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# Humboldt's *Tableau Physique* revisited

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Alexander von Humboldt's *Tableau Physique* (1807) has been one of the most influential diagrams in the history of environmental sciences. In particular, detailed observations of the altitudinal distribution of plant species in the equatorial Andes, depicted on a cross-section of Mt. Chimborazo, allowed Humboldt to establish the concept of vegetation belt, thereby laying the foundations of biogeography. Surprisingly, Humboldt's original data have never been critically revisited, probably due to the difficulty of gathering and interpreting dispersed archives. By unearthing and analyzing overlooked historical documents, we show that the top section of the *Tableau Physique*, above the tree line, is an intuitive construct based on unverified and therefore partly false field data that Humboldt constantly tried to revise in subsequent publications. This finding has implications for the documentation of climate change effects in the tropical Andes. We found that Humboldt's primary plant data above tree line were mostly collected on Mt. Antisana, not Chimborazo, which allows a comparison with current records. Our resurvey at Mt. Antisana revealed a 215- to 266-m altitudinal shift over 215 y. This estimate is about twice lower than previous estimates for the region but is consistent with the 10- to 12-m/decade upslope range shift observed worldwide. Our results show the cautious approach needed to interpret historical data and to use them as a resource for documenting environmental changes. They also profoundly renew our understanding of Humboldt's scientific thinking, methods, and modern relevance.

Humboldt | historical ecology | global warming | range shift | tropical Andes

Between 1799 and 1804, the physical geographer Alexander von Humboldt and the botanist Aimé Bonpland spent 5 y exploring the forests and mountains of tropical America, where they conducted accurate physical measurements, natural history observations, and plant collections (1, 2). A few years after his return to Europe, Humboldt coauthored with Bonpland in 1807 an *Essay on the Geography of Plants* (3) where, in addition to descriptions and tables, he presented their amassed data by means of an innovative diagram: the *Tableau Physique* (TP). This diagram combined a pictorial view of Chimborazo and Cotopaxi volcanoes (Ecuador) with text denoting the names of plants typical of different elevations in equatorial Andes (Fig. 1*A* and *SI Appendix*, section 1). It was flanked on each side with columns marked off by elevation in meters and in *toises* (an old French unit of length; fathom), which provided other relevant information such as the lower limit of perpetual snow.

The concept of vertical zonation of plants in montane environments already existed in the first years of the 19th century (4, 5), and as early as 1789, the French geologist and botanist Ramond de Carbonnières compared the upper limit of vegetation in European mountains and in equatorial Andes (6). But by providing for the first time a unified view of physical and ecological implications of mountains' verticality, the TP has become an iconic milestone, almost a foundation myth, in the history of ecology (7–9) and biogeography (5, 10). It has also influenced generations of artists and fascinated historians who have thoroughly explored its aesthetic and intellectual background and significance (11, 12). Surprisingly, despite such intensive examinations, both the production process of

the TP and the reliability of the hard scientific data included in it—namely, the association between plant taxa and elevation—have never been examined carefully and critically. The taxonomic corrections and the new distribution data introduced by Humboldt in successive publications have generally been overlooked. Moreover, Humboldt's statement that the information assembled in the TP covered the whole equatorial Andes area, from 10°N to 10°S (3), was rapidly forgotten and the TP is often thought to be the depiction of the plant belt succession on Mt. Chimborazo only (10, 13). As an example, a recent study has compared current records on Mt. Chimborazo with the botanical data of the TP to assess vegetation upslope shift over two centuries (14).

Here we revisited Humboldt's data, specifically those at highest elevations, with the objectives to (i) understand the complex process through which Humboldt developed and modified over more than 20 y his model of plant belt succession and (ii) assess the reliability of these historical data to quantify the ecological effects of climate change. Quantifying the exact elevation of the upper limit of vegetation is particularly crucial for evaluating upslope shifts due to global warming, a critical issue of global change biology research in the tropical Andes (15). To achieve these objectives, we combined expertise and methodologies from history, botany, and ecology fields.

