



HAL
open science

Humboldt's Tableau Physique revisited

Pierre Moret, Priscilla Muriel, Ricardo Jaramillo, Olivier Dangles

► **To cite this version:**

Pierre Moret, Priscilla Muriel, Ricardo Jaramillo, Olivier Dangles. Humboldt's Tableau Physique revisited. Proceedings of the National Academy of Sciences of the United States of America, 2019, 116 (26), pp.12889-12894. 10.1073/pnas.1904585116 . hal-02148885

HAL Id: hal-02148885

<https://hal.science/hal-02148885>

Submitted on 29 Dec 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Humboldt's *Tableau Physique* revisited

Pierre Moret^{a,1,2}, Priscilla Muriel^b, Ricardo Jaramillo^b, and Olivier Dangles^{c,d,1}

^aLaboratoire Traces UMR 5608, CNRS, Toulouse University, 31058 Toulouse, France; ^bLaboratorio de Ecofisiología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, 17-01-2184 Quito, Ecuador; ^cCentre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS, Université de Montpellier, Ecole Pratique des Hautes Etudes, Institut de Recherche pour le Développement, 34095 Montpellier, France; and ^dDepartment of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853

Edited by Nils C. Stenseth, University of Oslo, Oslo, Norway, and approved May 1, 2019 (received for review March 16, 2019)

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 By unearthing and analyzing overlooked historical documents, we show that the top section of the *Tableau Physique*, above the tree line, is an intuitive construct based on unverified and therefore partly false field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. 1A 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.

Author contributions: P. Moret and O.D. designed research; P. Moret, P. Muriel, R.J., and O.D. performed research; P. Moret, P. Muriel, R.J., and O.D. analyzed data; and P. Moret and O.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

¹P. Moret and O.D. contributed equally to this work.

²To whom correspondence may be addressed. Email: pierre.moret@univ-tlse2.fr.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1904585116/-DCSupplemental.

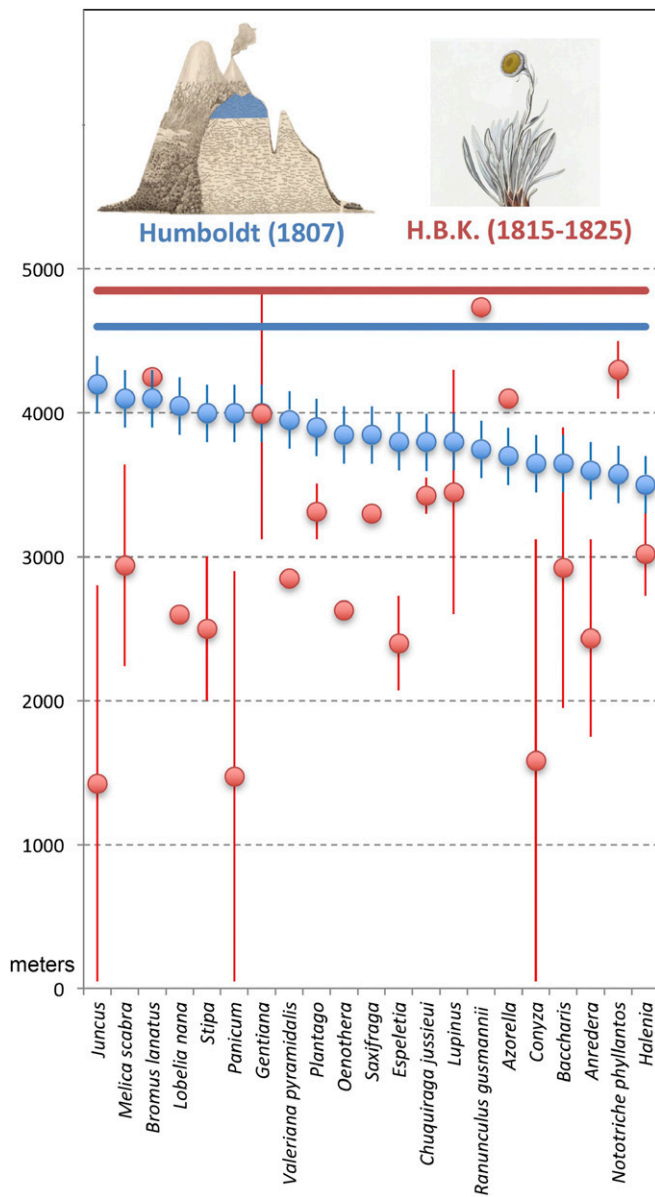


Fig. 2. Elevations of the plants placed above the tree line in 1807 in the *Tableau Physique* (3), in blue, compared with their elevation ranges in 1815–1825 in *Nova genera et species plantarum* (18), in red. Nine plants presented in 1807 as living above the tree line (approximately 3,550 m) were actually collected below 3,000 m. The horizontal lines indicate the elevation of the bottom limit of permanent snow according to ref. 3, in blue, and to ref. 18, in red. Supporting information: *SI Appendix*, section 2 and Table S3.

