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Challenges and opportunities for biogeography - what can we still learn from von Humboldt?

Running title: Biogeography challenges and opportunities

Authors: Franziska Schrodt[1,*], Joseph J. Bailey[2], Maria J. Santos[3], Richard Field[1]
* - corresponding author

Affiliations:
[1] School of Geography, University of Nottingham, UK
[2] Geography, School of Humanities, Religion and Philosophy, York St John University, YO31 7EX, UK
[3] University Research Priority Program in Global Change and Biodiversity and Department of Geography, University of Zürich, Switzerland

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Abstract

Alexander von Humboldt was arguably the most influential scientist of his day. Although his fame has since lessened relative to some of his contemporaries, we argue that his influence remains strong – mainly because his approach to science inspired others and was instrumental in furthering other scientific disciplines (such as evolution, through Darwin, and conservation science, through Muir) – and that he changed the way that large areas of science are done and communicated. Indeed, he has been called the father of a range of fields, including environmental science, earth system science, plant geography, ecology and conservation. His approach was characterized by making connections between non-living and living nature (including humans), based on interdisciplinary thinking and informed by large amounts of data from systematic, accurate measurements in a geographical framework. Although his approach largely lacked an evolutionary perspective, he was fundamental to creating the circumstances for Darwin and Wallace to advance evolutionary science. He devoted considerable effort to illustrating, communicating and popularising science, centred on the excitement of pure science. In biogeography, his influence remains strong, including in relating climate to species distributions (e.g. biomes and latitudinal and elevational gradients) and use of remote sensing and species distribution modelling in macroecology. However, some key aspects of his approach have faded, particularly as science fragmented into specific disciplines and became more reductionist. We argue that asking questions in a more Humboldtian way is important for addressing current global challenges. This is well exemplified by researching links between geodiversity and biodiversity. Progress on this can be made by (i) systematic data collection to improve our knowledge of biodiversity and geodiversity around the world; (ii) improving our understanding of the linkages between biodiversity and geodiversity; and (iii) developing our understanding of the interactions of geological, biological, ecological, environmental and evolutionary processes in biogeography.

Keywords: Alexander von Humboldt, biogeography, geodiversity, biodiversity, outreach, science communication, integrated perspectives, earth system science

Introduction

During their meeting in 1804, Napoleon Bonaparte famously quipped to the young Alexander von Humboldt: "You collect flowers? So does my wife" (Osterhammel, 1999). Yet Humboldt (1769-1859) was not only a trained botanist, he was a true polymath scholar with a career in the mining industry, expertise in geology, astronomy, anatomy, biology, languages and anthropology, and great skills in the maintenance and invention of scientific instruments (Buttimer, 2001). Humboldt has been pronounced the father/godfather of many disciplines, including modern geography (Egerton, 2009), plant geography (Nicolson, 2013), rock coating research (Dorn, Krinsley, & Dirro, 2011) and earth system science (Clifford & Richards, 2005). Arguably, he was one of the first scientists to empirically observe and describe intimate links between vegetation and abiotic environmental conditions over large spatial scales and in different ecosystems (von Humboldt & Bonpland, 1807) and, consequently, large-scale gradients in vegetation and environmental conditions. Observing the highly erosive practices of monoculture, overfishing and overhunting in South America, perhaps most remarkably for an 18th century scholar, he also recognized and warned about the degree to which humans could act as agents of change and destruction of biodiversity (Buttimer, 2001; Egerton, 2009). Humboldt recognised the need not only to perform rigorous research but also to popularize science, although this only came to him later, after his travels in South America. He "did not think at the time that these jotted-down notes would form the basis of a work offered to the public" but after his return "realized that even scientific men, after presenting their researches, feel that they have not satisfied their public if they do not also write up their journal" (Wilson, 1995). Undoubtedly, together with his image as an adventurous young polymath with a keen sense of humour and engaging writing and oratory skills, this helped his popularity and enhanced his scientific influence. Thus, he represents an early example of the importance of science communication and potentially wide-ranging influence of outreach.

Yet, Humboldt is not without controversies. In the public sphere, he was appropriated as a figurehead by such diverse political movements and geographical locations as Nazi Germany and many Latin American countries, including Mexico, Argentina and Colombia (Rupke, 2008). In the natural sciences, Humboldt's direct contributions have been questioned. Some have argued that he collected data "without developing a major theory" (Rillig et al., 2015) or publishing a truly ground-breaking piece of work such as Darwin's "Origin of Species" (Osterhammel, 1999). Even his famous botanical map (von Humboldt & Bonpland, 1807) was preceded by earlier, similar biogeographical maps (e.g. by Giraud-Soulavie, Ebach, & Goujet, 2006). Georg Forster (1754-1794) was described by Humboldt himself as the "parent of a grand progeny of scientific travellers" and "the first to describe with charm the varying stages of vegetation, the climatic conditions, the nutrients in relation to the customs of people in different localities" (Wilson, 1995).

On the other hand, Humboldt has been credited with notable academic advances across a wide range of scientific disciplines. For example, he developed a hypothesis for one of the most prominent patterns in biogeography: the water–energy dynamics hypothesis for the latitudinal diversity gradient. He is credited with discovering magnetic storms and, through promoting coordinated and strategically placed scientific measurements, proving "prescient in the development of modern networks of geospace observatories" (Lotko, 2017). Some of his hypotheses and approaches are now well established (e.g. the morphological species concept

(Nicolson, 1987)), some are still subject to discussion (e.g. latitudinal/elevational diversity gradients (Kinlock et al., 2018)) and some have only gained momentum relatively recently (e.g. the “Conserving Nature’s Stage” concept (Lawler et al., 2015)) and the importance of geodiversity for biodiversity (e.g. Bailey, Boyd, Hjort, Lavers, & Field, 2017).

