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GEOGRAPHY OF PLANTS IN THE
NEW WORLD: HUMBOLDT'S
RELEVANCE IN THE AGE OF
BIG DATA¹

Naia Morueta-Holme^{2*} and
Jens-Christian Svenning^{3,4}

ABSTRACT

Plant geography seeks to describe the patterns of species distributions and understand the underlying mechanisms. The foundation of the field is attributed to Alexander von Humboldt following the broad-scale insights he gained on his explorations of the New World two centuries ago. Today, in the age of “Big Data,” advances in methods and data availability allow us to better assess the complex drivers of species distributions. In this essay, we give an overview of the relevant legacy of Humboldt in the field of plant geography. Comparing the foremost insights and approaches of Humboldt’s time and of today, we highlight areas in which major changes have taken place and areas in which Humboldt’s approach is still relevant. We present advances in the description and understanding of plant geography, which have changed our entire worldview to a much more dynamic one. Further, we present some of the outstanding challenges of the field, and how solving them requires going back to the “Humboldtian” approach to science, i.e., combining precise, quantitative empirical studies with a holistic approach. Finally, we discuss how our recognition of the planetary impact of humans in the Anthropocene means that much of our research is no longer exclusively driven by curiosity, but also by the societal need to make predictions of ecosystem responses to environmental change. There is thus a strong need for combining quantitative empiricism with a holistic perspective to address the complex challenges of the current epoch.

Key words: Alexander von Humboldt, Anthropocene, biogeography, history of science, species distributions.

Alexander von Humboldt (1769–1859) traveled for over five years throughout the Americas, observing, measuring, counting, and describing all the physical and biological phenomena he came across. During his

explorations together with the botanist Aimé Bonpland (1773–1858), he was struck by the changes in vegetation as he moved north and south across both continents, and as he climbed up and down mountains. Different

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species of plants and animals replaced each other, from the thick forests covering the lowlands east of the Andes, through the temperate and alpine shrubs and herbs on the slopes, until only grasses and lichens were left near the highest elevations covered by perpetual snow. Humboldt also noticed that many more species existed in tropical regions compared to higher latitudes. He recorded his observations of the changes in geology, air pressure, humidity, chemical composition of the atmosphere, distribution of animals, light intensity, human land use, gravity, and even the blueness of the sky. Although the early history of biogeography was shaped by a series of innovative naturalists, Humboldt was able to integrate the state-of-the-art knowledge in physical, earth, and biological sciences of his time into a unique synthesis (Jackson, 2009a, 2009b). His novel, simultaneously interdisciplinary, holistic, quantitative, and empirical approach toward understanding nature defines what was later termed “Humboldtian science” (Cannon, 1978; cf., Nicolson, 1987). Doubtless, Humboldt’s legacy and works have provided a major cornerstone—if not the foundation—of the field of plant geography (Anonymous, 1888).

Humboldt himself defines the field of plant geography as “the science that concerns itself with plants in their local association in the various climates. This science, as vast as its object, paints with a broad brush the immense space occupied by plants” (von Humboldt & Bonpland, [1807] 2009: 64). A painting, his *Tableau Physique*, was in fact one of his main additions to science. By summarizing his findings on the profile of the Ecuadorian volcano, Mount Chimborazo (6268 m.s.m.), he managed to unify abstract concepts from botany, geography, physics, and other fields. The graphical depiction enabled him to communicate his research to a broad audience. His work formed the basis of the first world maps of the geography of plants (Schouw, 1822, 1824; Berghaus, 1852) (Fig. 1). The driving force behind Humboldt’s work was a fascination with the natural world, a desire to understand it “once and for all,” to gain “intellectual pleasure” and “moral freedom” through research, and to use this knowledge to communicate (through art) “with all the peoples of the earth,” since “enlightenment and civilization have the greatest impact on our individual happiness” (von Humboldt & Bonpland, [1807] 2009: 75). The aim of Humboldt’s research and of the science of plant geography in general was to answer a simple question still relevant today: What grows where, and why?

Given Humboldt’s seminal importance for plant geography and ecology broadly, it is interesting to consider the extent to which his work is still relevant today. Are Humboldt’s original insights still valid now? What has changed in our perception of the geography of plants? Are the driving forces behind today’s research the same

as Humboldt’s? How far are we from answering the “what grows where and why” question?

This essay seeks to present an overview of the status of the field of plant geography, with specific attention to the continued relevancy of Humboldt’s work and approach. It is divided in three sections. The first part focuses on the *description of patterns* in plant geography—how Humboldt and his peers saw them, and how we infer them today. The second part looks into the *understanding of processes* behind the patterns, looking into major ways in which our methods and insights have changed or stayed the same relative to Humboldt’s. The third section moves on to the *prediction of patterns*. The latter is arguably a major shift in the focus of the field, in large part driven by the current awareness of the strong environmental changes humans are driving to the point of defining a new geologic era: the Anthropocene. Throughout the essay, we will discuss ways of addressing the challenges of today to advance the field and further improve our understanding, ability to predict, and ultimately manage future changes in plant geography.

