

Wallace's legacy: from biogeography to conservation biology

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Figure 1. Alfred Russel Wallace as a young man in Singapore in 1862, at the start of his expedition around the Malay Archipelago.

Alfred Russel Wallace (Figure 1) is best known as the co-discoverer of evolution by natural selection. While suffering from a malarial fever somewhere near the remote island of Ternate, he realised that if heritable variation between individuals in a species existed, and furthermore that if this variation had some impact on survival, then species should gradually evolve to become adapted to their environments. These ideas, hastily assembled into a paper that he sent to Charles Darwin, whom he knew had some interest in evolution, were subsequently published with Darwin as a co-author in the *Journal of the Proceedings of the Linnean Society of London* (Darwin and Wallace 1858), and the world of biological sciences was changed forever.

However, Wallace wrote on an extraordinarily wide range of subjects, and it is unfortunate that these contributions have been somewhat overshadowed by his co-discovery of natural selection. He was instrumental in founding the field of biogeography, the study of the factors driving the geographical distributions of plants and animals, and his ideas relating to conservation biology were surprisingly wide-ranging. He also wrote extensively on such diverse topics as politics, spiritualism, astrobiology and anthropology. Here we will focus on his contributions to the two linked fields of conservation biology and biogeography.

Even in his famous paper on natural selection, there is a hint that he is aware that man's impact on the natural world is not a positive one: "*Even the least prolific of animals would increase rapidly if left unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing.*" (Darwin and Wallace 1858). Indeed, he documented the negative impacts of the "*fast diminishing forests*" on St Helena (Wallace 1880). He also worried that although the King Bird-of-paradise (*Cicinnurus regius*) was a stunningly beautiful creature, which Europeans would flock to the Aru

Islands (part of present-day Indonesia) to see, that this would result in the destruction of this species' habitat, and its eventual loss: "*... should civilized man ever reach these distant lands ... we may be sure that he will so disturb the nicely-balanced relations of organic and inorganic nature as to cause the disappearance, and finally the extinction, of these very beings whose wonderful structure and beauty he alone is fitted to appreciate and enjoy.*" (Wallace 1869). Presumably, however, Wallace would be pleased to have known that this species would go on to survive for at least another 150 years, with it currently being listed by the IUCN as a species of "least concern" (BirdLife International 2012).

Perhaps as a result of his concerns over habitat loss, Wallace was an early advocate of environmental vegetarianism. In a letter he states, "*I believe in it [vegetarianism] as certain to be adopted in the future ... far less land is needed to supply vegetable than to supply animal food.*" (Wallace 1900). Subsequent assessments quantifying the impacts of dietary choices on the environment have proved him to have been correct, although interestingly it seems that to be most efficient one should consume a small amount of meat or dairy products, since marginal

areas of land are often only suitable for grazing (Peters et al. 2007).

Wallace also noticed that disturbance by humans often led to increased vulnerability of habitats to invasion by species from elsewhere, and that this could make it difficult for native species to recolonize these areas. Specifically, he observed that clearance of forests in North America had led to the spread of imported weeds (Wallace 1891), and that the introduction of goats onto St Helena had been catastrophic, with the destruction of many native tree species and "*...with them all the insects, mollusca, and perhaps birds directly or indirectly dependent on them.*" (Wallace 1876). This shows an advanced degree of understanding of the way that the interconnected nature of ecosystems can affect their resilience to perturbation.

We think of human-induced climate change as something of which we, as a species, have only recently become aware, but Wallace was worrying about this in the 19th century. He noticed an article in a gardening periodical in which some subscribers had collated records indicating that certain types of fruits and vegetables could no longer be grown, and ascribed this to human impacts on the climate: "*... clearly*



Figure 2. A map of South East Asia from Wallace's book *On the Physical Geography of the Malay Archipelago* (Wallace 1863) showing what would become known as the Wallace line, separating faunas with oriental affinities from those with Australian affinities.