In his time, Humboldt was highly influential (Baron & Doherr, 2006; Buttimer, 2001; Jackson, 2009). Indeed, while few theories or scientific processes bear his name, more species, both scientific (e.g. Humboldt penguin (S*pheniscus humboldti*)) and common names (e.g. Humboldt squid (*Dosidicus gigas*)) and minerals, places or natural features (e.g. Humboldt current, Humboldt Glacier and a sea on the moon) are named after him than any other scientist (Wulf, 2015). His influence stems more from his approach to science than from the specific advances he made, and arguably this influence was, and remains, even greater than that of other prominent figures such as Darwin and Wallace.

Whether we may still learn from Humboldt’s approach to science is rarely considered (but see Morueta-Holme & Svenning, 2018). Here we aim to highlight key aspects of Humboldtian science, primarily from a macroecologist’s view (focusing on those aspects most relevant to biogeography and macroecology), and indicate what it means to ‘ask Humboldtian questions’. In so doing, we discuss recent advances and ways to move towards a more holistic, transdisciplinary “Humboldtian BIOGEOgraphy”, emphasizing the relationship between biodiversity and geodiversity (defined as the variety of geology, geomorphology, pedology/edaphology and hydrology).

Humboldtian science and its influence on biogeography today

We do not attempt to be comprehensive; much has been written about what constitutes Humboldtian Science and how it differed from what came before (e.g. Bowen, 1970; Buttimer, 2001; Jackson, 2009; Morueta-Holme & Svenning, 2018; Nicolson, 1987; Zimmerer, 2006a). Instead, we distil Humboldt’s approach into five key aspects or pillars (Figure 1, Table S1) that are highly relevant to biogeography (especially ecological biogeography and macroecology), and that we consider key to researching the links between geodiversity and biodiversity. Figure 1 illustrates these five pillars in the context of modern environmental science. It emphasizes the holistic, interconnected nature of both the subject matter and how it is researched and disseminated. For each pillar of Humboldtian science, Table S1 identifies scientific papers that make the link with Humboldt, and that identify a need for that aspect to be adopted more in today’s science.

Humboldt made an extraordinary quantity and range of detailed measurements, which he used to infer underlying mathematical laws of nature – a macroecological approach, in modern parlance. His approach was also strongly geographical, with emphasis on maps, isolines and other geographical illustrations such as his famous “Physical Tableau of Equatorial Regions” (Figure S1). Humboldt (and colleagues) recorded distributional patterns of vegetation in mountainous areas of the world, particularly in the Andes, Himalayas, Alps, Pyrenees and Tenerife (Figure 2). These early plant-geographical drawings describe distinct vegetation bands along elevational gradients. This emphasis on the connections between living organisms and non-living nature can be linked to the concept of biomes – Humboldt defined global vegetation zones, in sharp contrast to the Linnaean-style taxonomic classification and cataloguing that was dominant in science in his day. We may draw similar connections to the emergence of phytosociology and the notions of deterministic plant associations and Clementsian climax communities (where a plant community is considered analogous to an organism, in which species associations deliver the functions of organs, and an end-point is reached that is determined by climate (Eliot, 2007)). Importantly, however, Humboldt and his colleagues recorded each species as having its own place along the elevational gradient (Figure S1), in a rather individualistic way. This is analogous to, and may be regarded as a precursor for, a more Gleasonian view (where the plants present in a location are an assemblage of species that interact with their environment individualistically (Crawley et al., 2002)).