PATTERNS IN PLANT GEOGRAPHY

THE FIRST DESCRIPTIONS

Humboldt’s era was one of exploration. His urge to describe and measure the natural world was a reflection of the development of modern science, sparked at the end of the 17th century in Europe during the Age of Enlightenment. With trade systems growing outside of Europe, recognition of the complexity of the natural world pushed the interest to conduct expeditions to the New World and other continents and to gather information about these poorly known regions. The gathering of knowledge was thus strongly driven by curiosity and the general search for first principles characteristic of the Enlightenment (Buttimer, 2012).

During these explorations, some of the most fundamental observations in plant and animal geography were made. During his second voyage with Captain James Cook (1728–1779) in 1772–1775, Johann R. Forster (1729–1798) noted the latitudinal increase in species richness toward the equator, as well as the changing composition of the flora with environmental conditions (see Briggs & Humphries, 2004). Also around this time, Georges-Louis Leclerc Comte de Buffon (1707–1788) made the observation that geographically distant regions often have different biotas despite having similar climates (see Briggs & Humphries, 2004). Already in the mid-1700s, Carl von Linné (1707–1778) had recorded his observations on the changes in vegetation along elevation gradients (see Briggs & Humphries, 2004). Humboldt also observed that some regions in the temperate zone have species that are common across large extensions, whereas the tropics harbor more species



Figure 1. First atlas of the geography of plants in the New World, largely informed by Humboldt's collections. By Joakim F. Schouw (1789–1852), published in 1824 (excerpt of Panel XII in Schouw, 1824), after a draft was published in 1822. Visible Danish annotations translate into “Kingdom of the Breadfruit” over the Pacific islands, the “Saxifrages” in northern North America, and “Kingdom of Cacti, Pepper species and Melastomes” across Central and South America.

with small distributions (von Humboldt & Bonpland, [1807] 2009). The observations of Humboldt confirmed and added both detail and novel insights to the general patterns reported by preceding and contemporary naturalists (Jackson, 2009a).

The data and observations collected by Humboldt and Bonpland during their travels constitute a benchmark for today's knowledge of the “what grows where” question in the New World. The two explorers collected plant specimens and rigorously described the places in the New World where these specimens were collected. Their collections were described and classified together with Carl S. Kunth (1788–1850), following the system developed by Linné, a classification system still used in

modern systematics. The result was seven volumes of descriptions and illustrations (Kunth et al., 1815)—a major contribution, which formed the basis of the first world maps of the geography of plants in 1824 (Fig. 1) (Schouw, 1822, 1824) and 1852 (Berghaus, 1852). These maps depicted the distribution of individual species or genera, as well as the distribution of vegetation types, classified according to the physiognomy and function of plants. They laid the foundation for the later maps by Alfred R. Wallace (1823–1913) of biogeographic regions delimited based on the relatedness of species, which followed the development of the theory of evolution by Charles Darwin (1809–1882) and Wallace himself (see Briggs & Humphries, 2004).

The description of major patterns in the distribution of plants laid the basis for understanding the underlying mechanisms. As Andreas F. W. Schimper (1856–1901) and colleagues wrote a century after Humboldt, “The delimitation of separate floral districts and their grouping into more comprehensive combinations are nearly completed, and the time is not far distant when all species of plants and their geographical distribution will be well known. [...] a foundation [...] will have been laid on which science can construct a larger edifice. The essential aim of geographical botany will then be an inquiry into the causes of differences existing among the various floras” (Schimper et al., 1903: v).

However, in spite of Schimper’s statement, another century later we still have large gaps in our knowledge. We still do not know exactly how many species exist in the world (May, 2010). Many species remain undescribed or undiscovered (the “Linnean shortfall”; Raven & Wilson, 1992), and information on the distribution of those we do know is far from complete (the “Wallacean shortfall”; Lomolino, 2004; see also Kier et al., 2005; Feeley & Silman, 2011; Feeley, 2015).

GETTING CLOSER TO ANSWERING “WHAT GROWS WHERE” IN THE AGE OF BIG DATA

Being able to describe, map, and classify the distribution of plant species and vegetation types is as relevant today as it was in Humboldt’s time. It is on such descriptions that we base our fundamental understanding of the forces shaping the world surrounding us. Only with this understanding can we address the increasing need to document plant dynamics as communities respond to global environmental change (Franklin et al., 2017). Basic data on the distribution of species have been much improved thanks to the cumulative efforts in field collections by naturalists like Humboldt and his successors. We are now in the age of Big Data (Ward & Barker, 2013), a time with a steady increase in the amounts of data and computational power (Hampton et al., 2013). Due to the revolution in informatics (Michener & Jones, 2012), we now have the capacity to assemble and analyze the data on plants and their distributions collected across the past three centuries. How does this influence our inference of the geography of plants? What are the challenges for filling the gaps in our knowledge of distributions, and what resources do we have today that Humboldt lacked to address the data voids?

