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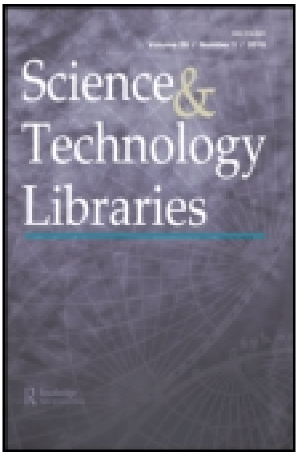

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Biogeography, the study of animal and plant distribution, has a history extending back to at least the eighteenth century. But it was not until the work of Charles Darwin and Alfred Russel Wallace in the mid-nineteenth century that it really came into its own as a science. Darwin's importance notwithstanding, it was really Wallace who put the field on the map, and many of today's research threads can be traced back to his influence. This article provides a summary review of Wallace's life and work and biogeography as a field of study, including Wallace's role in its development.

KEYWORDS *biogeography, biography of scientists, Alfred Russel Wallace, history of science, evolution, natural history, geographical distribution*

SOME BASICS

Biogeography as a study does not have quite the popular name recognition that chemistry or physics has, but it is a distinct field of science and has its own rich history of important discoveries. It is also arguably the most interdisciplinary scientific study, a fitting characterization as it examines the most complex natural systems on Earth.

It is, most simply stated, the study of "what lives where, and why." As such, it examines the reasons behind the spatial and temporal distribution of living things, especially at their greater scales of organization (population, higher taxonomic levels, communities and ecosystems, and

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world). At its outer reaches of coverage it blends seamlessly into a variety of other fields, especially ecology, paleobiology, geology, epidemiology, paleontology, physical geography, conservation, and ethnography and human geography. It is not entirely a "natural science" study either; as with most "geographies" a direct connection with the human world is often implicit—as, for example, with the subject of bioinvasions, the single most costly problem afflicting human existence.

There are two common ways of breaking biogeography down into sub-studies. One recognizes a difference of emphasis on the kinds of causalities involved. Thus, on the one hand, we have "historical biogeography," which concentrates either on changing events and landscapes of the deep geological past, or on the historical progression of events (both physical and biological) leading to today's observed distribution patterns. On the other hand, there is "ecological biogeography," which concentrates on the more immediate causes of distribution; that is, those contributing to a present-day ecological system including the forms under study.

Another general subdivision of a primarily ecological type is also commonly recognized: cultural biogeography. Human beings are, after all, animals, and most of the principles that govern the distribution of other animals (and plants as well) also pertain to us. But we also introduce many "curves" into the study of distribution that are peculiar to our species. Many cultural biogeographers are anthropology-trained and study human systems evolution, including such environment-integrating subjects as the domestication of animals, and the origins of crop agriculture.

The other common way of dividing biogeography into sub-studies is to recognize the fields of zoogeography, pertaining to animal/faunal distribution patterns, and plant (or "phyto-") geography, concerning plants/floras. Although both may be dealt with in either ecological or historical terms, the differing nature of the organisms involved (for example, the simple fact that most animals are individually mobile, whereas plants are not) necessitates many special considerations.

Biogeography has a very large technical literature, with thousands of related books and papers published annually. Nevertheless, in some respects, the field is rather fragmented as a professional discipline. There are relatively few investigators who call themselves *primarily* biogeographers; the vast majority of individuals who contribute to the literature have advanced degrees in the subjects listed in the second paragraph above and come to the field only secondarily, as a logical outcome of particular studies in their main areas. For example, those investigators delving into the evolutionary systematics of a particular group of animals will often enlist a biogeographic approach to help them understand speciation trends over time within that group.

As a result there are also essentially no "departments of biogeography" in the world's universities. Those relatively few individuals who train

FIGURE 1 Alfred Russel Wallace.

deliberately as "biogeographers" practically all come from geography departments, not biology- or geology-emphasizing ones. Geography is a relatively small professional field as compared with biology or even geology, and it is also a peculiarity of geography-trained biogeographers that most are ecological biogeographers whose main emphasis is phytogeography (although this is slowly changing). Thus, almost all historical biogeography comes from workers with primary backgrounds in biological systematics (especially as related to evolutionary biology studies) or in geology. Complicating the picture further is the fact that much of the ecological biogeography work being done by geography-trained biogeographers closely resembles ecological studies performed by biologists.

Before turning to an overview of the history of the field and its most significant literature, it is useful at this point to take a quick look at the biography of its "father" as a scientific study: Alfred Russel Wallace (see Figure 1).