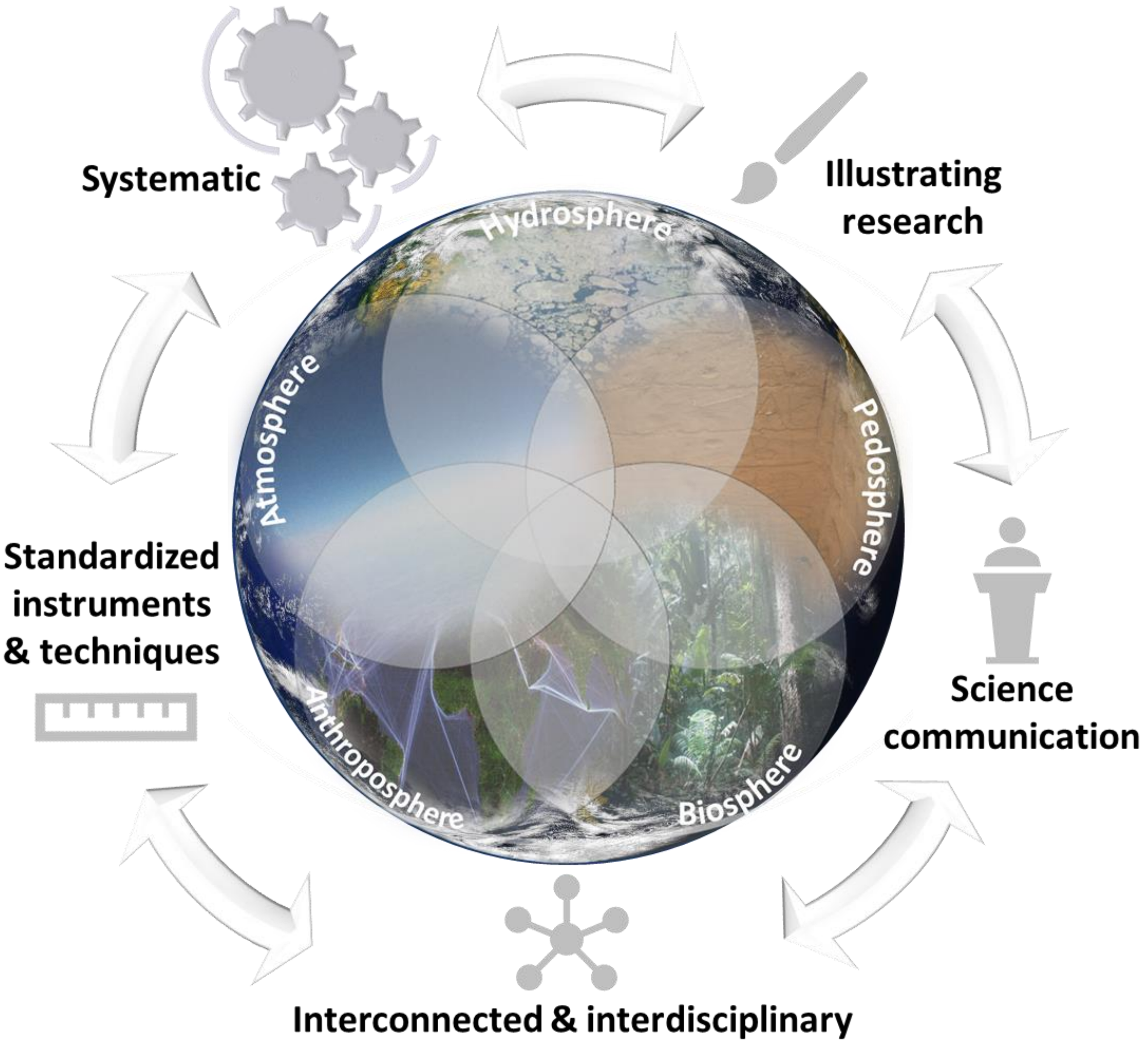

Figure 1 Humboldtian approach to science, integrating all 5 spheres of the Earth system (Hydro-, Atmos-, Bio-, Pedo- and Anthroposphere) using a holistic approach based on systematic measurements using standardized instruments and techniques to explore interconnected and interdisciplinary phenomena, and using outreach and artistic illustrations for research dissemination. The arrows depict holistic relationships between all five aspects, rather than linkages between pairs of aspects.

Humboldt’s emphasis on linking organisms and their environment may also be considered a progenitor of the Hutchinsonian niche concept. He explicitly incorporated information on elevation, temperature, electrical phenomena, soil cultivation, gravity, aspect, air humidity and pressure, light intensity, atmospheric composition, animals typically encountered and geology (von Humboldt & Bonpland, 1807, p. 146-155). Consequently, species distribution models – one of the most commonly used tools in attempts to understand and predict effects of climate change on biodiversity – are recognizably Humboldtian (Morueta-Holme & Svenning, 2018).

Humboldt's research on latitudinal diversity gradients was seminal. Although not the first to observe the gradient, he is considered to have been the first to propose not only a general hypothesis for it (climate) but also both a specific causal factor (winter temperature) and a mechanism (loss of fluidity) (Hawkins, 2001). In explicitly stating that fluidity is essential to life (see von Humboldt, Bohn, & Otté, 1850), Humboldt pinpointed the dynamic relationship between water and temperature that is crucial to life on Earth: biological processes such as photosynthesis and metabolism require water to be in liquid state, which is controlled by temperature. This is the foundation of the water–energy dynamics hypothesis for spatial patterns of species richness (O'Brien, 2006; O'Brien, Whittaker, & Field, 1998). The emphasis on water freezing is also foundational to the tropical (niche) conservatism hypothesis; that neither Wiens & Donoghue (2004) nor Wiens & Graham (2005) cited Humboldt is a good illustration of how Humboldt's influence remains strong but often not directly acknowledged. That Wiens and his colleagues have approached niche conservatism from an evolutionary standpoint also reminds us that the concept of evolution was only poorly developed during Humboldt's lifetime, resulting in his primary focus being macroecological rather than historical-biogeographical. His contributions to advancing macroecology and evolutionary biology, however, have been widely acknowledged, not least due to his direct inspiration and influence on Charles Darwin (Egerton, 1970).

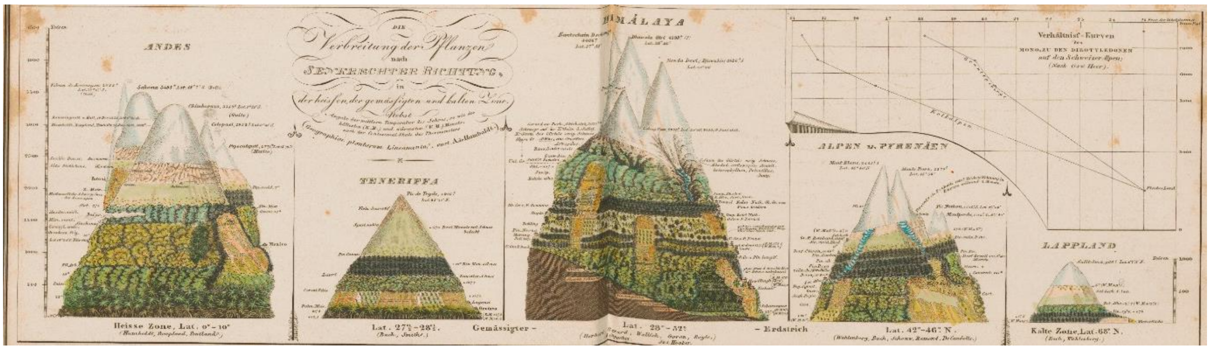

Figure 2 Physical Tableau of mountain ranges showing elevation bands in vegetation and characteristics of the physical environment in the Andes, Tenerife, the Himalayas, the Alps and Lappland (Berghaus, 1892).

With respect to elevational gradients, Humboldt's descriptions of plant distributions in mountains are fundamental to current approaches to modelling and predicting species migration in response to environmental change. Most directly linking to Humboldt, Morueta-Holme et al. (2015) resurveyed Mount Chimborazo 210 years after Humboldt and found strong upslope shifts in the distribution of vegetation and increases in maximum elevational limits of plants. Many have recently studied elevational patterns in plant and animal diversity (e.g. Alexander et al., 2018; Fadrique et al., 2018; Santos, Smith, Thorne, & Moritz, 2017; Steinbauer et al., 2018). However, few such studies incorporate changes in cultivation, geology, age of the terrain, etc., simultaneously; while Humboldt tended to consider elevational changes holistically, in biogeography today we tend to relate them primarily to climate.