The “expert based” method that Humboldt used to characterize the distribution of species is today being replaced by more data-driven approaches. Descriptions made by Humboldt were translated into qualitative hand-drawn maps (Schouw, 1822, 1824; Berghaus, 1852) and paintings of the elevation zones of vegetation types (or life zones) based on the dominance of species

he observed (Fig. 2). With the current geographic information systems (GIS), we are now able to plot more precise maps based on plant occurrences localized with global positioning systems (GPS). The use of digitized expert maps (e.g., Little, 1971; Henderson et al., 1995) is still widespread (e.g., Bjorholm et al., 2005; Morin & Lechowicz, 2011). However, based on the occurrence data, we can go a step further and map distribution patterns using the raw data directly (Morueta-Holme et al., 2013; Maitner et al., 2018) or models if needed (Kreft & Jetz, 2007).

The accuracy of botanical maps is contingent on the quality of the information we have on species and their distributions, and several challenges stand in the way for a complete knowledge of what grows where. Uneven data collection across space, changes in species definitions, and errors in species names or locality information are some of the major issues that need to be resolved (Maitner et al., 2018). If the basic unit of biogeography is the geographic range of a species, then these deficiencies in defining species and their distributions unavoidably affect our research (Brown et al., 1996).

Sampling biases in large datasets can stem either from biases in field collections (e.g., toward accessible regions or specific taxonomic groups) or from underrepresentation of regions when assembling data from different sources. For instance, the Botanical Information and Ecology Network, BIEN (Fig. 3) (Enquist et al., 2016), while currently the largest dataset of New World plants, has only published clean coordinate information on 19,317 flowering plant species for Brazil (BIEN database version 3.4.5; Maitner et al., 2018), whereas the country harbors 31,162 recognized native angiosperm species (Forzza et al., 2012). Uneven data compilation due to, for example, country-based data contribution policies in large online databanks can lead to stronger Wallacean shortfalls than independent data compilations in which coverage of rare species and under-sampled regions can be targeted more easily (Beck et al., 2013). Biased patterns can affect the conclusions we draw on the processes driving them (Yang et al., 2013; Engemann et al., 2015), especially if the sampling is biased with respect to the factors we are trying to infer as drivers of the distribution of species. Accounting for sampling effort (Kadmon et al., 2004), or using modeling approaches to estimate species and distributions in poorly sampled regions (Bini et al., 2006), can partly address the issue, but only to a certain degree (Engemann et al., 2015).

A second challenge is related to the definition of species, which are somewhat artificial constructs. Not only can the same species be named differently in the countries in which it is found, but definitions of species often change through time. Many of the species names

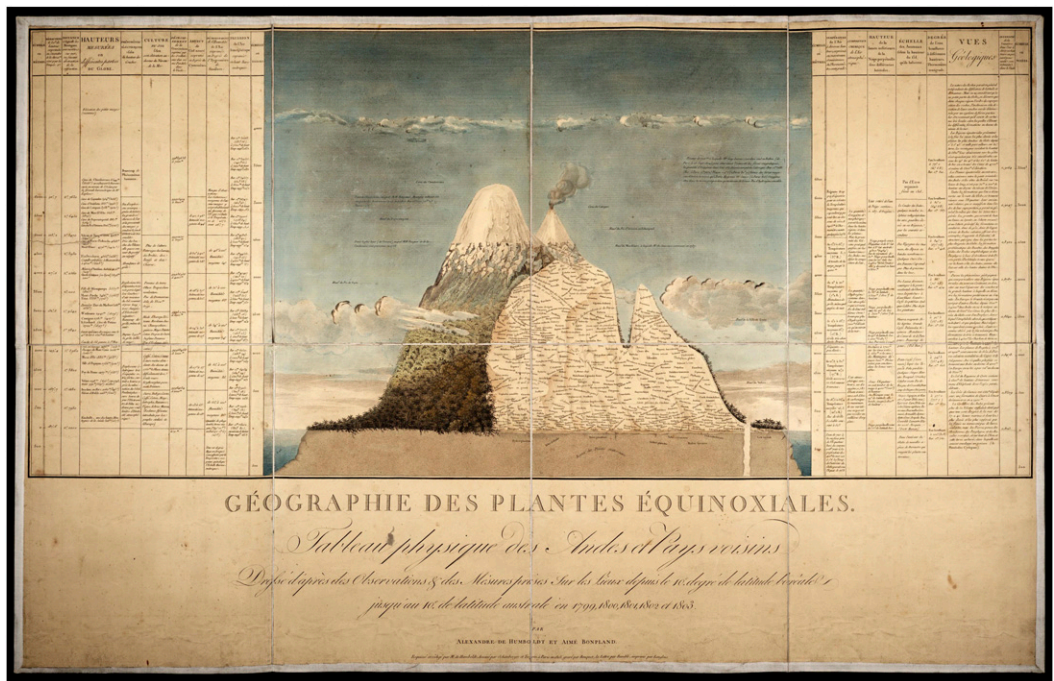


Figure 2. Humboldt's *Tableau Physique*, with the distribution of plants of the Andes depicted on the slopes of Mount Chimborazo and corresponding measures of environmental variables specified in the columns on each side (von Humboldt & Bonpland, [1807] 2009). Digital image courtesy of the Peter H. Raven Library/Missouri Botanical Garden.

that Humboldt used for his collections have thus changed (Morueta-Holme et al., 2015). Whereas tools like the Taxonomic Name Resolution Service (Boyle et al., 2013) can resolve nomenclatural synonyms (though the tools are still prone to errors), taxonomic synonyms are more challenging. Cases in which species definitions have changed from one to several can make comparisons of current and historic data difficult (Morueta-Holme et al., 2015), especially if the historic record is not documented with collections or descriptions. Besides temporal changes in species definitions, inconsistencies across space and taxonomic groups may bias the analysis of ecological and evolutionary patterns (Faurby et al., 2016).

