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Humboldt and the reinvention of nature

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Abstract

1. Alexander von Humboldt is a key figure in the history of ecology and biogeography who contributed to shape what is today ecology, as well as the environmentalist movement. His observation that the world's vegetation varies systematically with climate was one of his many contributions to science.
2. Here, we question to what extent Humboldt's view biased our vision of nature. The current emphasis on the role of climate and soils in ecological and evolutionary studies, and the emphasis on forests as the potential and most important vegetation, suggests that we still view nature through the eyes of Humboldt.
3. Over the last 20 years, diverse studies have shown that many open non-forested ecosystems (savannas, grasslands, and shrublands) cannot be predicted by climate and are ancient and diverse systems maintained by fire and/or vertebrate herbivory. Paleoecological and phylogenetic studies have shown the key role of these plant consumers at geological time scales. This has major implications for how we understand and manage our ecosystems.
4. *Synthesis.* We need to consciously probe the long-standing idea that climate and soils are the only major factors shaping broad-scale patterns in nature. We propose to move beyond the legacy of Humboldt by embracing fire and large mammal herbivory as additional key factors in explaining the ecology and evolution of world vegetation.

KEYWORDS
Darwin, disturbance, fire, herbivory, history of ecology, Humboldt, megafauna

1 | RECOGNITION

Alexander von Humboldt (1769–1859) is a key figure for understanding the history and evolution of natural science; and his contributions to this area were unprecedented. Humboldt was the first to understand the dynamic links between geological movement and the distribution of plants and animals. He described, for the first time, the similarities in vegetation along altitudinal gradients across different mountains of the world, and similarities with latitude. He also emphasised the importance of understanding that all organisms are interconnected and form a "web of life." Humboldt invented isotherms and isobars. He was the first scientist to go into the field with scientific instruments to precisely measure physical and environmental variables (e.g. altitude, temperature, magnetism, electricity, boiling point of water, and the blueness of the sky), and to link these measurements with observed biota. That is, he set the basis for a correlational science that explained how environmental factors affect species distribution. In short, he was the first global ecologist and biogeographer, and Ernst Haeckel was thinking of Humboldt's work when he coined the term "ecology." Wulf's book (*The Invention of Nature* 2015) provides a vivid description of his life and his diverse influences on science and society. Stellar figures such as Henry David Thoreau, Charles Darwin, George Perkins Marsh, John Muir, Rachel Carlson, Frederic E. Clements, and Henry A. Gleason were all inspired by Humboldt (Nicolson, 2013; Wulf, 2015) and, in spreading a vision, they shaped what is today mainstream ecology—as well as the environmental movement. Humboldt was, without doubt, a great and inspiring scientist, the best naturalist of his time, and a key voice in the rise of ecological science from early naturalists. Now that we are approaching the 250th anniversary of Humboldt's birth, it is instructive to ask to what extent our vision of nature has been distorted by Humboldt's eloquence. We suggest that it is time to consciously query and move beyond the legacy of Humboldt.

2 | THE HUMBOLDTIAN VIEW OF NATURE

Humboldt was the first to recognize consistent patterns of vegetation—such as vegetation bands ascending mountains. He interpreted the distribution of vegetation as being controlled by climate with forest as the logical climatic climax. During his time, timber was a key resource that powered the growth of industry, and Humboldt was very sensitive to the threat of a deforested Europe and carried these concerns with him on his travels. When he first encountered a savanna (in Venezuela, during the dry season), he immediately thought of a human-deforested landscape, and assumed that tree clearing caused drought. This view of "non-forested" ecosystems as degraded and deforested is common in environmental policy and still prevalent in the literature (Figure 1; Taubert et al., 2018). Humboldt promoted the belief that deforestation changes climate and dries rivers and that "reforestation" would ameliorate climate and promote streamflow. Certainly, some ecosystems have complex water-vegetation feedbacks; however, many experiments and observations have since shown that forests reduce streamflow, and that large-scale afforestation dries rivers (e.g. Bosch & Hewlett, 1982; Jackson et al., 2005). There is also evidence that wildfires destroying large tree plantations increase streamflow. Yet the belief that planting trees increases water supply is still popular and influential among environmentalists (see Bennett & Barton, 2018 for an historical review).