“plains carpeted with grass” and “huge lawns” of grasses “rarely mixed with dicotyledon plants” at elevations from 3,146 to 3,615 m on the southeast slope of the Chimborazo (21); he located the upper limit of the grassland at Mt. Puracé (Colombia) at 3,800 m (20), and he mentioned “dense lawns” at about 3,900 m in the mountains of Azuay (22). As early as 1831, Francis Hall, an adventurer and naturalist who spent several years in Ecuador and collected many plants at high altitude, felt puzzled by Humboldt’s description of high-altitude vegetation zones in the TP, pointing out “several inaccuracies” and concluding that “the reverse is the fact,” as the grasslands “are surmounted by the region of alpine plants, which extends to the limit of perpetual snow” (23). Humboldt must have realized his mistake, which could explain why from the eight genera of grasses placed in 1807 in the uppermost alpine zone,

none is mentioned in the 1817 list, and only one appears in the updated cross-section of 1824 (*SI Appendix*, section 1, Table S2). This set of evidence invalidates a recent assumption based on the 1807 TP, that high-elevation grasslands of Chimborazo have expanded their distributions downslope by several hundreds of meters over two centuries (14, 24). All this shows that the TP was a schematic construction that contradicted part of the observations made in the field, to such an extent that Humboldt had to introduce in-depth changes in two subsequent publications on the geography of plants. Consequently, any study aiming at comparing Humboldt’s historical data with current observations should discard the data contained in the TP of 1807.

Resurvey. We performed an in-depth analysis of primary data in Bonpland’s *Journal Botanique* and on herbarium labels, complemented with distribution data compiled in the final publication of the botanical results (*Materials and Methods*). We found that most tropical alpine plants reported in Humboldt’s publications were collected in March 1802 on Mt. Antisana. There, Humboldt and Bonpland spent 4 d at a place called Hacienda, at 4,100 m (*Materials and Methods* and *SI Appendix*, section 4) and climbed up to the snowline. In total, Bonpland collected more than 60 species of plants at different elevations from 3,000 m to 4,860 m (*SI Appendix*, sections 3 and 4 and *Dataset S1*). To recognize the central importance of Antisana in his fieldwork, Humboldt placed the Hacienda Antisana in the middle of a fictitious view of Mt. Chimborazo in his last cross-section of the Andes (ref. 25, Fig. 3). Based on these documents, we compiled a list of 31 plant species with unambiguous locality data and verifiable elevation information registered by Humboldt and Bonpland on Mt. Antisana (*SI Appendix*, section 3 and *Dataset S1*) and compared these data with contemporary records (*Materials and Methods*). Between March and December 2017, we performed several plant surveys at the exact same locations sampled by Humboldt and Bonpland 215 y ago (Fig. 4 A and B). To complement our dataset, we compiled 582 additional records in the same zone for the 31 selected plant species (*Dataset S2*).

The comparison of historical localities and current range of plant occurrence on Mt. Antisana provides two key results about plant distribution changes since Humboldt (Fig. 4D). First, as we know from Humboldt’s diary (20) that Bonpland collected plants on his way up to Mt. Antisana summit, it is likely that the elevation associated with a plant species refers to the first time he saw it, i.e., to its bottom range. Three plant species (*Werneria graminifolia*, *Nototriche phyllanthos*, and *Arenaria dicranoides*)