Big-data initiatives such as BIEN (Fig. 3) (<www.biendata.org>; Enquist et al., 2016), TRY (<www.try-db.org>), GBIF (<www.gbif.org>), Map of Life (<www.mappinglife.org>), RAINBIO (Dauby et al., 2016), European Vegetation Archive (EVA; Chytrý et al., 2016), GlobalTreeSearch (Beech et al., 2017), and GenBank (<www.ncbi.nlm.nih.gov/genbank/>) constitute important steps toward overcoming many of the data challenges. These efforts are only possible through the increase in cross-disciplinary collaborations observed in our time (Dong et al., 2017), taking advantage of the advances in informatics to assemble and enable access to a wealth of information on the distribution of

plants, functional traits, and genes. Such initiatives can help assess where data deficiencies are most prominent and guide future collections to address the Wallacean and Linnean shortfalls (e.g., Brito, 2010; Feeley, 2015). Parallel to the data assembly, web-based tools are being developed to correct and improve the quality of the data for nomenclatural issues, errors in geographic information, and resolving native status of species (Boyle et al., 2013; Maitner et al., 2018). The field of plant geography is indeed part of the age of Big Data.

As Humboldt declared, “for botanical maps [...] we can only make them more exact only inasmuch as we accumulate a greater number of good observations” (von Humboldt & Bonpland, [1807] 2009: 80). Ultimately, filling the gaps in our knowledge of species distributions can only be achieved by continuing Humboldt’s effort of data collection. On average, 2000 new plant species are being described each year (RBG Kew, 2016). Yet, there is still a long way to go, with museum collections—the feeders of digital infrastructure—strongly lagging behind in proper species identifications (Fontaine et al., 2012). Errors in species identifications propagate throughout web-based tools and databases and require revisions of the original specimens. Field-based collections, monitoring, and continued work on plant taxonomy, supplemented by advances in, for example, remote sensing, citizen science, and image recognition for species



Figure 3. The Botanical Information and Ecology Network (BIEN) working group, a collaborative effort of botanists, ecologists, and computer scientists active since 2008. To assemble the largest botanical dataset on New World plants, much of the work has moved to behind computer screens. The group also illustrates the movement of the field of plant geography toward collaborative, interdisciplinary work. Photo: Benjamin Blonder.

identifications (e.g., Carranza-Rojas et al., 2017) will help us get closer to Humboldt's and Schimper's visions of knowing where everything, everywhere, is living.

FROM DESCRIBING TO UNDERSTANDING

"I shall collect plants and fossils, I shall be able to make useful astronomic observations [...], I shall conduct chemical analyses of the air,—but all that is not the main purpose of my expedition. Above all, I will observe the interactions of forces, the influence of the inanimate environment on plant and animal life" (von Humboldt, 1799, in Knobloch, 2007). Although plant geography was mostly descriptive in its early days (Knapp, 2013), Humboldt's statement shows that his interest did not only reside in describing patterns in the distribution of plants. He, like the entire field of ecology, also sought to understand the processes driving them. What determines biodiversity is still seen as a major unanswered question in science (Pennisi, 2005). However, the advances in data and analytical tools and approaches since Humboldt's time have allowed us to get closer to the "why" species grow where they do. How has our view of the drivers of the geography of plants changed relative to that of Humboldt's? In this section, we highlight one major way in which our view has changed, and one in which we appear

to be going back to Humboldt's: first, that the world is now seen as more dynamic than was recognized by Humboldt and his contemporaries—with humans as an overwhelming force of change (Millenium Ecosystem Assessment, 2005; Steffen et al., 2005), and secondly, that a single universal explanation for the distribution of species probably does not exist. Before developing the two themes, we start by outlining the context of Humboldt's approach to understanding patterns.

SCIENTIFIC INFERENCE IN THE EARLY 1800S

Humboldt was attempting to get a complete picture of all the physical phenomena, and to understand their relationships. His methodology consisted of first recording information on temperature, humidity, atmospheric pressure, and other environmental parameters. Such measurements were only possible due to the technical advances of the time, with the invention of instruments such as the hygrometer, barometer, and thermometer. By then organizing the information in tables and drawing them on the same figure (e.g., Fig. 2) Humboldt inferred their relationships and set up hypotheses on the mechanisms behind them. This simple method supposed the onset of empirical inference.