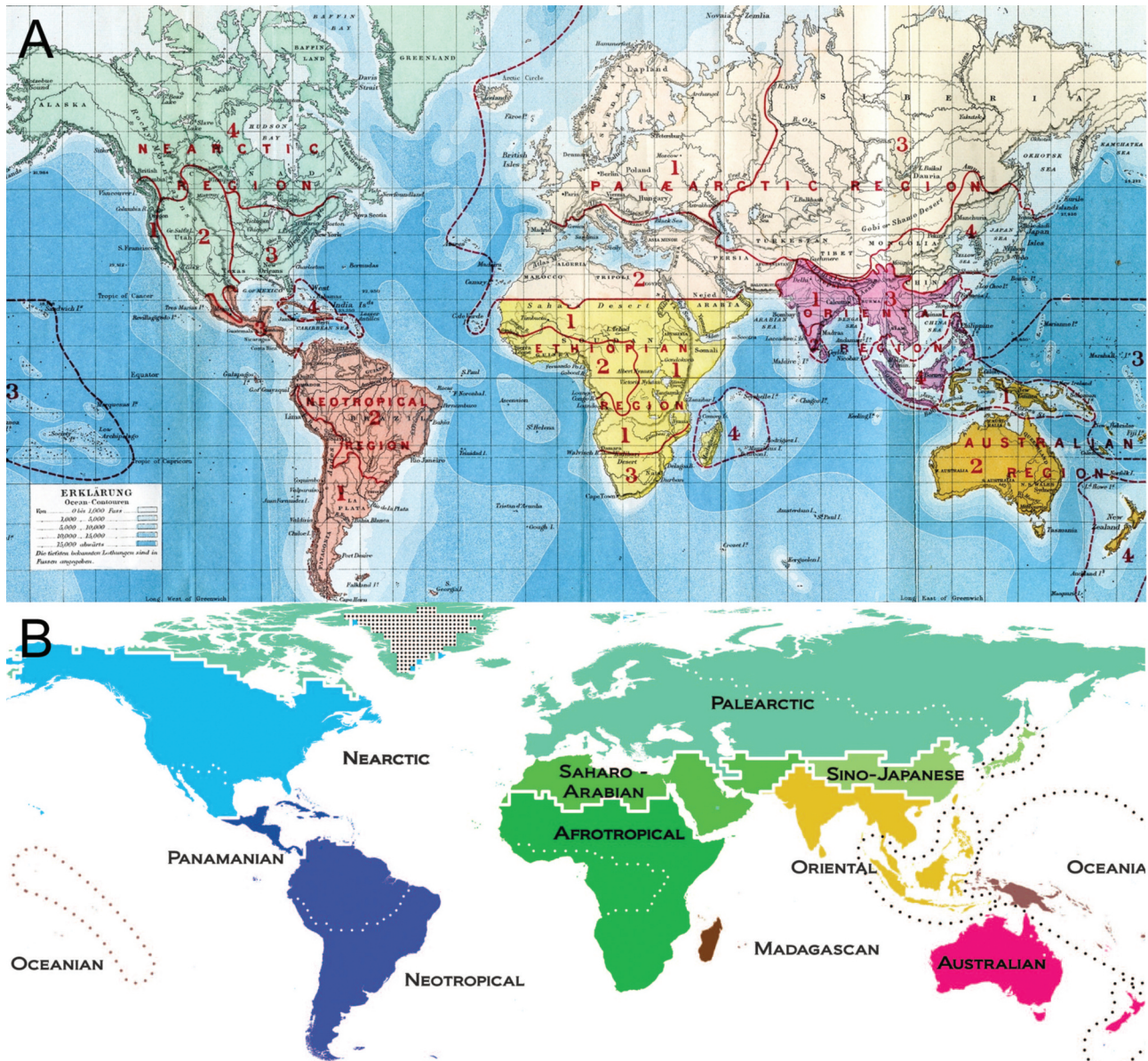


Figure 3. A) Wallace's map of biogeographic regions, based on records of vertebrates available to him in 1876, and his own observation (Wallace 1876). B) Biogeographic regions based on genetic data from Holt et al. (2013) An Update of Wallace's Zoogeographic Regions of the World. Science 339:74-78. Figure reprinted with permission from AAAS. The analytical method that generated this map did not use any prior information of the boundaries of Wallace's biogeographic regions. Note the differing projections of the two maps.

indicating a comparatively recent change of climate ... increase in cloud and consequent diminution of sunshine ... owing to the enormously increased amount of dust thrown into the atmosphere as our country has become more densely populated, and especially owing to the vast increase in our smoke producing manufactories." (Wallace 1898). More recent work has found that these worries were well-founded, and "global dimming", as it is now called, was a real phenomenon over the latter half of the 20th century, with particulate pollution both blocking sunlight directly and increasing the density of nuclei for condensation of water, and therefore increasing cloud cover (Mishchenko et al. 2007).