A BRIEF LOOK AT THE LIFE AND CAREER OF ALFRED RUSSEL WALLACE

Wallace was born on January 8, 1823; he has the same birthday as a previously featured writer in this series, Stephen Hawking. Wallace died on November 7, 1913, however, more than twenty-eight years before Hawking's birth in 1942. Wallace was, thus, a Victorian-period figure, although his long life spanned a period beginning before the initiation of regular train services and ending well into the period of automobiles and airplanes.

Wallace was born in Usk, Monmouthshire, and because of this some sources refer to him as Welsh. He was not. His family, of thoroughly English and Scottish roots, had moved there for financial reasons, a few years before he was born, and then moved back to England when he was aged five or six when a relative died and inexpensive housing became available. Wallace's father had been prepared to take up the law and actually was sworn into practice, but he never did so, preferring to live off a modest inheritance that permitted him a life of comparative leisure for some fifteen years (and, allegedly, acquaintances such as the infamous Beau Brummel). This changed in 1807 when he married and felt obligated to increase his income, which he barely managed to do. In the mid-1830s he was swindled out of his remaining inheritance, with the result that young Alfred was forced to leave school, move to London, and take up a trade. Eventually he landed in the surveying and map-making business, working for an older brother. This employment led him back to Wales for three years, where he also engaged himself in museum and library work and lecturing at local mechanics' institutes. In 1844, however, a slowdown caused his brother to let him go, whereupon he found work as an instructor at a private school in Leicester, England.

In Leicester he had the good fortune of running into another famous naturalist-to-be, Henry Walter Bates. Bates, two years younger than Wallace, was an avid beetle collector, and this avocation soon attracted Wallace's interest, which to that point had largely been consumed by plant identification activities. In 1845, Wallace's older brother suddenly died, and Alfred returned to Wales to tie up his affairs. But he also kept in touch with Bates, finally suggesting to him that they might "turn professional" and attempt a natural history–collecting expedition to Brazil. Bates liked the idea, and they left England in the spring of 1848, arriving in Pará (now Belém), at the mouth of the Amazon, on May 26.

Wallace's early endeavors are easily relatable to his future directions. During his short time in London as a teenager he fell in with followers of the utopian socialist Robert Owen and developed a permanent appreciation for his methods and teachings. In Wales, his surveying work exposed him to the indignities of the land-enclosure process, an experience that later informed his ideas on land reform and conservation. During his two periods there of surveying, map-making, and construction work he developed practical drafting, engineering, and mathematical skills. At Leicester he watched demonstrations of mesmerism, and himself became a skilled practitioner. Meanwhile, when time permitted, he carried on with his local collecting activities. In short, a wide range of experiences were beginning to stimulate his highly intellectual and intensely curious nature.

In 1844 or 1845, while in Leicester, Wallace read the sensational new book *Vestiges of the Natural History of Creation* (Anonymous 1844), which espoused evolutionary views, but was unable to suggest an underlying mechanism. On digesting its message Wallace quickly saw that the way to uncover such was to spend an extended period in the field, looking for clues. He stayed in South America for four years (Bates remained there a longer period, eventually accumulating evidence leading to his theory of mimetic resemblance, one of the first important proofs of Darwinian/Wallacean natural selection), but was unable to come to any conclusions. Furthermore, on the way back to England in 1852 the ship he was on caught fire and sank, destroying all of his recent collections. He escaped with his life—barely—but with little else.

After eighty days at sea Wallace finally made it back to England on October 1, 1852. Luckily his collections had been insured by his collections agent, so he was able to spend the next eighteen months writing, attending scientific meetings, and even vacationing. Two books (and several professional papers) were ultimately produced: the ethnobotanical *Palm Trees of the Amazon and Their Uses* and the scientific travel opus *A Narrative of Travels on the Amazon and Rio Negro,* both published in 1853. They were only modestly successful. Having succeeded in establishing a reputation as a traveler and naturalist, however, he was able to secure a small grant from the Royal Geographical Society covering a removal to Singapore, where he next set out to "look for clues."

Wallace's fourteen thousand miles of travel in what was then known as "the Malay Archipelago" consisted of some eighty separate expeditions. He remained there for eight years, headquartered in locations ranging in the west from Sumatra and Malaya to Aru and New Guinea on the east. He collected over 125,000 specimens, primarily of birds and insects (but also, somewhat infamously, of orangutans). Living among dozens of different peoples, he kept notes on their languages and cultural mores. Over the period 1854 to 1862 he sent back several dozen communications that found their way into print. Three of those were particularly important to the evolution of the field of biogeography.