Darwin, in his *The Voyage of the Beagle* (1839), recognized that he was looking at the world through the eyes of Humboldt. Both crossed and described savannas that we now know are strongly shaped by fire and herbivores, yet they were unable to recognize the ecological role of these plant consumers. Darwin, when visiting Australia (often considered the most flammable continent) mentioned that *we passed through large tracts of country in flames; volumes of smoke sweeping across the road* and that *I scarcely saw a place, without the marks of fires* (Nicholas & Nicholas, 2008). Yet he could not think of fire as a natural phenomenon acting as a selective pressure. The fact that our most prominent naturalists were blind to the ecological and evolutionary role of fire helps explain the difficulties that some scientists, especially in fire-free landscapes, are still experiencing.

In *Man and Nature*, Marsh (1865), an early conservationist, mentioned that "Humboldt was a great apostle." While Marsh rightly criticized anthropogenic deforestation, he also contributed to creating a romantic forest-centred culture of nature that fuelled the conservation movement. *Man and Nature* had a narrow view of nature; no single chapter was dedicated to any biome other than forest, despite the considerable terrestrial biodiversity found outside forests. Following this line, the 1873 Timber Culture Act in the US, which was inspired by *Man and Nature* (Wulf, 2015), encouraged planting trees on grasslands and prairies regardless of whether they were ancient old-growth systems with a long history of fires and large herbivores (Edwards, Osborne, Strömberg, & Smith, 2010; MacFadden, 2005; Veldman et al., 2015). Even today, global "forest restoration" programs are threatening many species-rich savannas and grasslands (Bond, 2016; Figure 1).

FIGURE 1 Forest-savanna mosaic under the same geology in the Serengeti, home to one of the world's richest remaining open habitat megafaunas. Savanna fires have killed some of the trees at the edge of the forests, and elephants have killed some of the trees in the savanna. The Serengeti is mapped as "deforested" and "degraded" in the *Atlas of Forest Landscape Restoration Opportunities* of the World Resources Institute (www.wri.org/applications/maps/flr-atlas/; see forest condition). The Atlas is used as a basis for global forest landscape "restoration" projects. This suggests persistent misunderstanding of ecosystem dynamics and the long-lasting legacy of Humboldt. Photo: W. Bond [Colour figure can be viewed at wileyonlinelibrary.com]

Humboldt and Marsh were the foundation on which John Muir, based in the western US forests, built a strong environmental awareness among Americans. Their legacy was a forest-centred view of nature that was probably the result of an ecological culture emerging from temperate ecosystems dominated by the forest biome in central Europe. Europeans grew up surrounded by dense forests and have a rich diversity of cultural and spiritual values associated with forests (Simončič, Spies, Deal, & Bončina, 2015). Deforestation led by an expanding industry in the 18th and 19th centuries increased forest conservation awareness, and Europeans spread their forest-centred view of nature to their colonies and neighbouring countries. There is plenty of evidence today that western society values forest more than any other biome, despite the very large proportion of global biodiversity found in grasslands, savannas, and shrublands (Fernandes et al., 2018; Murphy, Andersen, & Parr, 2016; Rundel et al., 2018). Fire was considered the enemy of forests, caused by humans, and a major agent of degradation. Fire suppression in American forests (and everywhere else) is an example of the consequences of this view. Only in the last few decades have we realized the extent to which ecosystems and their many constituent species depend on regular fires—and projects for restoring fire regimes are increasing worldwide (Barros, Ager, Day, Krawchuk, & Spies, 2018; Boisramé, Thompson, Collins, & Stephens, 2017).