## Results and Discussion

**Historical Study.** We first conducted a critical review of the scientific production of Humboldt and Bonpland to gather all reliable historical data on elevational ranges of vascular plants above the tree line in tropical Andes (*Materials and Methods*). The data contained

### Significance

Over the last decades, historical data have made significant contributions to assess the ecological effects of global warming. Alexander von Humboldt's *Tableau Physique* (1807) is by far the oldest existing dataset on altitudinal ranges of tropical mountain vegetation and represents a unique data source to assess vegetation shift in response to climate change. Yet, we show here that this exercise is not straightforward, and that partnerships between historians and ecologists are needed to tease out the intermeshing and discrepancies of past and present biodiversity records. Our findings reveal a generalized misinterpretation of Humboldt's most iconic work; provide new estimates of vegetation shifts for the tropical alpine Andes; and profoundly renew our understanding of Humboldt's scientific thinking, methods, and modern relevance.

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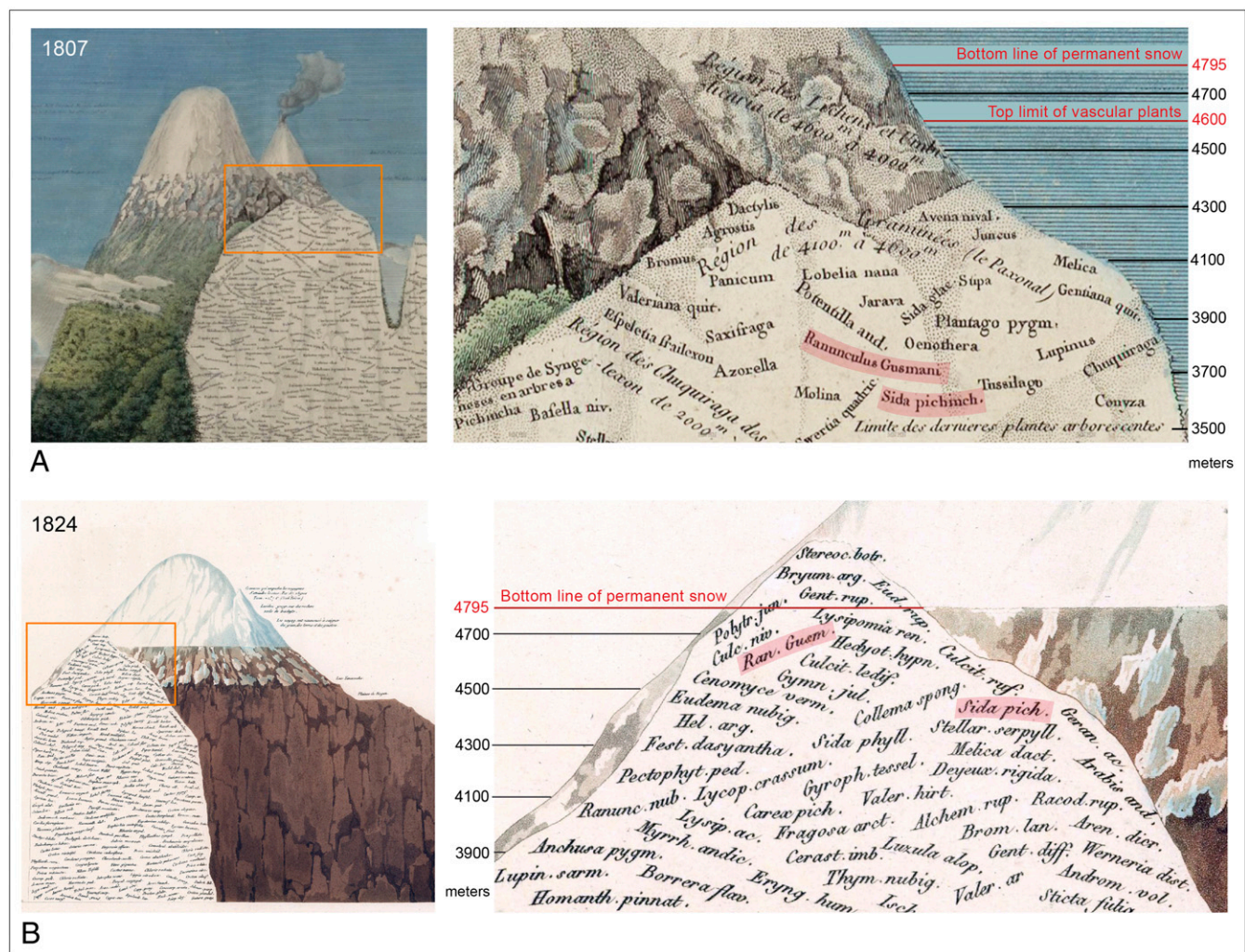
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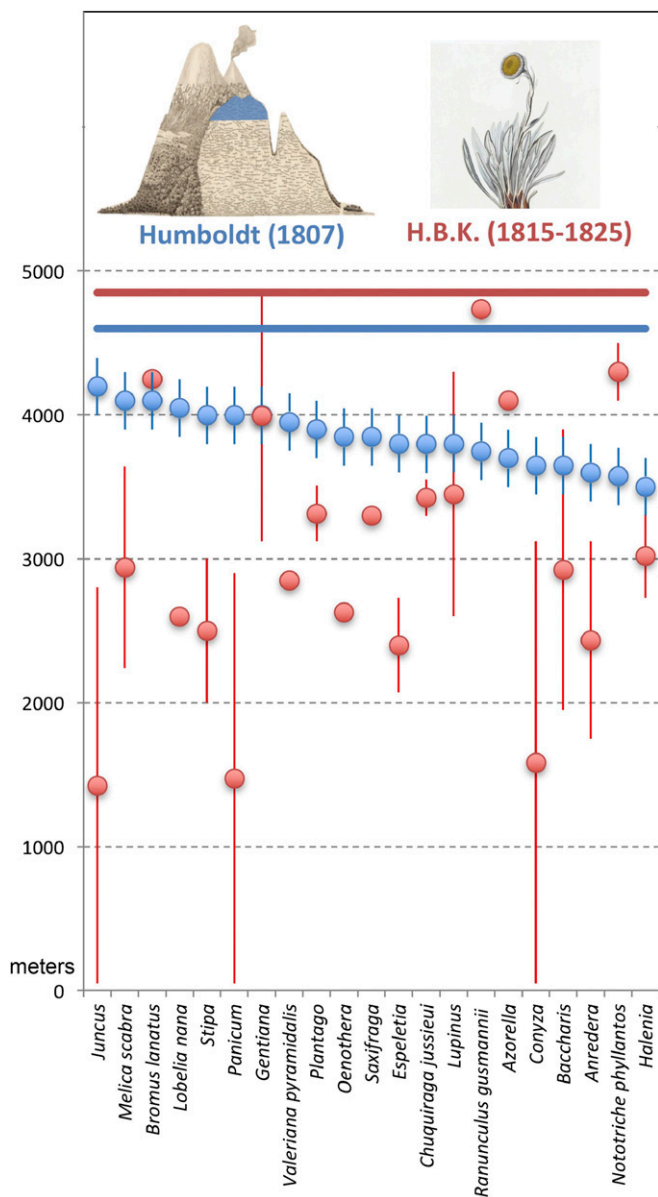
**Fig. 1.** Details of two sketches of the vegetation of the Andes by Humboldt. (A) From the *Tableau Physique*, 1807 (3). (B) From the *Sketch of the Geography of Plants in the Andes of Quito*, 1824 (17). On the enlarged panels, the added elevation lines are deduced from the lateral vertical scale of each *tableau*, not visible here (*SI Appendix*, section 1, Figs. S1 and S2). The bottom line of permanent snow at 4,795 m is the same in both cross-sections, but in 1824 two vascular plants were placed above this line, along with a moss and a lichen that are not included in our study. Species highlighted in red are examples of elevational shifts between the two sketches.