The first was composed in early 1855, while he was holed up during the rainy season in Sarawak. Written in response to a recent and rather dubious theory of global distribution patterns penned by the famous naturalist Edward Forbes (1819–1854), "On the Law which Has Regulated the Introduction of New Species" (Wallace 1855) was his first work hinting at an evolutionary interpretation of natural processes. It featured the "Every species has come into existence coincident both in space and time with a pre-existing closely allied species" law based on his realizations that: (1) there is a geological progression of closely allied forms, as revealed by the order of forms in the fossil record, and (2) there is a geographical association of closely allied forms, with the most closely related ones being nearest to one another in space. Only an evolutionary progression could produce such a combined outcome. This paper is widely regarded as the beginning of the modern field of biogeography and indeed provides, even now, one of the best proofs of the reality of biological evolution.

But it took Wallace another three years to figure out what kind of a mechanism, operating directly at the individual and population levels, might yield such spatial-temporal outcomes. In early 1858, while struggling through an episode of malaria in or near the island of Ternate in the Moluccas, he connected the ideas of Thomas Malthus on the checks on population levels in humans with the facts of variation and fecundity rates in plants and animals. Simply, it appeared likely that evolutionary change could be related to some individuals having the adaptations that gave them an advantage over others, especially to the extent of their then being more likely to reach maturity and (differentially) pass those traits along to their offspring. He quickly drafted up an essay he titled "On the Tendency of Varieties to Depart Indefinitely from the Original Type" (Wallace 1858) and sent it off to a correspondent he knew was interested in the subject—Charles Darwin—for comment. Darwin was devastated, having silently worked for many years on virtually the same idea, and sought advice from two of his closest friends, the naturalists Charles Lyell (1797–1875) and Joseph Hooker (1817–1911), on what to do. They suggested a solution: take Wallace's essay and some unpublished writings of Darwin's and have them read at the next meeting of the Linnean Society of London. This took place on July 1, 1858. Now it was possible to attach an ongoing, ecological, understanding to the observable spatial-temporal products of living nature: that is, to begin to understand how they and their composite patterns in time and space *had evolved*.

Wallace's third major biogeographical contribution came when he identified a sharp break in the pattern of distribution of animal forms between western and eastern Australasia. His years of visits to the important islands in the archipelago revealed a curious fact: that many genera or even families of creatures that were present in the western islands of Sumatra and Java did not extend eastward beyond Bali—and, conversely, that many typically Australian and New Guinea forms did not extend westward beyond it. Eventually termed "Wallace's Line" by T. H. Huxley (1868), this discontinuity has been a focal point of distribution studies ever since. Wallace interpreted his "line" as arising through historical geological changes, and the fact that it is along this line that the shallow Sunda Shelf seas meet the deeper ocean waters to the east. The zone of interaction has proved an instructive vehicle for the study of biogeographical processes, especially now that it is recognized that the land masses in the area have not only moved vertically (creating alternating periods of shallow sea and dry land), but horizontally (as understood through applications of plate tectonics theory) as well. Wallace's first summary of his "line" was included in a paper he sent to the Linnean Society in 1859 titled "On the Zoological Geography of the Malay Archipelago" (Wallace 1860).

Upon his return to England in the spring of 1862 Wallace quickly immersed himself in a wide range of studies, from the processes of biological evolution and physical geography to social science subjects and, surprisingly to most of his colleagues, spiritualism. But for about twenty years, his primary focus remained biogeography. Four books in particular represented his greatest legacy in that domain. The first, published in 1869, was *The Malay Archipelago*. This was a splendid accounting of his travels in the region, popular in style but scientific in scope, detail, and accuracy. In it he recounts his experiences among both settled and aboriginal peoples, his travails both at, and sailing between, dozens of places on the map, and his observations on floras, faunas, and individual organisms—all set within the framework of new evolutionary science. Beyond being a travel book it is, thus, a biogeography of the entire region, especially if one counts (as is sometimes done) the ethnological and ethnographic circumstances of human beings as being an element of study of the field as well.

In 1876 Wallace released the two-volume tome *The Geographical Distribution of Animals*, which became the standard work on the subject for the next seventy-five years. Central to the study is his classification of the world's biogeographical regions, based on the scheme of P. L. Sclater published in 1858 (to which Wallace himself made immediate adjustments in a letter from the field published in 1859). The work has three basic sections: an introductory portion summarizing the various forces producing geographical distribution (including their relation to evolution), and then long treatments of the biogeographical characteristics and histories of the regions ("zoological geography"), and similarly long treatments of the biogeographical aspects of the histories of individual animal groups ("geographical zoology").