Asking Humboldtian questions today

Can we still learn from Humboldt? The previous section illustrates (far from comprehensively) that Humboldt's influence on modern environmental science is strong, but there are key differences from Humboldtian science. We argue that his way of doing science is particularly relevant to current research needs and priorities for the 21st century. We do not claim to know

what Humboldt would do today, but several aspects of what he brought to science are highly relevant now. We first outline what we consider to be the most important of these aspects, and then expand on them in the subsections that follow, under headings defined by Figure 1.
Although polymaths have existed through time (e.g. Helmholtz), Humboldt was one of the last people to hold essentially all scientific knowledge in one head. As science advanced thereafter, by necessity scientists had to specialise, giving rise to different scientific disciplines. However, current global priorities – such as those embodied in the Sustainable Development Goals (Griggs et al., 2013) – require a reintegration of science. The interdisciplinarity so often called for must now be done by teams of researchers, rather than individuals possessing all the skills and knowledge. To ask Humboldtian questions, therefore, requires a level of interdisciplinarity rarely achieved today – a key challenge is to find ways for experts from different disciplines to communicate with each other so as to allow the sorts of connections that a single human brain can make, and to enable sufficient vision to stimulate major advances.
Much of the within-discipline scientific progress made since Humboldt has come from a reductionist approach, which contrasts with Humboldt's holism. We suggest that current global research priorities require emphasis on the interconnectedness of nature – all the 'spheres' of the Earth (Figure 1), including the human one. While lab-based research and manipulative experiments will surely remain important tools for establishing cause and effect, they are not sufficient to ask Humboldtian questions, which are more synoptic, holistic and concern the ever-changing real world. Importantly, scaling from the micro to the macro can be mathematically impossible (McGill, 2018; O'Neill, 1979). An integrative approach is needed, adopting a geographically oriented, synoptic view: the Humboldtian approach of systematically collecting large amounts of detailed measures, aimed at inferring causal relationships rather than merely finding patterns, is key. Combining high quality, systematic *in situ* measurement with remote sensing and DNA data is Humboldtian writ large, but even the synoptic, repeated geographical view provided by satellites is currently not as co-ordinated with other systematic measurements, nor as enabling of interdisciplinary science, as it could be. Following in Humboldt's footsteps would also require a renewed focus on inferring processes, rather than purely correlational patterns from these data sources – this main goal of biogeography is now more achievable than ever across large temporal and spatial scales (Pearse et al., 2018).
Macroecology, which has emerged and become prominent since 1989, is Humboldtian in its use of large datasets to infer underlying mathematical laws of nature. However, attempts to integrate (macro)ecology with earth science are still embryonic, especially at synoptic scales. Yet both ecosystem and geosystem services are key to addressing Sustainable Development Goals, and are strongly interconnected (Gray, 2018). An important focus in asking Humboldtian questions today should therefore be researching the links between biodiversity and geodiversity. For example, species distribution modelling has repeatedly been criticised as being overly simplistic and may benefit from a more Humboldtian approach of recognizing other interconnected factors likely to affect species distributions – including geodiversity (Bailey, Boyd, & Field, 2018; Hasui et al., 2017). Similarly, the degree to which human actions affect long-term biogeochemical cycles, mineralization processes and biodiversity patterns is highly relevant yet rarely evaluated simultaneously with comprehensive bio- and geodiversity assessments. (Aufdenkampe et al., 2011).
It is not sufficient to advance science; typically, public support, or at least trust, is needed if knowledge and evidence are to guide policy and practice. Humboldt's "Kosmos" was an international bestseller and he both popularized science and liaised directly with politicians such as Thomas Jefferson (Sachs, 2003). His concerns about human impact on the

environment led directly to the environmental movement (e.g. John Muir's ideas about conservation derived from Humboldt (Zimmerer, 2006b)). With the rise of social networks and growing mistrust of experts, the means to communicate and engage with people beyond science are very different today than in Humboldt's time, but the need to do so is even greater. Humboldt effectively used illustrative techniques for communicating science, and this is no less important today. He published paintings and worked with poets (e.g. Goethe) – such integration with the arts is an underutilized opportunity in modern science. A key aspect of Humboldt's approach to popularizing science was his belief that humans are enriched by scientific understanding; he was a great proponent of promoting *Naturphilosophie*, a 'romantic' appreciation of nature (Dettelbach, 1999). Thus, pure science was at the heart of his science communication.

Systematic sampling, standardized instruments and techniques

> *"We are all indebted to Alexander von Humboldt. Almost 200 years ago he described what he called elevational and latitudinal gradients in diversity that he thought were due to climate. He did not have the data to examine or test his ideas. So, instead, he devoted part of his life to promoting and building a global meteorological station network so that someday we would have them."* (O'Brien, 1998)

Much has improved since Humboldt's time. Nowadays we have (i) better fieldwork access (including to remote areas), (ii) new measurement technologies (e.g. remote sensing; environmental DNA), (iii) initiatives to harmonize (Garnier et al., 2017; Pérez-Harguindeguy et al., 2013) and collate *in situ* species distribution and trait measurements in global databases (e.g. Bruelheide et al., 2018; Gillespie, 2013; Harris, Jones, Osborn, & Lister, 2014; Iversen et al., 2018; Kattge et al., 2011; Madin et al., 2016), (iv) biogeography-specific numerical techniques (e.g. Blonder, Lamanna, Violle, & Enquist, 2014; Ogle et al., 2015; Schrodt et al., 2015), (v) reproducible computer code (Cooper & Hsing, 2017) and (vi) interoperable data guiding principles (Gries et al., 2018; Wilkinson et al., 2016). These developments promote integrated, Humboldtian assessment of multiple ecosystem properties simultaneously over large areas – though barriers remain, such as restricted access to data compilations and some of the structures and incentive systems within modern environmental science. However, despite this explosion in data standardization and analytics, and increasingly collaborative approaches, a recurring theme in discussions at scientific meetings is that we are still strongly data-limited in what we can do.

