	July 2, 1995	Sklenář	729	MO
Ecuador	Pichincha	2,800	00°07'S	078°30'W	September 10, 1995	Clark et al.	1460	MO, QCNE
Ecuador	Pichincha	4,000–4,400	00°35'S	078°31'W	March 13, 1993	Cerón et al.	21543	
Ecuador	Tungurahua	4,200–4,350	01°14'S	078°18'W	September 6, 1997	Sklenář	3747	MO
Ecuador	Tungurahua	4,280	01°13'S	078°17'W	November 14, 1999	Neill et al.	12123	MO, QCNE

For acronyms, refer to the Index Herbariorum ([sweetgum.nybg.org/science/ih/](http://sweetgum.nybg.org/science/ih/)).

REPLY TO SKLENÁŘ:

# Upward vegetation shifts on Chimborazo are robust

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

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).<sup>†</sup>

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,<sup>‡</sup> 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.

<sup>a</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; <sup>c</sup>Laboratorio de Ecología de Plantas, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Aptado 17-01-2184; <sup>d</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; <sup>e</sup>Department of Biology and Honors Chemistry, Tucson High Magnet School, Tucson, AZ 85705; and <sup>f</sup>Department of Biology, Stanford University, Stanford, CA 94305

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The authors declare no conflict of interest.

<sup>†</sup>To whom correspondence should be addressed. Email: morueta-holme@berkeley.edu.

\*herbarium.bgbm.org/object/B100243535.

‡specimens.kew.org/herbarium/K000471926.

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