Two years later, in 1878, Wallace put out his most important contribution to ecological biogeography, *Tropical Nature and Other Essays*. This was a natural subject for Wallace, who had spent twelve years in equatorial environs, and by a majority of scorecards ranks as the most acute tropical naturalist in history. The book consists of a series of essays treating both some of the feature characteristics of tropical ecology, and adaptations and life habits of the dominant organisms that live there. In one of the essays he discusses and suggests an explanation for the existence of what are known as latitudinal diversity gradients: the fact that within many groups of living things there is a decided tendency for the number of its representative species to increase as one approaches the equator. This matter, and its related issue of what factors influence species richness levels at different locations, is an increasingly hot topic of late within the realm of biodiversity studies.

Wallace's last great work on biogeography appeared in 1880 under the title *Island Life*. In this study Wallace shows his mettle as a physical geographer; beyond discussing several important ties among geology, climate and landscape and the distribution of living things, he spends three full chapters developing a theory of continental glaciation—the first such theory projecting a combination of astronomical and geographical causal factors. The remaining half of the book is given over to a discussion of the circumstances of a good number of representative individual islands, and how these have evolved the floras and faunas that we witness today.

After 1880 Wallace's attention drifted increasingly in other directions, although from time to time he would return to his favorite subject. And there was one more cause he took up that, although not involving "biogeography" *sensu stricto*, nevertheless did involve the *possible* distribution of living things.

Around the turn of the century several astronomers were reporting the existence of markings on the surface of the planet Mars that resembled canal structures. Primary among them was Percival Lowell (1855–1916), who in 1906 released a book called *Mars and Its Canals* that argued for the presence of actual Martians on the planet. Wallace, who a few years earlier had published a book (Wallace 1903) that on physical science grounds denied any likelihood to there being other advanced beings in our neck of the universe, was appalled by the inconsistencies of Lowell's argument. In 1907 he put out a slender volume (*Is Mars Habitable?*) that, applying basic principles of physical geography to deduce the probable conditions on the Martian surface, thoroughly debunked Lowell's theory. (Some years later it was determined that the "canals of Mars" were actually optical aberrations in the observing telescopes themselves.) For his efforts in both works Wallace is now recognized as one of the founding fathers of the field of astrobiology—perhaps, if one stretches definitions, a kind of "astro-biogeography."

Wallace's reputation rests, above all, on his contributions to evolutionary theory and, only semi-independently, biogeography. But in his own time he was known for his attraction to many other subjects (Smith 2010). He was a vocal spiritualist, for example, and published over a hundred writings related to this belief. He was president of the Land Nationalisation Society for over thirty years, becoming a potent advocate for land reform in an era dominated by large landholders. His writings on this matter number at least another hundred. A variety of other social issues were treated in a further two hundred or more publications, including four books. Wallace's involvement in so many subjects, both scientific and popular, made him quite famous in his own time. He was active all the way through to his death at the age of ninety—in fact, his published output in his final decade exceeded three thousand pages in print. By the end of his life he may well have been the most famous scientist in the world: the "Grand Old Man of Science," as he was frequently called.

BIOGEOGRAPHY: THEN AND NOW

Wallace's influence on the evolution of the field of biogeography has been considerable, but of course he was neither the first to take up all related questions, nor have all of his posed "solutions" proved to be final ones.

Even during the earliest days of civilized humankind it must have been obvious that not all plants and animals lived everywhere, but it was not until after the Renaissance that this fact began to take on its own significance.

Before this time, the facts of presence and absence had had practical implications, to the degree that many natural products that were coveted in places that did not produce them had to be traded for, generating economies that propelled the advancement of civilization. But it was not until later, when academic/intellectual institutions arose, that general patterns of presence and absence came to be noticed and related to possible causes. The voyages of discovery of the fifteenth through eighteenth centuries especially fueled the process, as large numbers of specimens of animal and plant life were brought back to Europe, along with stories of fabulous creatures in the new lands that were unlike any of those known at the time. Still, this was not of great concern to most observers, who simply accepted that the Creator had seen fit to populate the world with different creatures at different places.

A complication arose when enough of the world had been explored to make it apparent that once-existing forms, as evidenced by the fossil record, no longer roamed the Earth. In the eighteenth century some individuals began to wonder whether some process of change within the living world might be operating that involved the ongoing appearance of new forms and extinction of old ones. Buffon, Maupertuis, Hutton, and Erasmus Darwin, among others, hinted at a possible evolutionary process and how climate and other environmental factors might be driving it. In the early nineteenth century, Lamarck fashioned his famous hypothesis of evolutionary change through the differential exercise of particular organs and habits. He was wrong, but the idea got people thinking more about organic change. The geological studies of Charles Lyell also proved conducive to evolutionary thinking, as he promoted a view of surface change that relied on slow and relentless forces more than cataclysmic ones. Then along came Charles Darwin, and finally Wallace, and an operational model of evolution.