Thus, we have lots of data but often not the right sort, or not accessible. One reason is that large data compilations tend to be ad-hoc / post-hoc, rather than systematic and standardized; a more Humboldtian approach is needed. Some longstanding national and international initiatives have aimed to do so, including the National Ecological Observatory Network in the USA and the Biodiversity Exploratories in Germany. Fluxnet, an international network of gas flux towers which promotes well-coordinated measurements, frequent cross-calibration of instruments and sharing of data is another example of successful standardization of data collection and instrumentation. Yet, the usefulness of these initiatives could be greatly extended by more coordination between them. For example, although species records are available for over 20% of the Fluxnet sites, few have plant traits measured *in situ* (Musavi et al., 2015) and many permanent biodiversity sampling sites lack coordinated, standardized measurements of environmental data (but see Naeem & Bunker (2009) for TraitNET, an initiative aimed at linking plant trait with environmental data). This issue is largely due to a combination of funding restrictions, disparate aims of observatory networks and a continued lack of interdisciplinary groups working on setting up these networks.

Interdisciplinary and integrated approaches: linking geo- and biodiversity

All study of nature was broadly termed 'natural philosophy' until the 19th century, when modern disciplines with unique titles such as 'physics' and 'biology' developed. Humboldt was a polymath natural philosopher with expertise across science, and also a "cultural icon", proficient science communicator, diplomat and traveller (Shapin, 2006). However, he himself questioned the value of his interdisciplinary approach to science: "I was at fault to tackle from intellectual curiosity too great a variety of scientific interests" (Worster, 1998: 135). He has also been described as "a practitioner of disunified science and a man with no stable intellectual or political make-up" (Shapin, 2006). Yet the importance of interdisciplinary approaches to scientific questions has remained recognised (Daily & Ehrlich, 1999; Ignaciuk et al., 2012; Zimmerer, 2006a). Biogeographic research is inherently interdisciplinary, drawing on geography, evolution, palaeontology, ecology, biogeomorphology, geology, geomorphology, human geography and atmospheric sciences, amongst others. When studying biodiversity specifically, the importance of considering phylogenetic, taxonomic and functional aspects simultaneously, ideally accounting for differences according to their respective heritage, is increasingly recognised (Pauchard et al., 2018).

Taking the example of links between biodiversity and geodiversity: to establish why a landform, rock type or hydrological feature relates to either individual species' distributions or any aspect of biodiversity requires understanding of the abiotic properties surrounding that geofeature – for example, microclimate, pH, mineralogy how these properties change through time, and how they interact with biodiversity. Although such studies are starting to accumulate, the need for greater integration of biosphere, geosphere and hydrosphere persists (Antonelli et al., 2018; Badgley et al., 2017; Hoorn et al., 2010; Xing & Ree, 2017). Indeed, in her recent perspective, Renner (2016) pointed out the perils of ignoring geological history in biogeographic studies. She also found numerous cases where biogeographic studies mis-cited results, or used obsolete findings, from geological papers.

To avoid misuse of specialised data and approaches, scientific collaborations are typically needed to reliably and robustly research these intimate links between living and non-living nature (e.g. Hjort, Heikkinen, & Luoto, 2012; Räsänen et al., 2016; Tukiainen, Bailey, Field, Kangas, & Hjort, 2017). The gains in scope and expertise are counteracted by loss of unity of thought, so effective methods of combining wide-ranging expertise with clarity of thought should be pursued. Apart from supporting modern polymaths and well-balanced cross-disciplinary working groups, collective, in-depth development of integrative analytical methods that encourage interdisciplinary thinking will help – for example, logical trees (Platt, 1964), path analysis (Mitchell, 1992) and some of the thought processes involved in Bayesian approaches (Kulmala & Kuikka, 2012). Some of these analytical methods lend themselves to a Humboldtian approach of combining different scientific approaches, and different types of evidence, to investigate processes across scales of space and time.

Assessing the extent to which integrated approaches are used in biogeography is not straight-forward. Here, we attempt an indicative analysis by the use of path analysis/structural equation modelling in articles published in the Journal of Biogeography since 2003. These related statistical techniques allow (though are not always used for) testing of models in which chains or webs of direct and indirect causation are incorporated. Thus, they are appropriate for more integrated and holistic approaches to studying ecological systems than, for example, multiple regression (Mitchell, 1992). We recognize that there are other means of analysing natural patterns and phenomena in a holistic manner and that some limitations of path analysis reduce its usage (e.g. difficulty of modelling non-linear relationships); this analysis can nevertheless serve as an indication of the propensity for truly macroecological approaches *sensu* Humboldt. We used the following search terms: “Structural equation model*” OR “Path analy*” OR “Path diagram*”. After removing insignificant content (see Appendix for a full list), the most frequently used words within these articles were determined using the tm package (Feinerer & Hornik, 2018) in R version 3.4.0.

Of all papers published in the Journal of Biogeography between January 2003 and November 2018, 40 (~1%) include path diagrams and/or structural equation models. Within these 40 articles, which cover a range of organisms (Fig. 3), there is much more focus on species than the Humboldtian community (species is mentioned 4209 times compared to community (624 times)). Although environmental factors are considered in most studies, usually this refers predominately to climate (444 mentions). In contrast, aspects of geodiversity, such as soil (268), hydrology (21), geology (20), geomorphology (10) and landforms (7) are mentioned much less frequently, as are human-related words (e.g. anthropogenic, humanity: 67 times).

This exercise, combined with our own knowledge of the literature, suggests that even those studies using analytical techniques well suited to modelling interconnectedness tend to only model climate and/or soil, and not environment more widely.

