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

3 **Running title:** Biogeography challenges and opportunities
4

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20

21 **Abstract**

22 Alexander von Humboldt was arguably the most influential scientist of his day. Although his
23 fame has since lessened relative to some of his contemporaries, we argue that his influence
24 remains strong – mainly because his approach to science inspired others and was
25 instrumental in furthering other scientific disciplines (such as evolution, through Darwin, and
26 conservation science, through Muir) – and that he changed the way that large areas of science
27 are done and communicated. Indeed, he has been called the father of a range of fields,
28 including environmental science, earth system science, plant geography, ecology and
29 conservation. His approach was characterized by making connections between non-living and
30 living nature (including humans), based on interdisciplinary thinking and informed by large
31 amounts of data from systematic, accurate measurements in a geographical framework.
32 Although his approach largely lacked an evolutionary perspective, he was fundamental to
33 creating the circumstances for Darwin and Wallace to advance evolutionary science. He
34 devoted considerable effort to illustrating, communicating and popularising science, centred
35 on the excitement of pure science. In biogeography, his influence remains strong, including in
36 relating climate to species distributions (e.g. biomes and latitudinal and elevational gradients)
37 and use of remote sensing and species distribution modelling in macroecology. However,
38 some key aspects of his approach have faded, particularly as science fragmented into specific
39 disciplines and became more reductionist. We argue that asking questions in a more
40 Humboldtian way is important for addressing current global challenges. This is well
41 exemplified by researching links between geodiversity and biodiversity. Progress on this can
42 be made by (i) systematic data collection to improve our knowledge of biodiversity and
43 geodiversity around the world; (ii) improving our understanding of the linkages between
44 biodiversity and geodiversity; and (iii) developing our understanding of the interactions of
45 geological, biological, ecological, environmental and evolutionary processes in biogeography.
46

47 **Keywords:** Alexander von Humboldt, biogeography, geodiversity, biodiversity, outreach,
48 science communication, integrated perspectives, earth system science
49

50 **Introduction**

51 During their meeting in 1804, Napoleon Bonaparte famously quipped to the young Alexander
52 von Humboldt: “You collect flowers? So does my wife” (Osterhammel, 1999). Yet Humboldt
53 (1769-1859) was not only a trained botanist, he was a true polymath scholar with a career in
54 the mining industry, expertise in geology, astronomy, anatomy, biology, languages and
55 anthropology, and great skills in the maintenance and invention of scientific instruments
56 (Buttimer, 2001). Humboldt has been pronounced the father/godfather of many disciplines,
57 including modern geography (Egerton, 2009), plant geography (Nicolson, 2013), rock coating
58 research (Dorn, Krinsley, & Dirro, 2011) and earth system science (Clifford & Richards, 2005).
59 Arguably, he was one of the first scientists to empirically observe and describe intimate links
60 between vegetation and abiotic environmental conditions over large spatial scales and in
61 different ecosystems (von Humboldt & Bonpland, 1807) and, consequently, large-scale
62 gradients in vegetation and environmental conditions. Observing the highly erosive practices
63 of monoculture, overfishing and overhunting in South America, perhaps most remarkably for
64 an 18th century scholar, he also recognized and warned about the degree to which humans
65 could act as agents of change and destruction of biodiversity (Buttimer, 2001; Egerton, 2009).
66 Humboldt recognised the need not only to perform rigorous research but also to popularize
67 science, although this only came to him later, after his travels in South America. He “did not
68 think at the time that these jotted-down notes would form the basis of a work offered to the
69 public” but after his return “realized that even scientific men, after presenting their researches,
70 feel that they have not satisfied their public if they do not also write up their journal” (Wilson,
71 1995). Undoubtedly, together with his image as an adventurous young polymath with a keen
72 sense of humour and engaging writing and oratory skills, this helped his popularity and
73 enhanced his scientific influence. Thus, he represents an early example of the importance of
74 science communication and potentially wide-ranging influence of outreach.