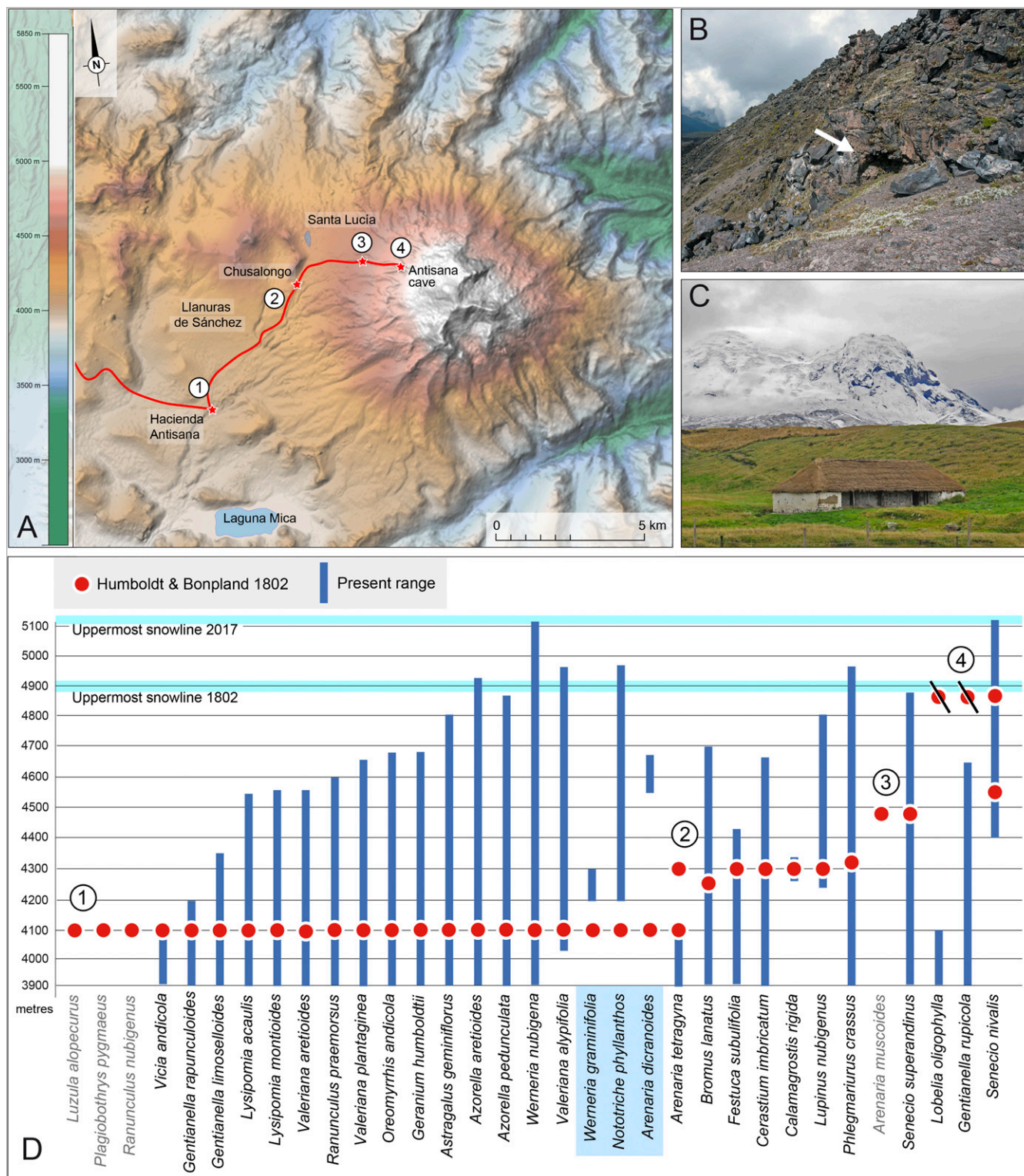
in the TP (3) were compared with two later works published by Humboldt (16, 17) (Fig. 1 and *SI Appendix*, section 1). Our analysis conveyed three key findings. First, the number of selected taxa placed above 3,900 m increases in each successive publication (17 in 1807, 23 in 1817, 32 in 1824), but these taxa are not the same. The 1807 set of vascular plants only shares one species-level taxon and two genera with that of 1817 and one species and four genera with that of 1824. Only one genus (*Gentiana*) and no species are present in all three sets (*SI Appendix*, section 1, Table S2). Second, most alpine plant records reported in the TP have inaccurate elevations, sometimes with a difference of more than 1,000 m compared with the baseline data later used by Humboldt in the final publication (18) of his botanical results (Fig. 2 and *SI Appendix*, section 2, Table S3). Third, in 1807 Humboldt set at 4,600 m the upper limit of vascular plants, “phanerogams” in his terms (3). However, the *Essay* is the only publication where Humboldt gave this figure. It is quite clear from later publications (16, 18) that Humboldt and Bonpland collected vascular plants far above the 4,600-m line, close to the limit of permanent snow: at Mt. Pichincha (4,678 m), Nudo de Azuay (4,732 m), and Mt. Antisana (4,860 m, *SI Appendix*, section 4). In this last case, plant collection elevation is even above the supposed limit of permanent snow, fixed by Humboldt at 4,795 m (3). These three