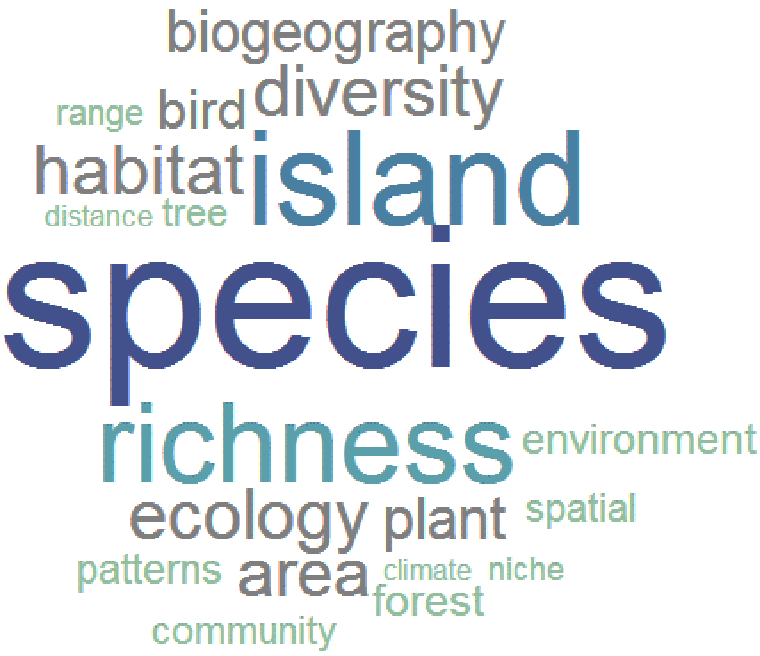

Figure 3 Words occurring at least 400 times in articles published between January 2003 and Nov 2018 in the Journal of Biogeography which discuss structural equation modelling and/or path models.

There is scope, therefore, for more Humboldtian thinking in biogeography, particularly with respect to Humboldt’s focus on the importance of considering unity: the connections among all natural and human phenomena (Buttimer, 2012). Humboldt wrote: "The principal impulse by which I was directed was the earnest endeavor to comprehend the phenomena of physical objects in their general connection and to represent nature as one great whole, moved and animated by internal forces” (Baron & Doherr, 2006). Throughout his work, he aimed to assess the environment in its totality, including various biota, humans (through commerce, culture, art and aesthetic considerations; Lubowski-Jahn (2011)), climate, soils and geology using contemporary as well as palaeo-evidence.

An important Humboldtian topic is the relationship between abiotic environmental heterogeneity and biodiversity. The general relationship is well established (Stein, Gerstner, & Kreft, 2014). However, heterogeneity metrics typically omit information about identity of the landscape, such as the geological setting and which landforms or hydrological features are present. Most are generalized digital elevation model (DEM)-based topographic parameters, such as range or variance in elevation and slope or topographic roughness. Biodiversity models can be improved, however, through explicit consideration of geofeatures (geomorphological landforms, geological types, hydrological features). This has been shown in analyses of both biodiversity and species' distributions using both expertly mapped geofeatures (Hjort et al., 2012) and semi-automated geomorphometric techniques across spatial scales (Bailey et al., 2018, 2017).

Although progress has been made in explicitly linking living and non-living nature using geodiversity, much remains to be done to integrate geodiversity into biogeography, conceptually and empirically – towards more fully realising Humboldt's vision, using twenty-first century databases, techniques and theories. For example: (i) At which spatio-temporal scales and for which taxa are the various geofeatures most relevant? (ii) How should we measure geodiversity? A study's theoretical focus, spatial scale, focal taxa and geographic setting directly affect how geofeatures are best quantified to capture the abiotic landscape. For example, in a study of plant biodiversity at the landscape scale, geological variety, geomorphological features and presence of waterbodies are relevant (Bailey et al., 2018; Hjort et al., 2012). However, for less mobile species, larger geofeatures such as valleys and mountain ridges may be more important. Shortage of geofeature field data means that broader-scale research may require modelled geodiversity (Tukiainen et al., 2017) or geomorphometric techniques (Bailey et al., 2017), which have only recently been applied to bio-geodiversity studies.

The benefits of linking geodiversity and biodiversity extend to practical conservation (Lawler et al., 2015) and services benefitting humans. Although the concept of ecosystem services is well advanced (Mace, Norris, & Fitter, 2012), geodiversity has been largely neglected. Few studies explicitly assess the importance of geofeatures for the provisioning of ecosystem services by supporting biodiversity (e.g. Alahuhta et al., 2018). Even fewer discuss direct benefits of geofeatures – geosystem services (Gray, 2018; van Ree & van Beukering, 2016). Indeed, some discussions on ecosystem services actively exclude consideration of geosciences (Gray, 2018).

Illustrating research and science communication

Communicating his scientific findings and approaches to the many was at the heart of Humboldt's approach. Indeed, his seminal work "Kosmos" was specifically aimed at enthusing the public about the "Liebe zum Naturstudium" (love of studying nature) (von Humboldt, 1845, p. XV). Today's scientists have more ways than ever to communicate research findings and ideas (e.g. blogs, social media, YouTube) and to produce beautiful illustrations (e.g. using R packages and/or other open access software). However, there are dangers to science and progress. 'Misinformation' was Dictionary.com's 2018 word of the year. Science communication and effective illustration of findings may be more important now than ever, not only for enthusing non-scientists – including politicians – and imbuing passion for the natural world, but also for ensuring accurate information is readily available to those who seek it.

The role of science communication is growing (Burns, O'Connor, & Stocklmayer, 2003). For example, Twitter is an effective tool for science communication (Côté & Darling, 2018) and various dedicated events and broadcasts help scientists communicate with interested members of the public. Scientists can also benefit from popular media and public figures such as Sir David Attenborough, whose documentaries move millions towards positive environmental action. Other visual media, such as YouTube, have been successfully used for outreach across the natural sciences (e.g. “Minute Physics” and “Minute Earth” which were initiated by the son of a University of Minnesota plant science professor or “The Brain Scoop” by the Chicago Field Museum (Bik et al., 2015)).