75 Yet, Humboldt is not without controversies. In the public sphere, he was appropriated as a
76 figurehead by such diverse political movements and geographical locations as Nazi Germany
77 and many Latin American countries, including Mexico, Argentina and Colombia (Rupke,
78 2008). In the natural sciences, Humboldt’s direct contributions have been questioned. Some
79 have argued that he collected data “without developing a major theory” (Rillig et al., 2015) or
80 publishing a truly ground-breaking piece of work such as Darwin’s “Origin of Species”
81 (Osterhammel, 1999). Even his famous botanical map (von Humboldt & Bonpland, 1807) was
82 preceded by earlier, similar biogeographical maps (e.g. by Giraud-Soulavie, Ebach, & Goujet,
83 2006). Georg Forster (1754-1794) was described by Humboldt himself as the “parent of a
84 grand progeny of scientific travellers” and “the first to describe with charm the varying stages
85 of vegetation, the climatic conditions, the nutrients in relation to the customs of people in
86 different localities” (Wilson, 1995).

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

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

98 In his time, Humboldt was highly influential (Baron & Doherr, 2006; Buttimer, 2001; Jackson,
99 2009). Indeed, while few theories or scientific processes bear his name, more species, both
100 scientific (e.g. Humboldt penguin (*Spheniscus humboldti*)) and common names (e.g.
101 Humboldt squid (*Dosidicus gigas*)) and minerals, places or natural features (e.g. Humboldt
102 current, Humboldt Glacier and a sea on the moon) are named after him than any other scientist
103 (Wulf, 2015). His influence stems more from his approach to science than from the specific
104 advances he made, and arguably this influence was, and remains, even greater than that of
105 other prominent figures such as Darwin and Wallace.

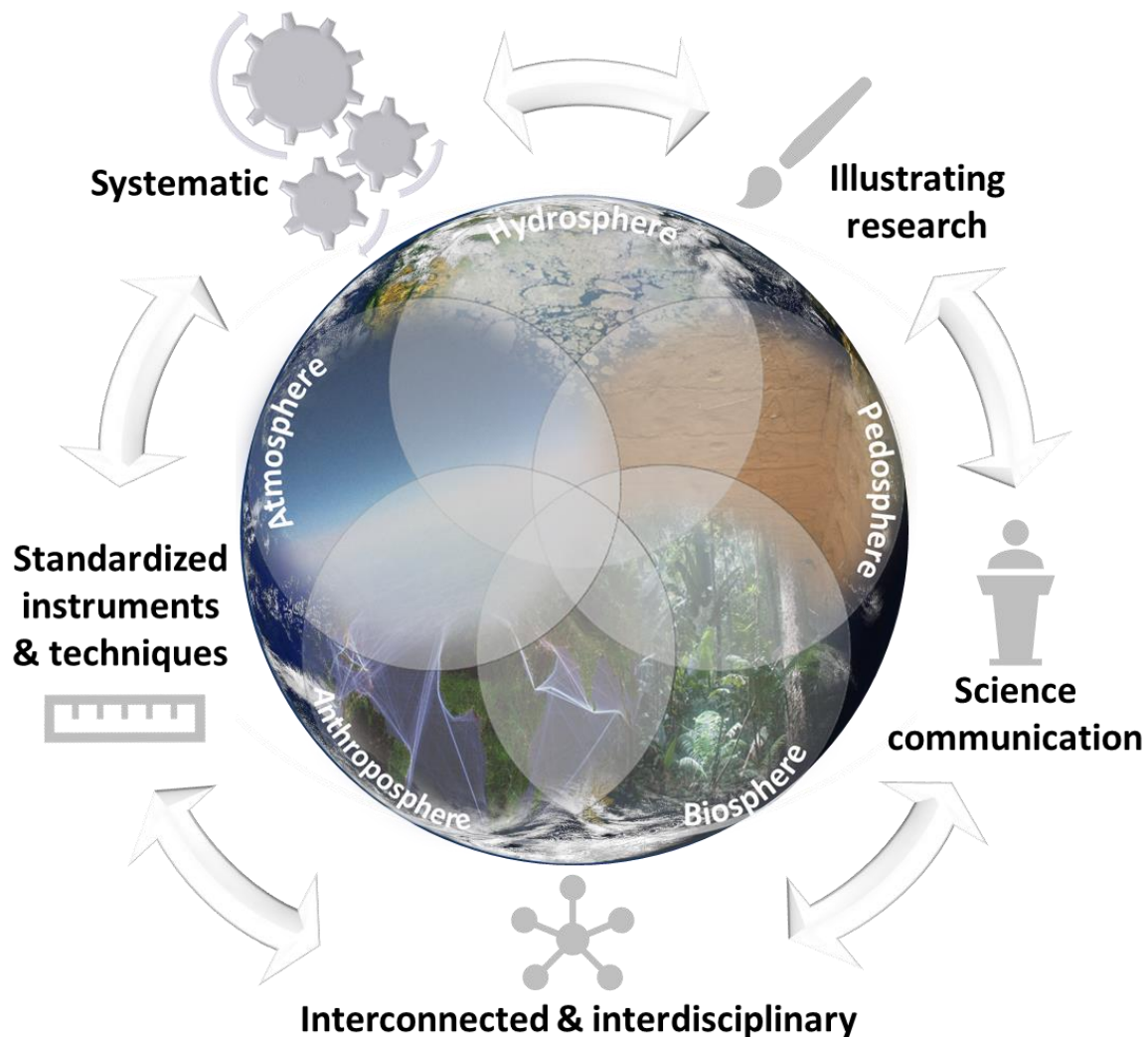
106 Whether we may still learn from Humboldt’s approach to science is rarely considered (but see
107 Morueta-Holme & Svenning, 2018). Here we aim to highlight key aspects of Humboldtian
108 science, primarily from a macroecologist’s view (focusing on those aspects most relevant to
109 biogeography and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