Through these observations, Humboldt set up hypotheses on which factors might influence the physiology—and in turn the distribution—of plants. Among the strongest relationships that he inferred was that between temperature and the distribution of plants. The physiological requirements of plants to ambient energy meant that the colder temperatures up elevational and latitudinal gradients restricted their survival (von Humboldt & Bonpland, [1807] 2009; see Hawkins et al., 2003). The relationship was not only linked to average temperature. Indeed, Humboldt noted also the effect of temperature seasonality on the distribution of species' range sizes and richness. He attributed the observation that the range of many species in temperate regions spread from valleys to high elevations to the fact that plants in these regions are exposed to the same low temperatures in winter and at high elevations, and thus have adapted to a wider range of temperatures (the same observation that led Janzen to later develop the classic hypothesis that tropical mountain passes are more effective barriers to organisms; Janzen, 1967). On the other hand, stable intra-annual temperature conditions in the tropics resulted in clearer vegetation bands up elevation, leading to higher richness of life forms relative to an equivalent zone on the slopes of a temperate mountain (von Humboldt & Bonpland, [1807] 2009).

Seldom is an idea original to any one person, and Humboldt's thinking on the effect of climate on the distribution of vegetation was strongly influenced by many preceding and contemporary peers (Jackson, 2009a). For instance, Linné had already noted the differential distribution of plants along elevation gradients, and Forster had invoked temperature to explain the latitudinal gradient in species richness (Briggs & Humphries, 2004). Humboldt developed these ideas further, finding support through extensive data collections and delineating the apparent causal links inferred through his observations. He drew the parallel of elevation and latitude, both in climate conditions and species distributions, and based on his work, the first isotherm map of the world was drawn in 1823.

SCIENTIFIC INFERENCE TODAY

Although Humboldt lacked the statistical tools we use today, his approach to infer causation was not very different from the correlative methods widely used today. Indeed, correlative species distribution models (SDMs), plant diversity regressions, multivariate analyses of species composition, and related numerical models in general rely on the same basic approach of linking, for example, environmental data to the occurrence of a species or certain plant community characteristics (Guisan & Thuiller, 2005; Elith & Leathwick,

2009; Lamanna et al., 2014). Still, there has been a strong development in approaches to infer processes from patterns. In particular, Popper's falsification theory (Popper, 1968) and developments within the formulation of scientific hypotheses and their testing, including techniques to test multiple competing hypotheses (Chamberlin, 1890; Burnham & Anderson, 2002), have shaped much of our current research. Other influential areas include progress within statistics, ecological theories, experimental work in the field and in laboratories, more systematic approaches to data collection, and use of simulations and null-models to separate patterns from chance events, to mention a few (see Brown & Maurer, 1989; Gotelli & Graves, 1996). The amount of data on factors that can potentially influence species' distributions has increased greatly, from climate, geology, soil conditions and topography, to genetic information, plant functional traits, and remote sensing products (Michener & Jones, 2012). The development of methodological approaches and the availability of data and computer resources have given us insights that were previously not possible to infer.

Toward a highly dynamic view of the world

Humboldt acknowledged that the history of the Earth must have an effect on the distribution of plants (Jackson, 2009a). For instance, he described the impact of geologic changes, such as “the great catastrophe which opened up the Strait of Gibraltar and fashioned the Mediterranean seabed” (von Humboldt & Bonpland, [1807] 2009: 66), in forming barriers to dispersal and described how plant geography could complement other approaches to help discern that separated islands or continents were once connected (von Humboldt & Bonpland, [1807] 2009: 67). However, he did not appear to fully recognize the sheer magnitude and multitude of mechanisms at play and the importance of time in shaping contemporary patterns of distribution. Rather, he saw the role of history as mostly insignificant for driving species distributions (Seberg, 1985), at least until later in his career (Jackson, 2009a), and thought, for example, the separation of Africa from South America had occurred “before the development of organized forms of beings” (von Humboldt & Bonpland, [1807] 2009: 67). The presence of shells and petrified corals found on mountain peaks over 4000 m.s.m. were already “posing difficult enigmas for geologists” (von Humboldt & Bonpland, [1807] 2009: 76). Humboldt mentioned that plant geography combined with earth history could help address these questions but saw mysteries like populations with disjoint distributions as unsolvable (Jackson, 2009a). Indeed, he largely shared the prevalent view in the beginning of the 19th century that the world was rather static—the geology, the climate, and

the distribution of species. Previous to Humboldt, literal readings of the Bible at the beginning of the Age of Enlightenment led Linné and others to the belief that species had spread from Mount Ararat rapidly after the deluge, creating a static pattern. Reconciling this idea with the observed distribution of species proved difficult. As explained in Briggs and Humphries (2004) and Seberg (1985), through the 1800s arguments grew more complex about the placement and number of centers of origin of species (Comte de Buffon and Augustin de Candolle [1778–1841]), about the means of species to disperse between continents (invoking land bridges by Joseph Hooker [1817–1911], Charles Lyell [1797–1875], and Edward Forbes [1815–1854] and long-distance dispersal [e.g., by Darwin]), and about the theory that species evolve and diversify through time (Darwin & Wallace, 1858). The idea of Noah's Ark and the deluge was sinking.