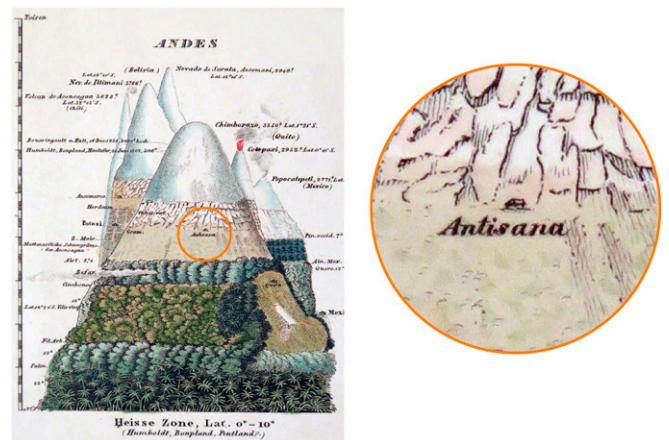


Fig. 3. Sketch of the vertical distribution of Andean vegetation in Berghaus’ Atlas (ref. 25, plate 5.1), which was published in 1845 as an illustration for Humboldt’s *Cosmos*.

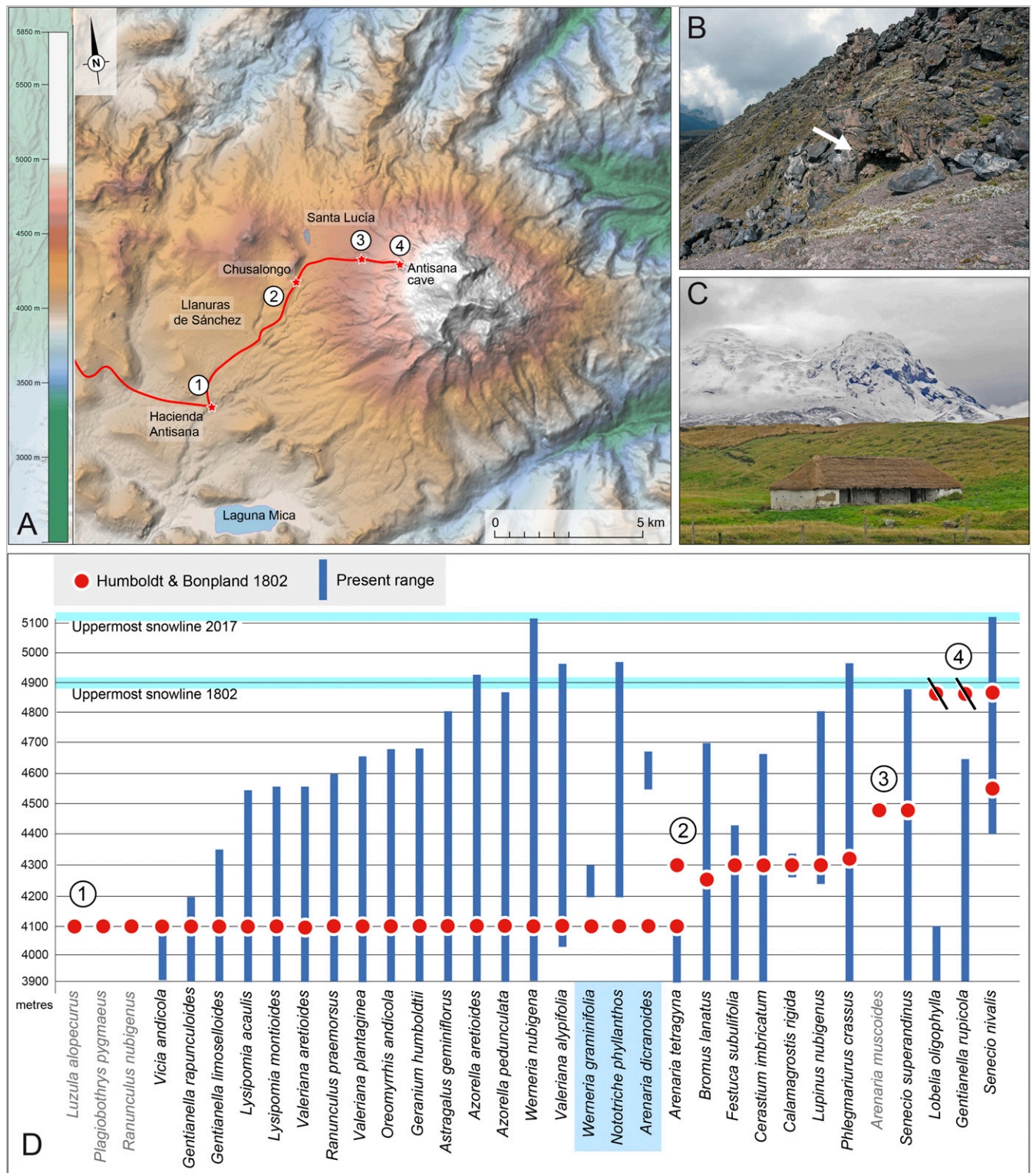


Fig. 4. Botanical resurvey of Mt. Antisana (Ecuador) guided by historical data. (A) Map of Antisana with the route taken by Humboldt and Bonpland in 1802 (in red). Place names and itinerary were retrieved from Humboldt's diary (*SI Appendix, section 4*). (B and C) Two pictures of the sites where Humboldt 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 ± 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 Antisana–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).

ACKNOWLEDGMENTS. We warmly thank Henrik Balslev, Jérôme Casas, Nelson Hairston Jr., and Petr Sklenář for useful feedback on a previous version of the manuscript, and Antoine Moret for the background map of Fig. 4. We also wish to acknowledge the constructive comments of five anonymous reviewers. The research was conducted under research permit 004-2017-IC-FLO-DNB/MA/RENOVACIÓN (Ministerio del Ambiente del Ecuador). We thank the Empresa Pública Municipal de Agua Potable y Saneamiento and the Fondo para la Protección del Agua for allowing the access to the research area. P. Moret was funded by the SUMMITEX project (CNRS, Institut National Ecologie et Environnement, PICS-06724, and Maison des Sciences de l'Homme et de la Société USR 3414) and the INSPYRAND project (CNRS, Réseau National des Maisons des Sciences de l'Homme); P. Muriel by the Pontificia Universidad Católica del Ecuador; and O.D. by the Écologie, Biodiversité et Fonctionnement des Écosystèmes Continentaux Department of Institut de Recherche pour le Développement during a stay at Cornell University (2017–2018).