Humboldt's view of climate as a primary driver of vegetation distribution paved the way for ecology to focus on changes along continuous environmental gradients; and the classical works by Clements, Gleason, and Whittaker, followed that path (Nicolson, 2013). We have now learned that a large part of the world's vegetation has less biomass than would be expected from climate and soil alone (Bond, Woodward, & Midgley, 2005), and that fire and mammalian megafauna are (and have been) major natural factors maintaining low biomass systems. The conscious replacement of the "balance of nature" by the "flux of nature" (Pickett & White, 1985) has helped replace the Humboldtian view of nature by one in which disturbance plays a central role.

The under-recognition of fire and megafauna (collectively called plant consumers) in shaping nature can be easily depicted from the biased terminology valuing forest vs. alternative vegetation types in many current popular and scientific publications. For instance, we often find in the literature the use of terms such as "more desired" or "luxurious" state when referring to forest (vs. savannas or shrublands), "arrested succession" and "degradation stages" for low-biomass vegetation, and the concept of "deforestation by fire" in fire-prone ecosystems. It is singularly inappropriate to use the word "deforestation" or "early successional" for non-forested ecosystems that have existed for millions of years (Cerling et al., 1997; Edwards et al., 2010; Keeley, Bond, Bradstock, Pausas, & Rundel, 2012). Of course, not all open ecosystems are ancient; for instance, the felling of tropical rainforests may generate savanna-like ecosystems lacking the specific flora and functional types that characterize ancient savannas (Veldman et al., 2015).; and anthropogenic disturbance of ancient shrublands may generate grasslands dominated by invasive species (Keeley et al., 2012); in such cases, the use of terms like "degradation" seems appropriate. Another indication of the lack of recognition of plant consumers as major shapers of vegetation is their limited coverage in general ecology and biogeography textbooks (e.g. Begon, Townsend, & Harper, 2006, Cox, Moore, & Ladle, 2016). This is especially evident for fire that is rarely treated as a major biogeographic and evolutionary agent filtering species and growth forms and selecting for traits compatible with the fire regime. The cultural bias can also be depicted in romantic stories about forests and myths on historical deforestation, like the myths of the ancient Great Scottish Woods which seems unsupported by palynological, dendrochonological, and carbon-dating studies (Smout, MacDonald, & Watson, 2004).

3 | THE REINVENTION OF NATURE

Perhaps, the major example of the Humboldtian perspective in ecology is the emphasis on the role of climate and soils in our

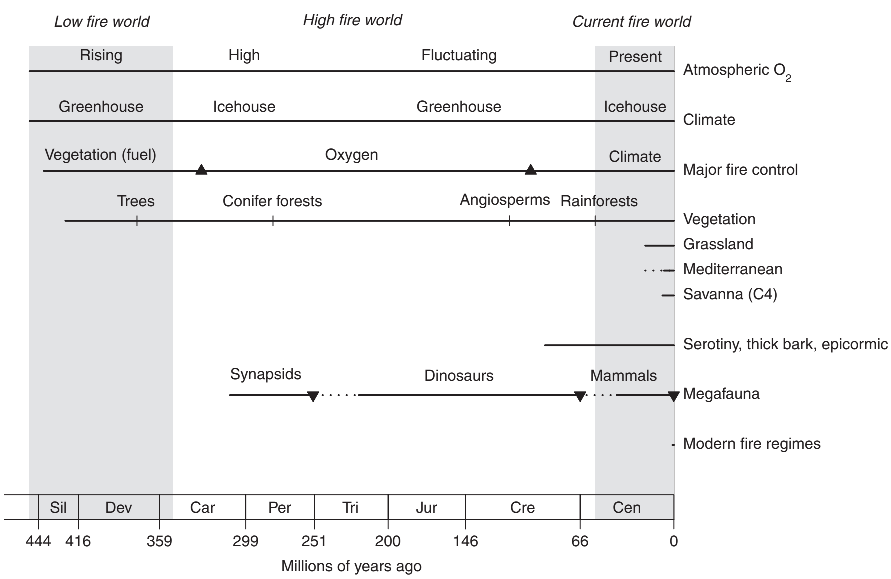

FIGURE 2 Changes in the drivers related to fire and herbivory, together with the evolution of different vegetation types, and some plant traits (serotiny and thick bark of pines, epicormic resprouting in eucalyptus), during the evolutionary history of plants (see main text for details). Upper pointing triangles are peaks of O_2 atmospheric concentration and fire activity; lower-pointing triangles are megafauna extinction events, also associated with fire activity peaks. Note that modern fire regimes are very recent and at this scale they are almost a point. Modified from Scott, Bowman, Bond, Pyne, and Alexander (2014)