Since Humboldt's time, we have learned that both the geology and climate of the Earth are dynamic entities. The movement of tectonic plates over millions of years (a theory developed by Alfred Wegener [1880–1930] in the early 1900s, but not accepted until the 1960s; Briggs & Humphries, 2004) has given us the key to understanding the formation of mountains, islands, and seas, and with that, explanations for long-term drivers of speciation and extinction, and for the disjunction of biotas. Besides the geology, deep-time climate changes have also greatly influenced diversification and extinction processes. For instance, decreasing CO₂ levels in the Cretaceous (145–65 Ma) are thought to have driven the radiation of angiosperms (Boyce et al., 2009), and the drought of the mid-Oligocene (33.9–23 Ma) lead to the evolution and radiation of C₄ photosynthesis in grasses (Sage, 2004). More *recently*, the glacier cycles of the Quaternary, starting 2.6 Ma, have created variation in environmental conditions, both in terms of global climate, sea levels, and expansion and recession of glaciers, alternately creating barriers and bridges to the dispersal of species. Species have responded to the changing conditions through time, moving (Svenning & Skov, 2004; Antonelli et al., 2009), adapting (e.g., Sage, 2004; Antonelli et al., 2009; Boyce et al., 2009), or going extinct (e.g., Svenning, 2003; Eiserhardt et al., 2015), ultimately creating the patterns of distribution we see today.

The realization of how dynamic the earth system is has influenced our understanding of ecological processes. Species might respond differently to climate changes, and so the species communities we see are not necessarily closed entities (*sensu* Clements, 1916), as evidenced by the no-analog communities in the paleorecord of past interglacials (Jackson et al., 2005; Williams & Jackson, 2007). The paleorecord and distribution models comparing the actual and potential

distribution of species have also shown that many are in disequilibrium with current climate, and actually still in the process of tracking climatic changes since the Last Glacial Maximum (Davis, 1986; Svenning et al., 2008; Normand et al., 2011). The species that do manage to track climate change often have either good dispersal ability or are more generalist (Normand et al., 2011). The higher frequency of widespread species that Humboldt observed in North America relative to the Andes (von Humboldt & Bonpland, [1807] 2009) indeed partly reflects the effect of long-term climate instability in promoting large ranges (Morueta-Holme et al., 2013).

Humboldt pointed out that humans could impact species and the environment. For instance, he noted that the distribution of species could change due to dispersal by humans (von Humboldt & Bonpland, [1807] 2009). Yet, he could not have guessed that the dynamic nature of species ranges would become apparent within a human lifetime and would be driven by human activities. Indeed, that species ranges are dynamic is also evidenced by the responses of species to recent anthropogenic climate warming (IPCC, 2014). Although migration lags are common (Bertrand et al., 2011), the distribution of plants and other organisms are generally moving upward in elevations (Lenoir et al., 2008; Moritz et al., 2008; Felde et al., 2012) or toward higher latitudes (Devictor et al., 2012; Lindström et al., 2013). Even the plant species that Humboldt studied, and on which he carefully based his classifications of vegetation along the slopes of Mount Chimborazo, have shifted upward by more than 500 m, as evidenced by a resurvey 210 years later (Fig. 4) (Morueta-Holme et al., 2015).

One distribution driver or many?

"In this great chain of causes and effects, no single fact can be considered in isolation" (von Humboldt & Bonpland, [1807] 2009: 79). Humboldt aimed to unify the physical sciences and to measure everything he could think of to grasp the big picture of their relations. Later, the focus of the sciences was on separate disciplines, with more emphasis on experimental inference and a reductionist search for universal laws (Jackson, 2009a). However, more recently there has been a shift toward a re-emphasis on the complexity and interconnection of the processes underlying not only species distributions but environmental science in general. We seem to be going back to the "Humboldtian" convergence of disciplines (Jackson, 2009a, 2009b).

Climate is often regarded as the main driver behind the distribution of biomes and species across the globe (Merriam, 1894; Whittaker, 1975; Wiens, 2011). Coinciding patterns of distribution of species and temperature conditions that Humboldt already observed



Figure 4. Resurveying the Chimborazo volcano 210 years after Humboldt from 3800 m elevation (top) to 5200 m (bottom). Despite the technical advances of the age of Big Data, fieldwork is still needed for understanding changes in plant geography driven by environmental change. Photos: Naia Morueta-Holme and Pablo Sandoval-Acuña.

support this view. Temperature can interact with water availability, driving the distribution of rainforests and deserts, for example (Holdridge, 1947; Whittaker, 1975). Another piece of evidence is the shift in species' distributions observed following past and current climatic changes (see previous section). Mechanistic links from experimental work can also provide physiological explanations, used to understand how the physiological limits that low temperatures or drought stress, for example, can impose on reproduction, growth, or survival are translated to constraints on distributions due to reduced fitness (Woodward et al., 1990; Pigott & Pigott, 1993). Thus, low temperatures often constrain the latitudinal and elevational distribution of species, as evidenced from the frost-intolerant palms (Eiserhardt et al., 2011) and saguaro cacti (*Carnegiea gigantea* (Engelm.) Britton & Rose; Shreve, 1911).