114 **Humboldtian science and its influence on biogeography today**

115 We do not attempt to be comprehensive; much has been written about what constitutes
116 Humboldtian Science and how it differed from what came before (e.g. Bowen, 1970; Buttimer,
117 2001; Jackson, 2009; Morueta-Holme & Svenning, 2018; Nicolson, 1987; Zimmerer, 2006a).
118 Instead, we distil Humboldt’s approach into five key aspects or pillars (Figure 1, Table S1) that
119 are highly relevant to biogeography (especially ecological biogeography and macroecology),
120 and that we consider key to researching the links between geodiversity and biodiversity. Figure
121 1 illustrates these five pillars in the context of modern environmental science. It emphasizes
122 the holistic, interconnected nature of both the subject matter and how it is researched and
123 disseminated. For each pillar of Humboldtian science, Table S1 identifies scientific papers that
124 make the link with Humboldt, and that identify a need for that aspect to be adopted more in
125 today’s science.

126 Humboldt made an extraordinary quantity and range of detailed measurements, which he used
127 to infer underlying mathematical laws of nature – a macroecological approach, in modern
128 parlance. His approach was also strongly geographical, with emphasis on maps, isolines and
129 other geographical illustrations such as his famous “Physical Tableau of Equatorial Regions”
130 (Figure S1). Humboldt (and colleagues) recorded distributional patterns of vegetation in
131 mountainous areas of the world, particularly in the Andes, Himalayas, Alps, Pyrenees and
132 Tenerife (Figure 2). These early plant-geographical drawings describe distinct vegetation
133 bands along elevational gradients. This emphasis on the connections between living
134 organisms and non-living nature can be linked to the concept of biomes – Humboldt defined
135 global vegetation zones, in sharp contrast to the Linnaean-style taxonomic classification and
136 cataloguing that was dominant in science in his day. We may draw similar connections to the
137 emergence of phytosociology and the notions of deterministic plant associations and
138 Clementsian climax communities (where a plant community is considered analogous to an
139 organism, in which species associations deliver the functions of organs, and an end-point is
140 reached that is determined by climate (Eliot, 2007)). Importantly, however, Humboldt and his