Humboldt excelled at producing scientific illustrations so good that they still adorn the walls of homes and universities. While few illustrative pieces in scientific papers today would look so attractive above a mantlepiece, separate accompanying illustrative pieces designed for communication to non-scientists are growing (e.g. NASA’s scientific visualization studio (https://svs.gsfc.nasa.gov/)). In social media, the illustrations that tend to get attention are eye-catching (e.g. infographics) and can be animated (e.g. GIFs). With the rise in ‘graphical abstracts’ and conference presentations in prose and cartoons, such integration of art and science is set to become more common. For example, the European Geophysical Union documented its annual assembly (the largest European scientific meeting) through art in 2018, for the first time.

If our science is to lead to meaningful progress, we need to enthuse the public and policy-makers about the science itself, as Humboldt did. Following erosion of trust in science by wide parts of the public, as exemplified by the “Climategate” (non-)scandal in 2009 (Tollefson, 2010), this is more important now than ever.

Extensions of Humboldtian science

In Humboldt’s own words: “Such is the spirit of the method by which I persuade myself that it will someday be possible to connect, by empirical and numerically expressed laws, vast series of apparently isolated facts, and to reveal their mutual dependence” (Zeller, 2006). Here we outline how Humboldtian science might be extended in the light of major advances in understanding since his time. Today, we understand nature as much more dynamic than in the world-view of Humboldt, so a sensible extension of his approach is to systematically collect accurately measured data on ecological communities repeatedly through time, along with associated changes in the variables likely to affect those communities.

Recent advances in remote sensing technology and data storage offer unprecedented opportunities to assess change in both living and non-living nature. For example, remote sensing has been used to assess changes in land cover (Amici, Marcantonio, La Porta, & Rocchini, 2017), species abundance (Paganini, Leidner, Geller, Turner, & Wegmann, 2016), functional traits (Lausch et al., 2016; van Cleemput, Vanierschot, Fernández-Castilla, Honnay, & Somers, 2018) and even phylogenetic composition of plant communities (Schweiger et al., 2018). It is increasingly used for abiotic aspects, such as soil (Rogge et al., 2018) and hydrological features (Bierkens et al., 2015). Analysis of environmental DNA (eDNA) is another now-established technique enabling us to follow Humboldt’s vision of holistic, integrated assessments across many geographic areas. It is a cost-effective and comprehensive way to assess regional biodiversity of terrestrial and aquatic systems (Harper et al., 2018). Still, many aspects of biological and abiotic factors remain inaccessible to remote or genetic assessments, and we will continue to rely on *in situ* measurements. Furthermore, improvements are still needed in calibrating and standardizing data from both remote sensing and eDNA (e.g. Hansen, Bekkevold, Clausen, & Nielsen, 2018), to improve comparison of datasets across space and time.

Another barrier to realizing Humboldt’s vision of a global database of standardized measurements is that many existing databases for *in situ* organismal or environmental data cannot currently support submission of repeat surveys (e.g. TRY (plant traits; Kattge et al., 2011), sPlot (plant communities; Bruelheide et al., 2018), WoSIS (soils; Batjes et al., 2017)). Recent initiatives to promote analysis of change through time are helpful (e.g. BioTIME (Dornelas et al., 2018), ForestRePlot (Verheyen et al., 2017)), Andean forest plot database (Fadrique et al., 2018)). However, challenges remain for long-term ecological networks, including securing funding over long time periods and reducing the impact on the environment (and thus our data) caused by repeated *in situ* sampling (Sayer & Silvertown, 2018).

On the other hand, the large increase in palaeo databases provides information on long-term changes in assemblages, allowing evolutionary inference and deep-time perspectives. This is particularly powerful when integrated with information on long-term geological change (Renner, 2016; Santucci, 2005), rather than just climate as is frequently the case (Nogués-Bravo et al., 2018).

Arguably, the geosciences are lagging behind ecological databases with respect to both easy access to internationally standardized data and databases of change. For example, conflicting international data classifications for water resources (Scanlon, Ruddell, Reed, Tidwell, & Siebert, 2017) and soils (Oudwater & Martin, 2003), as well as widespread inaccessibility of country-level high-resolution geology data, make international comparative studies extremely difficult. Remote sensing can alleviate some of these issues (Hjort & Luoto, 2012), especially with respect to topographic variables (Amatulli et al., 2018).

Overall, we remain far from a Humboldtian database of databases that integrates *in situ* and remotely sensed environmental and ecological data in space and time. This is a major challenge for the coming decade.

Conclusion

Humboldt noted a tendency for specialism in his contemporaries, a trend that has deepened and only been challenged relatively recently, with increased recognition of the importance of inter- or trans-disciplinarity. Despite this recognition, and demands by funding bodies for interdisciplinary work, calls for a more holistic approach and for truly interdisciplinary research continue (Gray, 2018; Opdam, Luque, Nassauer, Verburg, & Wu, 2018). To improve management and conservation of the world's flora and fauna, and preserve essential ecosystem services they provide, we need an integrated approach considering both biotic and abiotic nature – both biodiversity and geodiversity. Approaching Humboldt's 250th birthday, we have the capability to achieve integrated global observatory networks that he could only dream of, enabling a new phase of Humboldtian science. In times of rapid environmental change, gaining holistic, integrative insights into biodiversity–environment relationships is vital. Successfully converting such insights into policy and practice is more likely if we also follow Humboldt in striving to convey a "love of natural philosophy" in "all the peoples of the earth" by "vividly describing" the "awe-inspiring unity" of Nature (von Humboldt, 1845; von Humboldt & Bonpland, 1807)**.**

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Biosketch

Franziska Schrodt is a senior research fellow at the University of Nottingham. She works on the application of remote sensing, machine learning and non-linear statistical tools to study biogeochemical patterns. She is especially interested in correlations between biodiversity and geodiversity as well as associated implications for ecosystem structure, functioning and services.

Author contributions: F.S. conceived the idea and F.S., R.F. and M. J. S. designed the study; F.S. performed the analysis and produced the figures; F.S. and R.F. wrote the paper with substantial contributions from M.J.S. and J. J. B.