Meanwhile, in the late eighteenth and early nineteenth centuries, increased attention was being given to the immediate environmental conditions that might be responsible for producing presence and absence. Here, the focus was on plants. The earliest workers included the Frenchmen Aimé Bonpland (1773–1858) and A.-P. de Candolle (1778–1841), the Dane Joakim Frederik Schouw (1789–1852), and the Germans Karl Ludwig Willdenow (1765–1812) and Alexander von Humboldt (1769–1859). Climate, especially the effects of variation in temperature and precipitation, was looked to as the predominating influence on "what lived where, and why."

The study of animal distribution patterns continued to be dominated by historical approaches. Darwin's *On the Origin of Species* in 1859 did nothing to change this emphasis, but new kinds of models tied to evolutionary theory emerged. Darwin and Wallace themselves increasingly adopted dispersal to account for widespread faunal similarities, but although many workers went along with this understanding, not all were so quick to appreciate natural selection as the likely underlying process model. In the United States, in particular, many adopted a "neo-Larmarckian" view of organismal change in which climate and other environmental forces were thought to be the main driving mechanisms (the Darwin-Wallace model did not assume final supremacy until the 1930s, when input from the developing fields of population biology and genetics turned the tide). Still, a rapidly expanding knowledge base within the field of paleontology made it possible to develop more complete area-specific models of faunal evolution, and many of the best known of these followed the basic Darwin-Wallace line when it came to evolution and dispersal (e.g., Matthew 1915; Simpson 1940, 1943; Darlington 1957).

Despite such efforts, it can be argued that the first half of the twentieth century witnessed something of a progressive stagnation in biogeography studies. This is not the place for a detailed accounting, but it can be suggested that there were two main reasons. For one, the geological model of Earth's surface-shaping processes did not progress beyond an understanding rooted in local causes—that is, in vertical movements of land or sea only. Second, limited advances were made in the means of assessing degree of phylogenetic (or other) relations within and among groups of related forms. This situation changed dramatically in the 1960s, with two developments.

First, it was discovered that the old ideas of Alfred Wegener (1924) on continental drift were essentially correct. Over a period of less than ten years the new theory of plate tectonics was erected—a theory that recognized the existence of *horizontally* moving, not to mention emerging and disappearing, crustal masses. It was quickly recognized that populations did not necessarily have to physically disperse from place to place but could also effectively "raft in place," as neo-oceans appeared and split continents apart, or be passively divided by the rise of mountain ranges or the development of hostile climates.

Second, and nearly contemporaneously, the German entomologist Willi Hennig (1966) developed an approach to classification ("cladistics") that more closely followed principles of evolutionary relation. Once it became possible to more accurately trace the sequence of divergence within particular groups, it also became possible to associate that sequence with a history of environmental events such as newly opening oceans or rapid mountain-building. Within biogeographical studies, a parallel revolution therefore occurred with the emergence of what is known as "vicariance biogeography," the linking of evolutionary divergence patterns to particular Earth history events of this kind.

Using vicariance biogeography approaches it is often possible to view entire lineages in relation to the environmental forces that most apparently caused them to come about. Yet, this method still has weaknesses. First, it assumes initial divergences without worrying about the particular relations between environment and selection and genetic change that are occurring at the population level to sustain them. Second, it does not consider other possible conditions related to evolutionary change: for example, the role of dispersal or possible speciation processes not related to overt changes in physical milieu. At present biogeographers are working through this incomplete state of affairs, searching for new and more complete models.

Another reason for the decay of interest in biogeography through the early 1900s was the increasing emergence of the field of ecology. New forms of "evolution," related to the population, community, and ecosystem scales came under scrutiny, with investigators concentrating on developing new means of measurement of organization and using these to relate observed natural patterns to local ambient conditions and histories. Among the earliest and best known of those understandings were the theory of ecological (plant) succession, as introduced by Henry Cowles (1899) and Frederic Clements (1916), and the geographical cycle of landform development advanced by physical geographer William Morris Davis (1899). Eventually, these "organism-by-analogy" approaches were replaced by more abstract appreciations such as the ecosystem concept (Tansley 1935), the "law of tolerance" (Shelford 1913), and the Eltonian niche (Elton 1927), which addressed rather more explorable relations between organism and environment.

By the 1950s, with the advent of digital computers, interest was growing in the statistical analysis of spatial trends in species richness. Geographers had long been interested in how distance relations affected rates of interaction, but the field of geographical ecology was developed primarily by ecologists and biologists. A central figure in this movement was the mathematics-trained ecologist Robert MacArthur, who in the late 1950s and 1960s, often working with other biologists and ecologists, developed what is known as the theory of island biogeography (MacArthur and Wilson 1963, 1967). With this model it became possible to make predictions about the faunal or floral makeup of island groups (or islandlike settings such as groups of mountaintops or spatially separated conservation/refuge areas), including variations in diversity and extinction rates based on size of island and distance from populating source. Before this advance biogeography had been largely a descriptive science, but with this work investigators turned increasingly to predictive modeling.