141 colleagues recorded each species as having its own place along the elevational gradient
 142 (Figure S1), in a rather individualistic way. This is analogous to, and may be regarded as a
 143 precursor for, a more Gleasonian view (where the plants present in a location are an
 144 assemblage of species that interact with their environment individually (Crawley et al.,
 145 2002)).



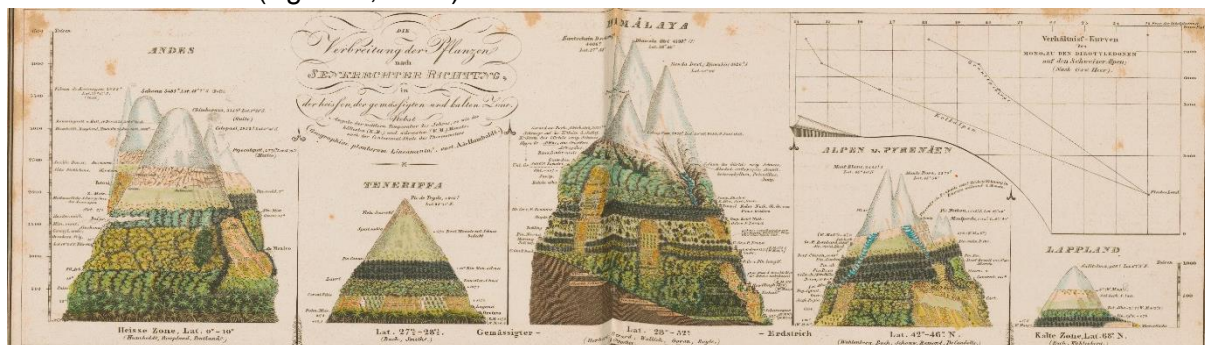
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147 *Figure 1 Humboldtian approach to science, integrating all 5 spheres of the Earth system (Hydro-,*
 148 *Atmos-, Bio-, Pedo- and Anthroposphere) using a holistic approach based on systematic*
 149 *measurements using standardized instruments and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

153

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

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



179
 180 *Figure 2 Physical Tableau of mountain ranges showing elevation bands in vegetation and*
 181 *characteristics of the physical environment in the Andes, Tenerife, the Himalayas, the Alps and*
 182 *Lappland (Berghaus, 1892).*

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

194 **Asking Humboldtian questions today**

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

199 what Humboldt would do today, but several aspects of what he brought to science are highly
200 relevant now. We first outline what we consider to be the most important of these aspects, and
201 then expand on them in the subsections that follow, under headings defined by Figure 1.

202 Although polymaths have existed through time (e.g. Helmholtz), Humboldt was one of the last
203 people to hold essentially all scientific knowledge in one head. As science advanced
204 thereafter, by necessity scientists had to specialise, giving rise to different scientific disciplines.
205 However, current global priorities – such as those embodied in the Sustainable Development
206 Goals (Griggs et al., 2013) – require a reintegration of science. The interdisciplinarity so often
207 called for must now be done by teams of researchers, rather than individuals possessing all
208 the skills and knowledge. To ask Humboldtian questions, therefore, requires a level of
209 interdisciplinarity rarely achieved today – a key challenge is to find ways for experts from
210 different disciplines to communicate with each other so as to allow the sorts of connections
211 that a single human brain can make, and to enable sufficient vision to stimulate major
212 advances.