Appendix

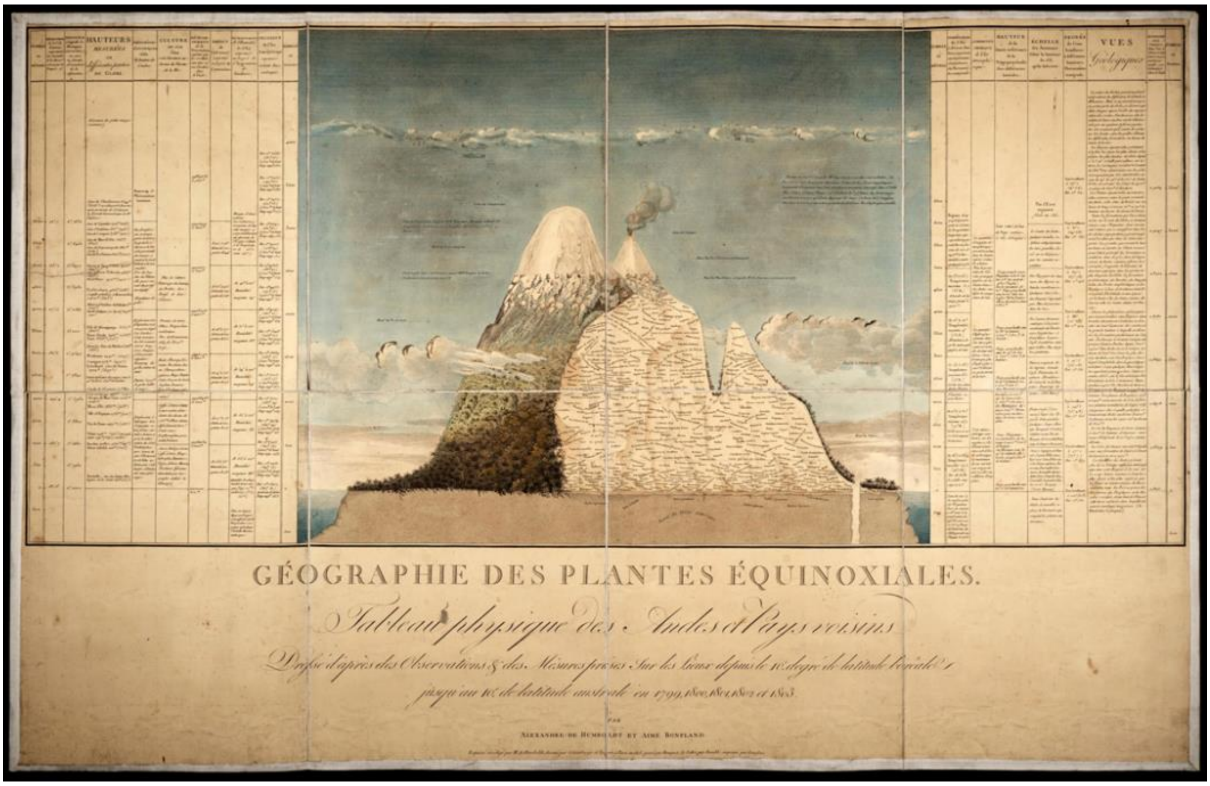

Figure S1 Humboldt and Bonplant's Physical Tableau of Equatorial Regions. Note the species names and plant communities depicted on the right-hand side of the mountain as well as environmental *variables measured along the slopes in the left and right-hand panels (von Humboldt & Bonpland, [1807] 2009). Digital image courtesy of the Peter H. Raven Library/Missouri Botanical Garden.*

Table S1. Published works supporting the importance of different aspects of a "Humboldtian approach" to science. The second column refers to articles showing Humboldt's support for the respective approach; the third column refers to articles drawing attention to a need to take up the respective aspect of a Humboldtian approach

Aspect	Humboldt references	Current references
Systematic	(Buttimer, 2001; Morueta-Holme & Svenning, 2018; Zimmerer, 2006a)	(Gray, Gordon, & Brown, 2013)
Interdisciplinarity	(Baron & Doherr, 2006; Jackson, 2009; Lubowski-Jahn, 2011; Zeller, 2006)	(Bracken & Oughton, 2009; Daily & Ehrlich, 1999; Ignaciuk et al., 2012; Ladle, Malhado, Correia, dos Santos, & Santos, 2015; Rhoten, 2003)
Illustrating research	(Anthony, 2018; Debarbieux, 2012)	Importance of: (Fox & Hendler, 2011; McCosker & Wilken, 2014; McInerny et al., 2014; Morseletto, 2017) Tools: (Chang, Cheng, Allaire, Xie, & McPherson, 2018; Kelleher & Wagener, 2011; Shneiderman, 1996; Wickham, 2016)
Outreach, Science communication	(Morueta-Holme & Svenning, 2018; von Humboldt, 1804, P. 76)	(Lesen, Rogan, & Blum, 2016; Saunders et al., 2017)
Standardized instruments & techniques	(Buttimer, 2001; Doherr & Jankowski, 2018; Lotko, 2017)	(Batjes et al., 2017; Berger, 1997; Cord et al., 2017; Garnier et al., 2017; Meyer, Koch, & Weisser, 2015; Pérez-Harguindeguy et al., 2013; Wilkinson et al., 2016)

List of "stopwords" removed in the text mining exercise using the tm package in R:
"journal", "using", "data", "variables", "results", "also", "figure", "mean", "may", "maybe", "significant", "study", "used", "fig", "specific", "number", "relative", "relate", "table", "model", "analysis", "effect", "small", "relationship", "two", "see", "ltd", "across", "within", "university", "among", "structure", "path", "total", "can", "sites", "relationships", "significant", "high", "variation", "effects", "models", "size", "different", "new", "values", "found", "publishing", "blackwell", "one", "factors", "analyses", "however", "appendix", "based", "studies", "large", "direct", "three"