elevation data are highly reliable, as they are based on barometric measurements made at the sampling spots (19), as confirmed by Humboldt’s diary (20) and by Bonpland’s *Journal Botanique* (*SI Appendix*, section 4).

These findings show that part of the data published in the TP were contradicted in later publications. This diagram was an intuitive construct based on unverified, incorrectly recorded field data, hardly modified from a sketch drawn at Guayaquil in 1803 before Humboldt and Bonpland left South America (*SI Appendix*, section 1, Fig. S1 and Table S1). Humboldt himself pointed out that the system of high-altitude floristic belts proposed in the TP was preliminary and “perfectible” (3). He gave one reason for these inconsistencies: in 1804–1806, when the TP was redrawn by a professional artist and engraved, the taxonomic study of his plant collection had barely begun, and the names of the many new genera to be described were still unavailable (3). However, our analysis reveals other major contradictions that are not related to plant taxonomy. Humboldt placed the “grassland region” in the TP at the highest elevation of vascular plant distribution (4,100–4,600 m), above the region of “alpine plants” (3,500–4,100 m), and below the region of lichens (4,600–4,795 m). This is not consistent with first-hand observations in his diary. Humboldt described







**Fig. 4.** Botanical resurvey of Mt. Antisana (Ecuador) guided by historical data. (A) Map of Antisana with the route taken by Humboldt and Bonpland in 1802 (in red). Place names and itinerary were retrieved from Humboldt's diary (*SI Appendix, section 4*). (B and C) Two pictures of the sites where Humboldt and Bonpland botanized (B: site 4, cave on the northwestern flank of Mt. Antisana; C: site 1, Hacienda Antisana with the volcano in the background). (D) Past (1802) and current elevational range of the species collected by Bonpland and Humboldt at Antisana. Names in gray: not resampled species (*SI Appendix, section 3.4*); struck-through red dots: wrong data (*SI Appendix, section 3.3*); blue box: suggested upslope shift of the bottom limit.

had their current lower elevational limit 100–450 m higher than the 1802 record, suggesting a bottom contraction of their ranges. Nevertheless, the case of *W. graminifolia* requires caution, since

this species is known only from one additional record besides the type specimen (Dataset S2), and its status is uncertain (*SI Appendix*, section 3 and Dataset S1, sheet 2).



Second, five plant species (*Werneria nubigena*, *N. phyllanthos*, *Valeriana alypifolia*, *Phlegmariurus crassus*, and *Senecio nivalis*) have now extended their elevational range above the 1802 snowline limit. The most interesting case is that of *S. nivalis*, as Bonpland collected it at 4,860 m and noted in his diary “this is the plant we have found at the highest elevation above the snow level” (*SI Appendix, section 3.1*). For this species, we can estimate a 216- to 266-m upslope expansion in 215 y. This result is consistent with changes in the freezing level height on the Antisana over the past decades (+10.7 m/decade) (26), and with the mean upward shift of 11 m/decade observed at a worldwide scale for both plant and animals (27). The barometric measurements made at the uppermost site where Bonpland and Humboldt collected vascular plants (19) indicate an upper limit of vascular plants in the first years of the 19th century around  $4,850 \pm 50$  m, depending on local climate conditions. Despite reports that many species lag behind climate change (27, 28), we found that *S. nivalis* was able to track the pace of glacier retreat in the Antisana. This plant can colonize recently deglaciated forefronts through aerial dispersion and its upslope shift therefore coincides with the displacement of glacier front (28). While a mean upslope migration rate of about 11 m per decade can be calculated for *S. nivalis* between the two sampling dates (1802 and 2017), it is likely that this displacement was not linear over the two centuries. Indeed, a break point in the trend of glacier retreat in the tropical Andes appeared in the late 1970s with mean annual mass balance per year almost quadrupling in the period 1976–2010 compared with the period 1964–1975 (26). This suggests that the potential migration rate of this plant is underestimated.