1. N. A. Rupke, *Alexander von Humboldt: A Meta-Biography* (University of Chicago Press, 2008).
2. S. T. Jackson, "Introduction: Humboldt, ecology, and the Cosmos" in *Essay on the Geography of Plants*, S. T. Jackson, Ed. (University of Chicago Press, Chicago, 2009), pp. 1–52.
3. A. von Humboldt, A. Bonpland, *Essai sur la géographie des plantes, accompagné d'un tableau physique des régions équinoxiales* (Levrault & Schoell, Paris, 1807).
4. N. Güttler, "Drawing the line: Mapping cultivated plants and seeing nature in Nineteenth-Century plant geography" in *New Perspectives on the History of Life Sciences and Agriculture*, D. Phillips, S. Kingsland, Eds. (Springer, New York, 2015), pp. 27–52.
5. M. C. Ebach, *Origins of biogeography. The role of biological classification in early plant and animal geography* (Springer, Dordrecht, 2015).
6. L. Ramond de Carbonnières, *Observations faites dans les Pyrénées, pour servir de suite à des observations sur les Alpes* (Belin, Paris, 1789).
7. M. Nicolson, Alexander von Humboldt, humboldtian science and the origins of the study of vegetation. *Hist. Sci.* **25**, 167–194 (1987).
8. J. G. Pausas, W. J. Bond, Humboldt and the reinvention of nature. *J. Ecol.* **107**, 1031–1037 (2019).
9. N. Morueta-Holme, J.-C. Svenning, Geography of plants in the New World: Humboldt's relevance in the age of Big Data. *Ann. Mo. Bot. Gard.* **103**, 315–329 (2018).
10. M. Lomolino, B. C. Pijanowski, A. Gasc, The silence of biogeography. *J. Biogeogr.* **42**, 1187–1196 (2015).
11. E. V. Bunkse, Humboldt and an aesthetic tradition in geography. *Geogr. Rev.* **71**, 127–146 (1981).
12. O. Lubrich, "Fascinating voids: Alexander von Humboldt and the myth of Chimborazo" in *Heights of Reflection: Mountains in the German Imagination from the Middle Ages to the Twenty-First Century*, S. Ireton, C. Schaumann, Eds. (Boydell & Brewer, 2012), pp. 153–175.
13. A. Wulf, *The Invention of Nature: Alexander von Humboldt's New World* (Alfred Knopf, New York, 2015).
14. N. Morueta-Holme et al., Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 12741–12745 (2015).
15. F. Cuesta et al., Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. *Ecography* **40**, 1381–1394 (2017).
16. A. von Humboldt, *De distributione geographica plantarum secundum coeli temperiem et altitudinem montium, prolegomena* (Libreria Graeco-Latino-Germanica, Paris, 1817).
17. A. von Humboldt, *Voyage vers la cime du Chimborazo, tenté le 23 juin 1802 par Alexandre de Humboldt, Aimé Bonpland et Carlos Montúfar. Esquisse de la Géographie des plantes dans les Andes de Quito, entre les 0° 20 de lat. bor. et les 4° 12 de lat. austr.* (Schoell, Paris, 1824).
18. A. von Humboldt, A. Bonpland, K. Kunth, *Nova Genera et Species Plantarum* (Lutetiae Parisiorum, Paris, 1815–1825), vols. 1–7.
19. A. von Humboldt, J. Oltmanns, *Voyage de Humboldt et Bonpland. Quatrième partie. Astronomie* (Schoell, Paris, 1810), vol. 1.