213 Much of the within-discipline scientific progress made since Humboldt has come from a
214 reductionist approach, which contrasts with Humboldt's holism. We suggest that current global
215 research priorities require emphasis on the interconnectedness of nature – all the 'spheres' of
216 the Earth (Figure 1), including the human one. While lab-based research and manipulative
217 experiments will surely remain important tools for establishing cause and effect, they are not
218 sufficient to ask Humboldtian questions, which are more synoptic, holistic and concern the
219 ever-changing real world. Importantly, scaling from the micro to the macro can be
220 mathematically impossible (McGill, 2018; O'Neill, 1979). An integrative approach is needed,
221 adopting a geographically oriented, synoptic view: the Humboldtian approach of systematically
222 collecting large amounts of detailed measures, aimed at inferring causal relationships rather
223 than merely finding patterns, is key. Combining high quality, systematic *in situ* measurement
224 with remote sensing and DNA data is Humboldtian writ large, but even the synoptic, repeated
225 geographical view provided by satellites is currently not as co-ordinated with other systematic
226 measurements, nor as enabling of interdisciplinary science, as it could be. Following in
227 Humboldt's footsteps would also require a renewed focus on inferring processes, rather than
228 purely correlational patterns from these data sources – this main goal of biogeography is now
229 more achievable than ever across large temporal and spatial scales (Pearse et al., 2018).

230 Macroecology, which has emerged and become prominent since 1989, is Humboldtian in its
231 use of large datasets to infer underlying mathematical laws of nature. However, attempts to
232 integrate (macro)ecology with earth science are still embryonic, especially at synoptic scales.
233 Yet both ecosystem and geosystem services are key to addressing Sustainable Development
234 Goals, and are strongly interconnected (Gray, 2018). An important focus in asking
235 Humboldtian questions today should therefore be researching the links between biodiversity
236 and geodiversity. For example, species distribution modelling has repeatedly been criticised
237 as being overly simplistic and may benefit from a more Humboldtian approach of recognizing
238 other interconnected factors likely to affect species distributions – including geodiversity
239 (Bailey, Boyd, & Field, 2018; Hasui et al., 2017). Similarly, the degree to which human actions
240 affect long-term biogeochemical cycles, mineralization processes and biodiversity patterns is
241 highly relevant yet rarely evaluated simultaneously with comprehensive bio- and geodiversity
242 assessments. (Aufdenkampe et al., 2011).

243 It is not sufficient to advance science; typically, public support, or at least trust, is needed if
244 knowledge and evidence are to guide policy and practice. Humboldt's "Kosmos" was an
245 international bestseller and he both popularized science and liaised directly with politicians
246 such as Thomas Jefferson (Sachs, 2003). His concerns about human impact on the

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

258 *Systematic sampling, standardized instruments and techniques*

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

264 Much has improved since Humboldt’s time. Nowadays we have (i) better fieldwork access
265 (including to remote areas), (ii) new measurement technologies (e.g. remote sensing;
266 environmental DNA), (iii) initiatives to harmonize (Garnier et al., 2017; Pérez-Harguindeguy et
267 al., 2013) and collate *in situ* species distribution and trait measurements in global databases
268 (e.g. Bruelheide et al., 2018; Gillespie, 2013; Harris, Jones, Osborn, & Lister, 2014; Iversen et
269 al., 2018; Kattge et al., 2011; Madin et al., 2016), (iv) biogeography-specific numerical
270 techniques (e.g. Blonder, Lamanna, Violle, & Enquist, 2014; Ogle et al., 2015; Schrodte et al.,
271 2015), (v) reproducible computer code (Cooper & Hsing, 2017) and (vi) interoperable data
272 guiding principles (Gries et al., 2018; Wilkinson et al., 2016). These developments promote
273 integrated, Humboldtian assessment of multiple ecosystem properties simultaneously over
274 large areas – though barriers remain, such as restricted access to data compilations and some
275 of the structures and incentive systems within modern environmental science. However,
276 despite this explosion in data standardization and analytics, and increasingly collaborative
277 approaches, a recurring theme in discussions at scientific meetings is that we are still strongly
278 data-limited in what we can do.