However, the magnitude of global dimming is now much decreased, following the introduction of laws on emissions.

Although his awareness of conservation issues was impressively broad for the period, the main focus of much of Wallace's work was the study of the distributions of animals and plants. The initial indications that he was aware of the importance of geography in driving the distributions of species came on his first trip to the tropics, to the Amazon. Here he noticed that some species of monkey were present on one side of the larger rivers, but not on the other: "...the Amazon, the Rio Negro and the Madeira formed the limit beyond which certain

species never passed. The native hunters are perfectly acquainted with this fact, and always cross over the river when they want to procure particular animals, which are found even on the river's bank on one side, but never by any chance on the other." (Wallace 1852). These observations inspired a quantitative study 140 years later, which showed that this was indeed the case, and furthermore that the wider, and faster-flowing the river, the more different the sets of species of monkeys from opposite banks (Ayres and Clutton-Brock 1992).

While Wallace's Amazon expedition was ill-fated, with the loss of the majority of his specimens due to the sinking of his ship, he would go on to

develop extensively the biogeographical ideas initiated during that period, in particular during his second tropical expedition, to SE Asia (Figure 1). In Sarawak, then the domain of the Rajah Brooke, now a state in Malaysian North Borneo, he formulated what would become known as his Sarawak Law. He stated, “*Every species has come into existence coincident both in time and space with a pre-existing closely allied species.*” (Wallace 1855). This deduction, which preceded his revelation regarding natural selection, came about as a result of his extensive observations of the distributions of species, and his painstaking work studying the minute differences between them. Here was a first indication that the evolutionary history of species (and groups of species) could have some bearing on their present day distributions.

As he travelled further around the Malay Archipelago, mainly through what is now Indonesia, Wallace noticed that there was a sharp demarcation in the flora and fauna present on either side of a line running between the islands of Bali and Lombok, north between Borneo and Sulawesi, and then to the south of the Philippines. The areas on either side of this line did not differ consistently in terms of volcanic activity, climate, or any other factor that might directly influence the distributions of species. However, many of the islands on the west side of the line sat on a shallow shelf in the ocean

connected to the Asian mainland, while many of those to the east were connected by a similar shelf to the islands of Australia and New Guinea. Combining his ideas regarding the influence of geographical barriers, and the potential for species’ evolutionary histories to affect their present-day distributions, Wallace concluded that changes in the level of the land relative to that of the sea had given rise to these two nearby, but very different, floras and faunas (Wallace 1863). The boundary between these two regions subsequently became known as the Wallace Line (Figure 2).

When Wallace returned from his travels he continued to collate information on the global distributions of animals and plants, and eventually constructed a map, based on the distribution of vertebrates, delineating regions within which the sets of species present were similar, and between which they were not (Wallace 1876). These biogeographic regions, as they became known, have been in use ever since. Over the last twenty years an enormous amount of information on the evolutionary histories of species has become available through the assessment of genetic similarities between them. A recent study in the journal *Science* used these data to reassess the validity of Wallace’s regions, and found a remarkable agreement between the two maps (Holt et al. 2013; Figure 3). It is quite

extraordinary that Wallace, having access to relatively limited records of animal distributions, and using morphological information to determine species’ evolutionary relationships, constructed a map so similar to that generated from molecular data today.

The man known to many solely for hurrying a procrastinating Darwin into the publication of the theory of evolution by natural selection was in fact a polymath, with interests in many areas. His ideas relating to the conservation of animals and plants were many decades ahead of their time, and his theories on the factors driving the distributions of these groups founded the discipline of biogeography.

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