20. A. von Humboldt, *Reise auf dem Rio Magdalena, durch die Anden und Mexico. Teil I: Texte* (Akademie Verlag, Berlin, 1986).
21. A. von Humboldt, *Notice de deux tentatives d'ascension du Chimborazo* (Pihan de la Forest, Paris, 1838).
22. A. von Humboldt, *Vues des Cordillères, et monumens des peuples de l'Amérique* (F. Schoell, Paris, 1810).
23. F. Hall, Excursions in the neighbourhood of Quito, and towards the summit of Chimborazo, in 1831. *J. Bot.*, **1**, 327–354 (1834).
24. K. J. Feeley, E. M. Rehm, Downward shift of montane grasslands exemplifies the dual threat of human disturbances to cloud forest biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **112**, E6084 (2015).
25. H. Berghaus, *Physikalischer Atlas, oder Sammlung von Karten, auf denen die Hauptsächlichen Erscheinungen der anorganischen und organischen Natur nach ihrer geographischen Verbreitung und Vertheilung bildlich dargestellt sind* (Justus Perthes, Gotha, 1845), vol. 1.
26. A. Rabatel et al., Current state of glaciers in the tropical Andes: A multi-century perspective on glacier evolution and climate change. *Cryosphere* **7**, 81–102 (2013).
27. I.-C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
28. A. Zimmer et al., Time lag between glacial retreat and upward migration alters tropical alpine communities. *Perspect. Plant Ecol. Syst.* **30**, 89–102 (2018).
29. J. Kapfer et al., Resurveying historical vegetation data—Opportunities and challenges. *Appl. Veg. Sci.* **20**, 164–171 (2016).
30. V. Stöckli, S. Wipf, C. Nilsson, C. Rixen, Using historical plant surveys to track biodiversity on mountain summits. *Plant Ecol. Divers.* **4**, 415–425 (2011).
31. M. J. Steinbauer et al., Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* **556**, 231–234 (2018).
32. M. Vellend, C. D. Brown, H. M. Kharouba, J. L. McCune, I. H. Myers-Smith, Historical ecology: Using unconventional data sources to test for effects of global environmental change. *Am. J. Bot.* **100**, 1294–1305 (2013).
33. R. Kwok, Hidden in the past. *Nature* **549**, 419–421 (2017).
34. N. L. Stepan, *Picturing Tropical Nature* (Reaction Books, London, 2001).
35. C. Debarbieux, The various figures of Mountains in Humboldt's Science and Rhetoric. *Cybergeo* (2012). <https://journals.openedition.org/cybergeo/25488?lang=en>. Accessed 7 May 2019.
36. D. A. Morrison, The invention of nature: Alexander von Humboldt's New World by Andrea Wulf. *Syst. Biol.* **65**, 1117–1119 (2016).
37. A. von Humboldt, A. Bonpland, *Plantae aequinoctiales, per regnum Mexici, in provinciis Caracurum et Novae Andalusiae, in Peruvianorum Quitensium, Novae Granatae Andibus, ad Orinoci, Fluvii Nigri, Fluminis Amazonum tipas nascentes*, (Paris & Tübingen, 1805–1817), vols. 1–2.
38. C. Ulloa Ulloa et al., An integrated assessment of the vascular plant species of the Americas. *Science* **358**, 1614–1617 (2017).
39. K. Romoleroux et al., Base de datos del Herbario QCA. (*Versión 1.0*, Pontificia Universidad Católica del Ecuador, Quito, 2018).