That climate is not the sole driver of plant geography was already obvious to the early naturalists of Humboldt's time. Buffon already discussed that dispersal limitation must explain why the biotas of different parts of the world were not the same even when they shared similar climates (Briggs & Humphries, 2004). The lagged responses of species' distributions to climate change (see previous section) are evidence today of the important role of dispersal limitation even in the absence of physical barriers.

Since the time of Humboldt, we have learned that several additional factors influence the broad-scale distribution of species. The role of biotic interactions such as competition and facilitation in shaping large-scale patterns is one major factor that is increasingly recognized (see Wisz et al., 2013). For instance, the smaller-than-expected range sizes of large-seeded trees in Amazonia are consistent with a reduction in dispersal following the extinction of megafauna frugivores in the Late Pleistocene (Doughty et al., 2016). Diseases and pests can also strongly reduce the distributions of species as in the case of the American chestnut blight, or the hemlock woolly adelgid (*Adelges tsugae* [Annand]) (see Svenning & Sandel, 2013). The expansion of the woolly adelgid with recent warming temperatures is driving range contractions in hemlock (*Tsuga canadensis* Carrière), exemplifying how different factors (here climate change and biotic interactions) interact with one another (Svenning & Sandel, 2013). Soil requirements of plants are often reflected on local-scale distributions but can also have imprints at coarser scales (Thuiller, 2013). At present, anthropogenic land use has a strong effect on the distribution of plant species and vegetation, for instance in confining forests to steep terrain in areas subject to intense human land use (Sandel & Svenning, 2013).

Although plant distributions are likely not directly affected by the blueness of the sky that Humboldt measured (von Humboldt & Bonpland, [1807] 2009),

his perception that many factors played a role was close to the notion we have today, even if he had not identified all important factors. The complexity not only stems from the long list of factors driving species distributions. Factors interact and influence each other, and their importance appears to vary across scales (Levin, 1992; Pearson & Dawson 2003; McGill, 2010); species (e.g., depending on dispersal traits [Normand et al., 2011] or ecological strategy [Grime, 1979]); and geographic regions (Morueta-Holme et al., 2013). The attempts to find simple, universal laws in ecology by mostly focusing on small-scale experimental ecology from the early 1970s (Brown & Maurer, 1989) are being replaced, or at least supplemented, by a "renaissance" of Humboldt's holistic approach: trying to grasp the whole picture, instead of considering processes in isolation (Jackson, 2009a). And then, "[s]ustained by previous discoveries, we can go forth into the future, and by foreseeing the consequences of phenomena, we can understand once and for all the laws to which nature subjected itself" (von Humboldt & Bonpland, [1807] 2009: 75).

MOVING ON TO PREDICTION

Humboldt focused on describing the patterns he saw and understanding their drivers. Today, much of the field is extending to predictions of how the patterns will change due to human-driven environmental change. With the Enlightenment came industrialization. The consequences of the following acceleration in human population growth and demands for natural resources are today discernible at the scale of the whole planet. Humans are responsible for the transformation of almost half of the land surface, and the greenhouse gas emissions from widespread use of fossil fuels is driving ongoing rapid climate change (Steffen et al., 2007; IPCC, 2014). The influence of humans on planetary functioning—to the point of leaving a stratigraphic signature—has led to the definition of a new geologic epoch: the Anthropocene (Crutzen, 2002; Steffen et al., 2007; Waters et al., 2016; Malhi, 2017). In this era, the forces or "laws to which nature subject[s] itself" (von Humboldt & Bonpland, [1807] 2009: 75) are being overwhelmed by humans. The rapid rates of change in biodiversity that human activities are driving are unprecedented in human history (Millennium Ecosystem Assessment, 2005; Steffen et al., 2005). Species extinction rates are alarming, up to 1000 times higher than background extinctions according to the fossil record (May, 2010), and species and ecosystems are already responding to the increases in mean global surface temperatures (see previous section). Almost within Humboldt's lifetime, scientists like George Perkins Marsh (1801–1882) in 1864 were already recognizing the impact of humankind's activities on the geology and

morphology of Earth (Steffen et al., 2007). Today, concerns about the impacts on biodiversity have never been stronger. A major change in the field of the science of geography is the increasing interest in using it for predictions of the effect of ongoing change and their application in conservation efforts (Knapp, 2013). Key to this is that we understand the underlying processes to understand what is possible and feasible for the future.

The pioneering ideas of Humboldt on the link between climate and plant geography have been translated into species distribution models (SDMs; Guisan & Thuiller, 2005). Such correlative models (not necessarily restricted to climate) are increasingly used for predicting distributions under future climate change scenarios (see Elith & Leathwick, 2009), and can also be used for reconstructing past distributions (e.g., Nogués-Bravo, 2009; Svenning et al., 2011), guiding fieldwork in the search of rare species (e.g., Pearson et al., 2007), or assessing the outcome of species introductions to new areas, either of invasive species (Peterson et al., 2003) or assisted colonization for conservation purposes (Fløjgaard et al., 2009; Svenning et al., 2009; Morueta-Holme et al., 2010). While SDMs are one of the few approaches we can use today in practice to predict distributions in space and time (Elith & Leathwick, 2009), predictions can be improved in several ways.