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

292 combination of funding restrictions, disparate aims of observatory networks and a continued
293 lack of interdisciplinary groups working on setting up these networks.

294 *Interdisciplinary and integrated approaches: linking geo- and biodiversity*

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

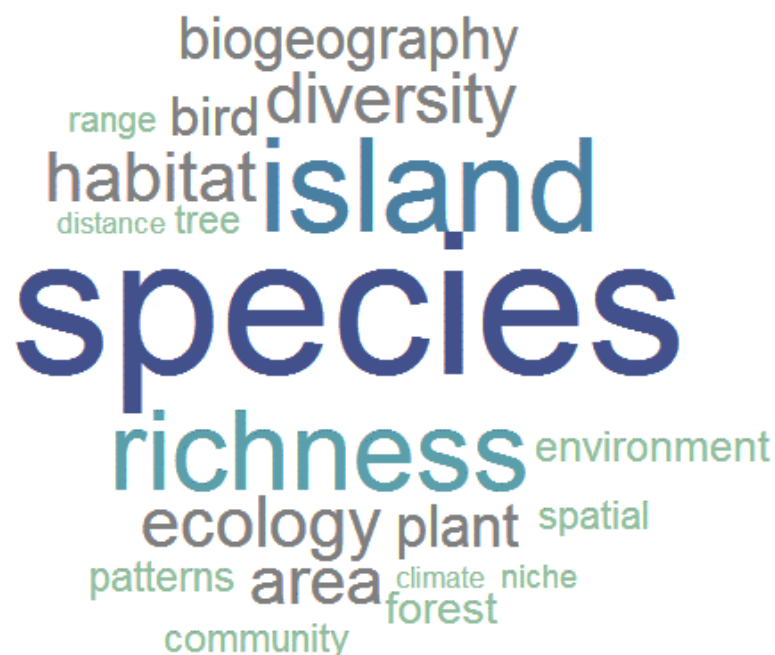
310 Taking the example of links between biodiversity and geodiversity: to establish why a
311 landform, rock type or hydrological feature relates to either individual species' distributions or
312 any aspect of biodiversity requires understanding of the abiotic properties surrounding that
313 geofeature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

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

332 Assessing the extent to which integrated approaches are used in biogeography is not straight-
333 forward. Here, we attempt an indicative analysis by the use of path analysis/structural equation
334 modelling in articles published in the Journal of Biogeography since 2003. These related
335 statistical techniques allow (though are not always used for) testing of models in which chains
336 or webs of direct and indirect causation are incorporated. Thus, they are appropriate for more
337 integrated and holistic approaches to studying ecological systems than, for example, multiple
338 regression (Mitchell, 1992). We recognize that there are other means of analysing natural

339 patterns and phenomena in a holistic manner and that some limitations of path analysis reduce
 340 its usage (e.g. difficulty of modelling non-linear relationships); this analysis can nevertheless
 341 serve as an indication of the propensity for truly macroecological approaches *sensu* Humboldt.
 342 We used the following search terms: “Structural equation model*” OR “Path analy*” OR “Path
 343 diagram*”. After removing insignificant content (see Appendix for a full list), the most frequently
 344 used words within these articles were determined using the tm package (Feinerer & Hornik,
 345 2018) in R version 3.4.0.