In the mid-1980s, the rise of the biodiversity studies movement gave biogeographical investigations a substantial shot in the arm. Although a concern for the environment had been accelerating at least since Rachel Carson's *Silent Spring* (1962), a conference held in 1986 (Wilson 1988) focused the scientific community's attention on the importance of (bio) diversity *per se*. As this importance rests on ethical and economic considerations as well as scientific ones, a rationale for a greater investment of attention was created; two of the fields that benefited most from this were biogeography (which deals with many of the causes of biodiversity) and conservation biology (which concerns itself with the societal implications of biodiversity—especially, biodiversity loss).

WALLACE AND BIOGEOGRAPHY STUDIES TODAY

It is not coincidental that the reemergence of biogeography has paralleled a resurrection of interest in Wallace, the field's "father." There is first the matter that dozens of Wallace's discoveries and theories, within and beyond biogeography, remain subjects of investigation today (for a quick tour, see the "Research Threads" feature at the author's *Alfred Russel Wallace Page* website). Within biogeography, and beyond the ideas mentioned earlier, considerable attention continues to be devoted to, for example, Wallace's "riverine barriers" hypothesis of the evolution of South American distribution patterns (Wallace 1852), his ideas on "corridor dispersal" along mountain chains (Wallace 1880, 1889), his hypotheses on the population of islands (Wallace 1880), his conclusions regarding the inadequacy of our information on distribution (the "Wallacean shortfall": Wallace 1879; Lomolino 2004), his linking of bird migration to natural selection (Wallace 1874), and his suggestion that the animal extinctions at the end of the Pleistocene Epoch might have been due to overhunting by prehistoric humans (Wallace 1876).

Beyond these associations, there is the possibility that some of Wallace's ideas and approaches may have yet unperceived relevancy. The glut of attention that has been lavished on the stodgier, more conservative Darwin has made it difficult for many to even entertain the notion that evolution might be organized around additional forces beyond natural selection. There is also the problem that generations of students of the subject have been inculcated with the misinformation that Wallace's and Darwin's ideas on both natural selection and evolution in general are nearly identical. They are not. Wallace's version of natural selection reduces to the more ecologically connected notion of the "elimination of the unfit"; that is, the apparently unassailable proposition that less well-adapted individuals should be more quickly removed from a population than better-equipped ones are. This leaves the question of just how the "better equipped" individuals contribute to an overall evolutionary process rather untouched—that is, without bringing into the matter complicated large-scale and long-term biogeographical causalities. Neither Wallace nor Darwin directly concerned themselves with this aspect of the problem, but it can be argued that Wallace's peculiar viewpoint makes it easier to connect the immediate facts to the larger scale (Smith 2008; in press). Darwin, by contrast, focused on relating particular adaptive structures to logical sequences of causation (for example, his sexual selection model, in which females of the species are attracted to males of showy or aggressive disposition, thus accounting for the development of colorful and/or flashy plumage or display in males, but not in females)—an approach that has caused some to characterize his model of natural selection as tautological or even teleological (Reiss 2009).

But this is only to contrast their ideas on natural selection *per se*. When it came to the more general matter of evolution overall, their positions were a good deal more different yet. Darwin was a rather conventional scientific materialist; if he had any significant religious beliefs, he kept them quite separate from his natural history theorizing. On the matter of the evolution of consciousness and advanced conscious acts he simply felt that these had emerged over evolution as had any other adaptive trait. Wallace, meanwhile, although rejecting purely theistic views (he had, in fact, a rather dim view of organized religion in general), thought he recognized a general progression in evolution, specifically in a direction leading to beings of advanced consciousness. In mid-life he became a spiritualist, ostensibly because he felt he had seen enough to convince him that the "natural world" extended beyond the immediately perceivable to realms outside of conventional materiality. At the same time and through the rest of his life, meanwhile, he continued to support the basic understanding of natural selection that he and Darwin had created. Wallace has sometimes been demonized as a theist, or as a purveyor of teleology, but in actuality he simply was an "ultra-naturalist" believer in the notion of final causes. He concluded that there is a "plan" to evolution—not one obeying godly first causes, however, but instead one organized according to ever-more remotely actualizing natural laws.