Our findings also invalidate the >500-m vegetation shift in Mt. Chimborazo, from 4,600 m in 1802 to 5,185 m in 2012, estimated using data from Humboldt’s TP (14), because no plant collection was made by Bonpland and Humboldt above 3,625 m on that mountain (*Materials and Methods*), and because the upper vegetation limit actually documented by Humboldt in 1802 was 260 m higher than (wrongly claimed) in the TP (3).

## Conclusion

Our results represent a compelling study case of the cautious interpretation needed when using historical data as a resource for documenting environmental changes (29–31). While the TP (3) contains the oldest historical dataset to document elevational ranges of mountain plant species, making use of these data is not straightforward: it requires the partnership between historians, botanists, and ecologists with extensive data checking from multiple sources (32, 33). Diagrams like the TP are powerful for representing conceptual frameworks but necessarily involve schematizations and selections (34), and their production is embedded in the historical and philosophical contexts of a period (5). Humboldt was well aware of these limitations as he wrote in the text accompanying the TP that, to build such a diagram, “one must consider two conflicting interests, appearance and exactitude” (3). Although most tropical alpine plant data in the TP came from other mountains, Humboldt gave a prominent place to Mt. Chimborazo in his diagrams, both in 1807 and in 1824 (Fig. 1), more to satisfy the “continuous questions” on his exploit of reaching the highest altitude so far attained by a man (21) and for aesthetic values of “the most majestic of all [mountains]” (22) than for scientific reasons (35).

Another important point of our analysis concerns how plant distribution changes could be estimated based on Humboldt’s data. Before him, botanical regions were defined by the presence of a few characteristic taxa, as the olive tree or the beech (4). Humboldt’s concept of vegetation belt was revolutionary as (i) it linked plants with a wide variety of abiotic factors and (ii) the definition of each belt was based on systematic measurements of the elevational ranges of individual taxa. Had Humboldt described

vegetation belts only in broad terms, as was usual in his time, it would have been impossible to use data from his expedition for assessing the impact of global warming over two centuries. Even though only a few taxa from Humboldt’s sampling could be used to infer vegetation shift, it is likely that plants in the higher part of Mt. Antisana present a heterogeneous range of responses to warming, some being able to follow the pace of retreating glaciers (e.g., *S. nivalis*), others being potentially delayed due to limitations in their dispersal at higher altitudes (28).

A last significant outcome of our study is that the TP should not be viewed as a fixed and exact representation of Humboldt’s theory of plant geography but rather as a dynamic framework. This framework mixed scientific evidence and inference and was used over several decades by Humboldt to refine his unitary view of phytogeography. The fact that the raw data used in successive publications were continuously changing between 1807 and 1824 suggests that he was searching for the evidence that would best support his intuition on plant zonation. However, only the first version, the one that contained serious errors, has remained in the collective memory of earth and life sciences as a seminal heritage. Not only were these errors offset by the novel message of a diagram that embodied the groundbreaking idea of the interconnectedness of all biotic and abiotic phenomena (36), but nobody even noticed them, such was the power of this mesmerizing image.

## Materials and Methods

**Historical Study.** The sources used for the historical analysis were of three types: (i) primary information provided by field notebooks and herbarium labels, in Latin, French, and German (*SI Appendix, sections 3 and 4*); (ii) taxonomic treatments of plant species in botanical monographs, in Latin (18, 37); and (iii) theoretical syntheses on plant geography, in French, German, and Latin (refs. 3 and 16, *SI Appendix, section 1*). Parts of Humboldt’s diary have been digitized and are available online or have been published (20), but Bonpland’s handwritten *Journal Botanique* had to be directly consulted at the Paris National History Museum Archives (*SI Appendix, section 3*). The Latin texts of the *Journal Botanique* and of the rarely commented treatise “On the geographic distribution of plants according to climate and altitude” (16) were translated by the first author. To estimate the elevational range of plant names in the TP, we measured the midpoint of each species or genus name, with a margin of error of  $\pm 200$  m. This margin was set to comprise the maximum elevation range that can be measured based on the obliquely written names in the TP (details in *SI Appendix, section 2*).