346 Of all papers published in the Journal of Biogeography between January 2003 and November
 347 2018, 40 (~1%) include path diagrams and/or structural equation models. Within these 40
 348 articles, which cover a range of organisms (Fig. 3), there is much more focus on species than
 349 the Humboldtian community (species is mentioned 4209 times compared to community (624
 350 times)). Although environmental factors are considered in most studies, usually this refers
 351 predominately to climate (444 mentions). In contrast, aspects of geodiversity, such as soil
 352 (268), hydrology (21), geology (20), geomorphology (10) and landforms (7) are mentioned
 353 much less frequently, as are human-related words (e.g. anthropogenic, humanity: 67 times).
 354 This exercise, combined with our own knowledge of the literature, suggests that even those
 355 studies using analytical techniques well suited to modelling interconnectedness tend to only
 356 model climate and/or soil, and not environment more widely.
 357



358

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

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

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

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

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

403 *Illustrating research and science communication*

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

414 The role of science communication is growing (Burns, O'Connor, & Stocklmayer, 2003). For
415 example, Twitter is an effective tool for science communication (Côté & Darling, 2018) and
416 various dedicated events and broadcasts help scientists communicate with interested

417 members of the public. Scientists can also benefit from popular media and public figures such
418 as Sir David Attenborough, whose documentaries move millions towards positive
419 environmental action. Other visual media, such as YouTube, have been successfully used for
420 outreach across the natural sciences (e.g. “Minute Physics” and “Minute Earth” which were
421 initiated by the son of a University of Minnesota plant science professor or “The Brain Scoop”
422 by the Chicago Field Museum (Bik et al., 2015)).

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

433 If our science is to lead to meaningful progress, we need to enthuse the public and policy-
434 makers about the science itself, as Humboldt did. Following erosion of trust in science by wide
435 parts of the public, as exemplified by the “Climategate” (non-)scandal in 2009 (Tollefson,
436 2010), this is more important now than ever.

437 **Extensions of Humboldtian science**

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

446 Recent advances in remote sensing technology and data storage offer unprecedented
447 opportunities to assess change in both living and non-living nature. For example, remote
448 sensing has been used to assess changes in land cover (Amici, Marcantonio, La Porta, &
449 Rocchini, 2017), species abundance (Paganini, Leidner, Geller, Turner, & Wegmann, 2016),
450 functional traits (Lausch et al., 2016; van Cleemput, Vanierschot, Fernández-Castilla, Honnay,
451 & Somers, 2018) and even phylogenetic composition of plant communities (Schweiger et al.,
452 2018). It is increasingly used for abiotic aspects, such as soil (Rogge et al., 2018) and
453 hydrological features (Bierkens et al., 2015). Analysis of environmental DNA (eDNA) is
454 another now-established technique enabling us to follow Humboldt’s vision of holistic,
455 integrated assessments across many geographic areas. It is a cost-effective and
456 comprehensive way to assess regional biodiversity of terrestrial and aquatic systems (Harper
457 et al., 2018). Still, many aspects of biological and abiotic factors remain inaccessible to remote
458 or genetic assessments, and we will continue to rely on *in situ* measurements. Furthermore,
459 improvements are still needed in calibrating and standardizing data from both remote sensing
460 and eDNA (e.g. Hansen, Bekkevold, Clausen, & Nielsen, 2018), to improve comparison of
461 datasets across space and time.

462 Another barrier to realizing Humboldt’s vision of a global database of standardized
463 measurements is that many existing databases for *in situ* organismal or environmental data

464 cannot currently support submission of repeat surveys (e.g. TRY (plant traits; Kattge et al.,
465 2011), sPlot (plant communities; Bruelheide et al., 2018), WoSIS (soils; Batjes et al., 2017)).
466 Recent initiatives to promote analysis of change through time are helpful (e.g. BioTIME
467 (Dornelas et al., 2018), ForestRePlot (Verheyen et al., 2017)), Andean forest plot database
468 (Fadrique et al., 2018)). However, challenges remain for long-term ecological networks,
469 including securing funding over long time periods and reducing the impact on the environment
470 (and thus our data) caused by repeated *in situ* sampling (Sayer & Silvertown, 2018).