This seems to move us away from the realm of biogeography, but as mentioned earlier this is a study whose subject is extremely complex. Clearly, there can be no complete model of biogeographical processes without a complete model of evolution, and any evolutionary position accepting some manner of mind-body duality would inevitably lead to an entirely different perspective on all those aspects of plant and animal distribution affected by human goals and activities.

Biogeographers of today, meanwhile, largely continue to explore directions set out in the last wave of major theory creation in the 1960s, 1970s, and 1980s, in so doing playing out many of the themes already present in the work of Wallace, Darwin, and others. But now they benefit from more advanced Earth systems models, field and laboratory techniques, and statistical analysis algorithms. They also benefit from an ever-increasing knowledge of "what lives where," both from current-day field studies of living things and from the paleontologic record. Thus, the connections between distribution and its many causes become more evident.

Societal pressures help propel this process. Biodiversity loss, for example, is a serious societal problem, and researchers are tackling it from a variety of directions: from economics and politics, to genetics and ecology. Biogeographers have a major role here, taking part in the monitoring of species population levels, the sorting out of phylogenies, the documentation and interpretation of large-scale diversity trends, and the search for environmental characteristics that can be linked to ecosystem health. We are a long way from understanding what forces conspire to produce mature patterns of distribution, much less from understanding exactly how things go wrong when these forces are tampered with.

WALLACE AND BIOGEOGRAPHY LITERATURE SOURCES

As far as Wallace goes, real progress has been made over the past ten or twenty years in redressing the imbalance of attention created by the "Darwin Industry." Although there had been previous biographies of Wallace, four very good ones appeared in rapid succession right after the millennium (Raby 2001; Shermer 2002; Fichman 2004; Slotten 2004); each has qualities to recommend it. Several anthologies of Wallace's writings have also been produced (Smith 1991; Berry 2002; Camerini 2002; Smith 2004), and an edited collection of writings on Wallace was published a few years back (Smith and Beccaloni 2008).

In addition, two, and shortly four, extensive websites on Wallace exist. The author's *The Alfred Russel Wallace Page* first went online in 1998, and has been expanding ever since. It features my own bibliographic investigation into Wallace's published materials, including nearly a thousand careful transcriptions of his writings (over six hundred of which I personally "rediscovered") and various secondary literature resources. George Beccaloni's *The Alfred Russel Wallace Website* opened a couple of years back, supported by the Natural History Museum (London) and the Alfred Russel Wallace Memorial Fund. Beccaloni's site features image galleries and a greater emphasis on Wallace as a popular figure in today's world than does mine; it hosts several blogs, interfaces with the Natural History Museum's collection of Wallace materials, and links to ongoing Wallace studies projects around the world.

Beccaloni, an entomologist, has also received a sizable grant to support a Wallace correspondence project, now underway and scheduled for completion on the anniversary of Wallace's death in 2013. The historian John van Wyhe, meanwhile, backed by the National University of Singapore, is developing a website on Wallace that will parallel his already operating *The Complete Works of Charles Darwin Online* resource. It, too, should be ready for access by 2013.

Access to the literature of biogeography is a more complicated matter. There is no dictionary of biogeography or encyclopedia of biogeography or indexing or abstracting service that does a good job of covering the entire field. Still, most of its significant publications can be identified through prudent use of the databases Biosis Previews, GEOBASE, OCLC WorldCat, Web of Science, and Scopus—or, in a pinch, the free online services Google Scholar and Google Books. The author provided a monographic review (Smith 2000) of the literature of the biodiversity studies movement that incorporates many biogeography topics; a year later, I published a review in *Choice* that included mention of many individual titles (Smith 2001).

Before 1974, there had only been a few abortive attempts to establish professional journals specifically dealing with subject. In that year the now best-known title was launched, the *Journal of Biogeography*

(Blackwell). In succeeding years a number of additional titles have appeared, including *Global Ecology and Biogeography* (Blackwell), *Diversity and Distributions* (Blackwell), *Systematics and Biodiversity* (Cambridge), *Plant Ecology and Evolution* (Royal Botanical Society of Belgium and the National Botanic Garden of Belgium), *Ecography* (Blackwell), and *Frontiers of Biogeography* (International Biogeography Society). Additional foreign language venues exist, but it almost goes without saying that the vast majority of biogeography-related articles still appear in journals that focus on a vast range of cognate subjects.

Several histories of biogeography have been written, and central aspects of its history (as related to evolutionary theory, for example) have been discussed in many other works. Janet Browne's *The Secular Ark: Studies in the History of Biogeography* (1983) is the best single volume study of the field's development up through the Darwin-Wallace revolution. David Quammen's *The Song of the Dodo: Island Biogeography in an Age of Extinctions* (1996) provides a good readable treatment of the history of island biogeography as related to present-day conservation biology. The best review in the cultural biogeography realm is Alfred W. Crosby's well-known 1972 work *The Columbian Exchange; Biological and Cultural Consequences of 1492*. Two excellent recent overviews of the history of the field as a whole are those by Williams and Ebach (2008) and McCarthy (2009).