**Selection of the Antisana Site.** In a recent study, the southeast slope of Mt. Chimborazo (Ecuador) was sampled to compare the current elevational distribution of plants with Humboldt and Bonpland’s historical data (14). However, there is strong evidence suggesting that Chimborazo only played a marginal role in the construction of Humboldt’s floristic zone system. If we consider all of the taxa listed by Humboldt in his three attempts (3, 16, 17) to define the páramo phytoregion (in his terms, both the “grassland region” and the “alpine plants region”), 31 species are from Antisana, 8 from Pichincha, 6 from Azuay, 4 from Puracé, and not one from Chimborazo (*SI Appendix, section 1, Table S2*). Due to a heavy snowfall that covered everything down to 4,160 m, Humboldt, Bonpland, and their companions only spent a few hours above 4,000 m on the Chimborazo (21) and not a single vascular plant was collected there above 3,625 m, as documented by the *Journal Botanique*, the herbarium, and distribution data in ref. 18. Actually, it was on another mountain, Mt. Antisana, that most of alpine plants reported in Humboldt’s publications were collected (*SI Appendix, section 4*). The herbarium labels, the *Journal Botanique*, and the final taxonomic publication (18) gave us the certainty that half of all of the high-altitude plants sampled by Humboldt and Bonpland in the equatorial Andes were collected on the slopes of Antisana, and that 26 of the 31 species selected for this study were only collected there (*SI Appendix, section 3 and Dataset S1*). It is also the only mountain where they collected at several elevations (around 3,900 m, 4,100 m, 4,300 m, 4,500 m, and 4,860 m), at least three of which are ensured by barometric readings. In addition, Humboldt’s account in his travel diary (20) makes it possible to trace with great precision the route they followed and the points where they stopped to botanize (Fig. 4 and *SI Appendix, section 4*).

**Selection of Taxa.** We first established the list of the 65 plants collected at Antisana, based on the cross-analysis of (i) Bonpland's field notebook, (ii) labels of type specimens in Bonpland's herbarium in Paris, and (iii) botanical publications of Humboldt's team (18, 37) (*SI Appendix, section 3* and *Dataset S1*).

We then compiled a list of 31 plant species with unambiguous locality data and verifiable elevation information registered by Humboldt and Bonpland on Mt. Antisana (Fig. 4 and *SI Appendix, sections 3* and *4*). We excluded the species collected in the Antisanilla–Muertepungu area at the beginning of their trip in March 1802, due to errors in their elevation measures. We only considered plants collected on sites that we could precisely identify from the descriptions of Humboldt's diary and maps, where he made barometer measurements and where we could repeat these measurements with a GPS. These 31 species were collected at approximately 4,100 m in the vicinity of Hacienda Antisana, and on the western slope of the volcano from 4,250 to 4,860 m (*SI Appendix, section 4*).

**Resurvey.** To quantify a potential shift in distribution of plant taxa on Mt. Antisana since Humboldt and Bonpland's visit in 1803, we conducted several botanical surveys between March and December 2017 (we made our first expedition on March 16, exactly 215 y after Humboldt and Bonpland's visit). Humboldt's account in his travel diary makes it possible to precisely trace the route they followed and to identify specific sites where they stopped to botanize (Fig. 4 A and B and *SI Appendix, section 4*): (i) Hacienda Antisana at 4,080 m; (ii) a saddle between Antisana and Chusalongo, at about 4,300 m; (iii) a first stop at approximately 4,500 m toward the summit; and (iv) a second stop at the edge of the snow, at the cave of Antisana at 4,860 m.

For site 1, two persons spent a day sampling vascular plants in a 100-m radius around the Hacienda. At sites 2 and 3, five people spent 3 h per

site sampling all vascular plants found in a vertical gradient of 100 m above and below the selected elevation (e.g., site 2: 4,300 ± 100 m). Finally, at site 4 three people surveyed a vertical gradient of 250 m from the cave upwards. Two parallel transects with different exposure and substrate were sampled every 20 elevational meters, the first one beginning at the cave, the second 100 m north of the cave. At each site, we recorded the lowest and highest elevations where plant taxa were found.

For all species, we made a nomenclatural and taxonomic validation, following up-to-date classification (38). In addition to our botanical survey, we compiled 582 records about the elevational range of the 31 selected plant taxa on the western slope of Mt. Antisana, based on available databases (*Dataset S2*) and herbarium specimens deposited at QCA (39).

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