We know that multiple factors other than climate determine species distributions. The way forward to improve predictions is to continue Humboldt's interdisciplinary approach and find ways to better integrate into models the ecological processes we have delineated during the past two centuries. The integration of disparate types of data enabled by developments in digital infrastructure and statistical approaches has opened new avenues for achieving this goal. For instance, phylogenetic information can help estimate functional traits for species missing information (Swenson, 2014; but see Molina-Venegas et al., 2018), avoiding the exclusion of many species from predictions based on trait-environment relationships. Co-occurrence patterns from plots can serve to infer pairwise species dependencies (e.g., Morueta-Holme et al., 2016 and references therein) to include the effect of biotic interactions in distribution modeling (Wisz et al., 2013). Going beyond simple correlative SDMs, information on dispersal and biotic interactions can be incorporated into process-based simulation models such as dynamic vegetation models (see Svenning et al., 2014). Although they are not without challenges, notably in terms of data requirements, these integrative approaches are enabling predictions based on the mechanisms thought to be important, moving beyond the correlative approach of SDMs and Humboldt's inference method.

Humboldt recognized the importance of nature for human well-being. In particular, he saw nature as

important for the intellectual mind, through the increase of knowledge it can provide, and for its aesthetic value. The latter is reflected in his great interest in communicating his science through artwork, which provided a medium to reach people that would never be able to travel to the places he had seen. Although these views are still valid today, there is increasing awareness of the services that ecosystems provide to humans (Millennium Ecosystem Assessment, 2005). Humboldt mentioned the value of "useful" plants (von Humboldt & Bonpland, [1807] 2009), perhaps in an attempt to increase the interest of society on plant geography, but we now know that the value of plants and other organisms goes well beyond the commercial value of crops (Daily, 1997; Cardinale et al., 2012; Cámara-Leret et al., 2017). We have realized that resources are limited, and that the welfare of societies depends on functioning ecosystems (Daily, 1997; RBC Kew, 2016). There is now a demand for knowledge that is applicable to societal and conservation needs, a demand for science to deliver predictions of the consequences of our actions that can guide decision-making. There are thus many good reasons in continuing Humboldt's quest and holistic perspective for understanding patterns and processes in nature and extending it to prediction.

CONCLUSIONS

Humboldt's lifelong observations and collections helped paint the first broad picture of the geography of plants in the New World. His systematic approach to data gathering has been used ever since. Today, we have much more detailed knowledge of the distribution of species, thanks to the cumulative efforts of naturalists in collecting primary data and the means of assembling them through the computer infrastructure of the age of Big Data. Still, there is a long way to go. Only by continuing to gather data in the way of Humboldt, with today's updated technologies, will we come closer to filling the gaps in our knowledge of "what grows where."

Even if methodologies and available data have improved greatly in the last two centuries, Humboldt's basic approach of inferring causal relationships bears similarities to our current statistical approaches. By linking the patterns of the distribution of plants and other physical factors, we can test hypotheses of their causal relationships. Since Humboldt, we have acquired a more dynamic view of the world, learned that the world's geology and climate have been changing through deep and recent time, in turn affecting the distribution, speciation, and extinction of species. Humboldt's appreciation of the complexity of ecological processes is re-emerging in today's views, which appear to be giving up on the search of reductionist universal laws. The constraints on the distribution of species are multidimensional, and the

importance of individual factors vary and interact across scales, species, and space. Disentangling these factors is still a challenge that calls for a continuation of Humboldt's holism and interdisciplinarity.

The development of human societies since the beginning of the industrialization has deeply changed the environment that Humboldt experienced two centuries ago. Concerns over the strong negative impacts human activities are having on the natural world and, in turn, the impacts they are having back on our own species have changed the focus of ecological science. There is now an increasing demand for science that can be applied to solve societal needs, to predict the outcome of conservation and management, and to guide decision-making. Methodological advances are improving our ability to include our knowledge on processes in predictions. However, such predictions must be founded on a solid understanding of our complex world, which can only be achieved by working across disciplines, in the broad way that Humboldt attempted to do. The more we improve our understanding of the processes, the better we will know how to act as a society if we wish to maintain the diversity of life.

Humboldt left the species-poor Germany of his youth, driven by curiosity. "The sight of exotic plants, even of dried specimens in a herbarium, fired my imagination and I longed to see the tropical vegetation in southern countries with my own eyes" (von Humboldt, 1806, in Buttner, 2012). The complexity and variation of the natural world became apparent to him as soon as he set foot on the New World. Like it did for Humboldt, biogeography, the science of the distribution of biodiversity, gives us a global, geographic perspective to the set of systems we need to explain. Maybe more importantly, biogeography inspires a sense of wonder about the world when we realize the planetary scale of things—that nature is not just a simple beech grove or a rye field, but instead a system of many species in diverse locations, developed by processes that are interconnected in ways we are just now discovering.

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