Throughout the years a good number of textbooks providing summary introductions to the field have appeared; at the moment the two most popular titles seem to be Cox and Moore (2010) and Lomolino (2010), both of which have been around for decades and have gone through several editions. A new treatment of the spin-off subject of conservation biogeography has also recently been released (Ladle and Whittaker 2011).

Online, a wide range of resources are available. The websites of the two main biogeography-centered societies, the International Biogeography Society and the Systematic and Evolutionary Biogeographical Society, are instructive as to entry into the professional side of the field. The author maintains three biogeography-centered websites: the historical/biographical-oriented *Some Biogeographers, Evolutionists and Ecologists: Chrono-Biographical Sketches*; and the historical/anthology-focused twin sites *Early Classics in Biogeography, Distribution, and Diversity Studies: To 1950* and *Early Classics in Biogeography, Distribution, and Diversity Studies: 1951–1975*. The first provides short biographical sketches of about 275 figures, whereas the second two concentrate on key works over the history of the field. A larger-scale effort is the *Biodiversity Heritage Library*, which although not restricted to biogeography alone, offers access to many related historical sources. Beyond this, there is an ever-increasing number of online projects providing information on individual species and conservation efforts; discussion of these in any detail would require a separate effort.

THE FUTURE?

Predicting the future is always a risky business, but for the time being, at least, it would appear that interest in biogeography—and Wallace—is likely to continue to maintain itself or increase. One of the byproducts of the recent Darwin bicentennial has been a heightened curiosity over Wallace and his work. A quick Google Scholar search reveals that his name comes up about 31 percent more often annually in articles published in 2008–2010 than it does in articles over the period 2001–2007; the increase between 1997–2000 and 2008–2010, moreover, is over 200 percent. This trend cannot be maintained indefinitely but should continue over the short term, at least, as 2013 will mark the centennial of his death, with corresponding publicity (books and conferences are in planning). Meanwhile, through the same period, 1997–2010, the word "biogeography" appears: (1) in the titles indexed by Google Scholar at a fairly consistent, or slightly increasing, rate and (2) as a keyword in all items indexed in Google Scholar at a continuing rate of increase of about 10 percent each year.

As to what students of Wallace and biogeography will be studying in coming years, only time will tell—but a couple of guesses might be made. My own investigations of Wallace bibliography are not exactly grinding to a halt (especially since additional full-text collections of Victorian period literature continue to emerge), but apart from his earliest period (say, circa 1841 to 1848), it seems unlikely that much more in the way of striking new information can be found in this direction. Attention will likely shift to the results of Beccaloni's project and the something-like five thousand letters he is tracking.

Biogeography as a systematic biology endeavor is likely to continue indefinitely: the diversity of life is enormous, extending, most likely, to several millions of species, most of which are still unknown and/or undescribed. For each of those species there is a story, not merely ecological, but historical as well. The exploration of this labyrinth of interrelations can be justified as basic science, but it is also true that such exploration can reveal characteristics of life that could be greatly beneficial to humankind (for example, within the world of pharmaceutical drug development).

It is the more abstract side of the field, however, that presents the greatest challenges for investigators. It is easy enough to identify correlations between distribution and various biological and physical factors, but quite another matter to discern which are significant and which are spurious. Further, what works for a species in the short-term sense as an adaptive ecological strategy may lead to disastrous longer-term results (for example, those animal species choosing to resemble a plant structure or some other, perhaps noxious, animal, may rapidly go extinct if something happens to wipe out the species they are mimicking). Evolution cares little about the temporary success of individual species groups; it is mostly about the Earth system.

I believe the biogeographers of the future must give greater attention to how the most basic elements of the ecosystem cycle through it and how this affects a population's ability to enter into ecological associations and disperse. Wallace (1858) saw how natural selection primarily operated to keep natural systems in balance; in this view, natural selection is more of a regulator than it is an originator. For any organism to be successful in the longer-term sense it must develop ways to be "in the right place, at the right time" to collect and process the resources it needs to survive. Where vital resources are difficult to find or infrequently available, much of the organism's genetic budget must be invested in developing specialized adaptations to obtain and/or store them; conversely, more benign environments sponsor a kind of evolution less tied down in this way. It is first and foremost a matter of determining what defines the word "benign" in this instance. I predict that this understanding of the natural order—one harkening back to Wallace's original vision—will eventually be the one that yields models more attuned to a lasting appreciation of what lives where, and why.

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