understanding of the ecology, evolution, and biogeography of species—and even for species restricted to fire-prone ecosystems (Pausas & Lamont, 2018). Many ecologists do not consider fire or megafauna as major evolutionary and ecological processes. However, fossil evidence suggests that wildfires were already present in the Silurian (420 Ma, Figure 2) and affected plants in the very first terrestrial communities on Earth (Glasspool, Edwards, & Axe, 2004). Fires increased in importance when vegetation increased in height and density (Devonian, 420–360 Ma), and become common in the Carboniferous (360–300 Ma) when atmospheric O_2 concentrations were higher than present (Scott, 2018, Figure 2). Throughout the evolutionary history of plants, fire activity has fluctuated in time and space (Pausas & Keeley, 2009; Scott, 2018) depending on changes in atmospheric oxygen concentration; the evolution of new plant forms altering the "fuel" (Bond & Scott, 2010); the consumption of vegetation by megafauna (e.g. megafaunal extinctions increased fire activity; Gill, Williams, Jackson, Lininger, & Robinson, 2009); and the changing climate (Figure 2).

While fossil charcoal provides evidence of the long history of fire as an ecological process, phylogenetic analyses are providing evidence on when it was frequent and predictable enough to have an evolutionary role. For instance, fire adaptive traits in pines (thick insulating bark, serotinous cones), in eucalyptus (epicormic resprouting), and in many Proteaceae, arose during the Cretaceous (Crisp, Burrows, Cook, Thornbill, & Bowman, 2011; He, Pausas, Belcher, Schwilk, & Lamont, c; Lamont & He, 2012), a period with a high atmospheric oxygen concentration and a high level of fire activity (Bond & Scott, 2010; Figure 2). More recently, fire has been implicated in the late Miocene (~7 Ma) spread of C_4 grasses and the rise of savannas (Keeley & Rundel, 2005; Maurin et al., 2014; Simon et al., 2009). The ancient role of fire in the ecology, evolution, and diversification of many lineages is now unquestionable (He & Lamont, 2018). A lack of consideration of the importance and influence of fire in Earth's history has led to misunderstandings over the mechanisms behind observed patterns. For instance, some patterns of plant mortality have been related to global warming, although fire history is likely to be the underlying mechanism (Schwilk & Keeley 2012). And different ecological and evolutionary studies of the Proteaceae plant family (ca. 1,700 species in the southern hemisphere) have failed to recognize the role of fire in their distribution and diversification—despite the family including many species that are clear examples of fire adaptation (reviewed by Pausas & Lamont, 2018).

The importance of megafauna in the past is also under-considered in relation to understanding the current and past vegetation patterns. The first herbivorous tetrapods only began to consume vegetation more than 100 million years after the first fires. Dinosaurs first appeared in the Mesozoic (245 Ma) and reached enormous sizes and diverse shapes before their extinction 65 Ma; this extinction gave way to the rise of large mammals (such as mammoths, bovids, and large African tetrapods). The impact of dinosaurs on vegetation is not well understood though, famously, Bakker (1978) argued that the evolution of short-necked dinosaurs prompted the evolution of angiosperms. Some 50 million years later, a switch in the mammalian fauna of Africa, when the continent drifted into Eurasia, has been implicated in the early (mid-Miocene) appearance of savannas. It is only at this time that spines, plant structural defences against bovid browsers, began to diversify in savanna trees (Charles-Dominique et al., 2016).