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

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

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

486 **Conclusion**

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

502

503 **References**

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844 **Biosketch**

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

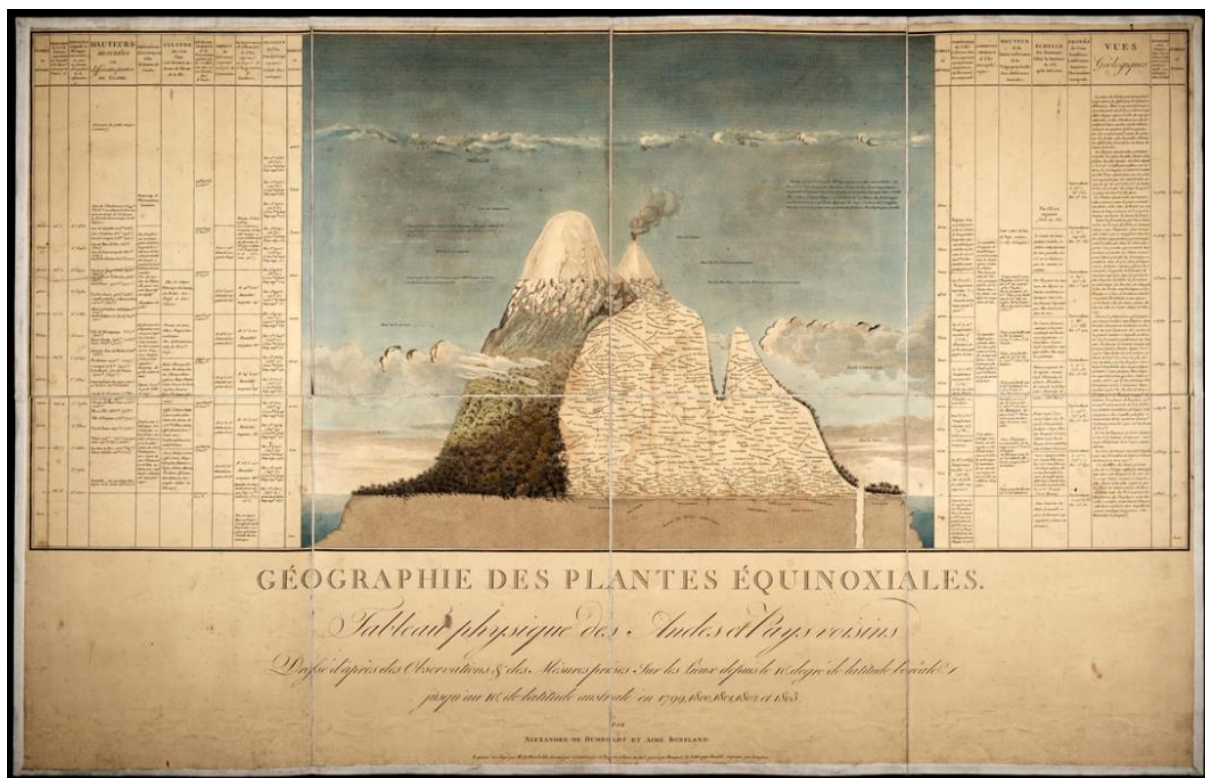
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851 Author contributions: F.S. conceived the idea and F.S., R.F. and M. J. S. designed the study;
 852 F.S. performed the analysis and produced the figures; F.S. and R.F. wrote the paper with
 853 substantial contributions from M.J.S. and J. J. B.

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856 **Appendix**



857

858 *Figure S1 Humboldt and Bonplant’s Physical Tableau of Equatorial Regions. Note the species names*
 859 *and plant communities depicted on the right-hand side of the mountain as well as environmental*

860 *variables measured along the slopes in the left and right-hand panels (von Humboldt & Bonpland, [1807]*
 861 *2009). Digital image courtesy of the Peter H. Raven Library/Missouri Botanical Garden.*

862

863 *Table S1. Published works supporting the importance of different aspects of a “Humboldtian approach”*
 864 *to science. The second column refers to articles showing Humboldt’s support for the respective*
 865 *approach; the third column refers to articles drawing attention to a need to take up the respective aspect*
 866 *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)

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

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