During the late Pleistocene and early Holocene, the Earth experienced an abrupt extinction of large vertebrates. For instance, in North America, all mammal species over 1,000 kg and over half of those over 32 kg became extinct (Koch & Barnosky, 2006); similar processes occurred in Eurasia and Australia (Barnosky, Koch, Feranec, Wing, & Shabel, 2004), and at the global scale, the present-day biomass of wild animals is about sevenfold lower than during the Pleistocene (Bar-On, Phillips, & Milo, 2018). That is, populations of large wild herbivores are currently at historical lows, yet they have a strong impact on vegetation (Jia et al., 2018). The megafaunal extinction disrupted many ecological interactions (Galetti et al., 2018), including the herbivore–plant interactions that are key for shaping landscapes and biomes (Sandom, Ejrnæs, Hansen, & Svenning, 2014). We live in a world analogous to an herbivore exclusion experiment, with most of the large herbivores removed. In many cases, the role of megafauna has been partly replaced by livestock, and thus some of the grassland-forest mosaics currently maintained by livestock may be a relic of the previous natural system (Hempson, Archibald, & Bond, 2017). Researchers on biotic interactions have long recognized the important role of past megafauna as dispersal agents; (seed dispersal anachronisms; Janzen & Martin, 1982; Galetti et al., 2018), yet many community ecologists and biogeographers have barely explored the role of these large mammal consumers in influencing habitats and biome distribution (Owen-Smith, 1987).

Perhaps, the clearest case of the role of consumers at the community scale is the existence of alternative stable vegetation states driven by fire and/or herbivory (Figure 1). This includes tropical savanna/forest mosaics (Bond, 2005; Dantas, Hirota, Oliveira, & Pausas, 2016; Hirota, Holmgren, Nes, & Scheffer, 2011; Sankaran et al., 2005; Staver, Archibald, & Levin, 2011) and some non-tropical ecosystems (Keeley et al., 2012; Pausas, 2015). Satellite imagery has contributed greatly to showing the global scale of the mismatches between climate and vegetation, while also revealing the global extent of vegetation fires. Forest/open habitat mosaics can no longer be dismissed as local aberrations; they are the natural landscapes in many places on Earth. Open communities (savannas, grasslands, and shrublands) include biodiversity hot spots harbouring a large diversity of light-demanding plants and animals that cannot survive in closed forests (Fernandes et al., 2018; Rundel et al., 2018). And changes in consumers (fire regime changes, extinction/exclusion of megafauna, etc.) are likely to have as much impact, or more, on nature as changes in climate (Pausas & Keeley, 2014). An open question that requires further research is how fire and grazing interact with each other in shaping species at the evolutionary scale.

Fire and herbivory are key disturbance factors for understanding our biosphere. We have referred to them as consumers (different from disturbances such as cyclones, floods, and landslides), since we believe that they are best studied in the context of trophic ecology. As trophic agents, these consumers can be very influential in shaping vegetation at broad scales. To do so, herbivores must escape regulation by predators or pathogens. In the Serengeti, for example, the wildebeest population grew from ~150 thousand to 1.5 million after the rinderpest epidemic was controlled, with cascading consequences on the ecosystem: Fires were suppressed as they were "outcompeted" by grazers, resulting in increases in trees and changes in the carbon sink (Holdo et al., 2009). The context of trophic ecology forces a wider understanding of biotic interactions within the physical environmental context (e.g. Estes et al., 2011; Hopcraft, Olff, & Sinclair, 2010). Fire has analogies with a generalist herbivore (Bond & Keeley, 2005) and it "competes" with large vertebrate herbivores for food (fuel) and, as for herbivores, has reciprocal feedbacks between the consumer and the vegetation consumed (Archibald et al., 2018).

We believe that plant consumers have been under-considered when explaining large-scale patterns; and we show that this view has its roots in the early history of ecological science. The time is ripe for a more integrated view of nature away from the idea that climate and soils are the major factors shaping nature. It is time to move beyond the "certainties" of Humboldt's explorations more than 200 years ago. The world is more complicated and a great deal more interesting.

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AUTHORS' CONTRIBUTIONS

J.G.P. conceived the idea and wrote the first draft; J.G.P. and W.J.B. wrote the final version and gave final approval for publication.

DATA ACCESSIBILITY

No original data was used in this study.

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