INTRODUCTION AND COMMENTARY

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Islands have long held a special place in our understanding of the natural world. By the mid-1700s, long before Charles Darwin and Alfred Russel Wallace made their world-shaking observations of the process of natural selection in the Galapagos Islands and the Malay Archipelago, biologists such as Joseph Banks, Alexander von Humboldt, Johann Forster, and George-Louis Leclerc, Comte de Buffon, were stunned to learn of the presence of a great many endemic species of plants and animals on individual islands or archipelagoes in deep waters, wherever such islands existed throughout the world's oceans. The presence of large numbers of unique species on small and isolated islands posed a great puzzle, given the widespread view of European society at the time that each species was the result of divine creation and placement in its native range. Fed by the "cabinets of curiosity" mania that existed in Europe at that time, discovery of progressively more previously unknown endemic island species posed an increasingly greater problem. How have so many species come to be present on the earth, and specifically, why are there so many unique species on islands?

The most widely known answer to the first part of that question arrived in 1858 with the simultaneous publication of papers by Wallace and Darwin on the process of evolution by means of natural selection. Biological diversity and distributions, they proposed, resulted not from special creation but rather from natural processes. Although the process of evolution by means of natural selection took decades to become widely accepted, and advances in understanding the details, complexity, and genetic basis of evolution continue to this day, it is widely hailed as one of the single most important scientific discoveries in the history of humankind. The second part of the question—the startling diversity and endemicity of insular biotas—was addressed by Wallace twenty-two years later, in 1880, in *Island Life: Or the Phenomena and Causes of Insular Faunas and Floras*.

For over 150 years, Wallace has been widely acclaimed as the codiscoverer of natural selection. But in doing so, he is often described as remaining in the shadow of Charles Darwin (e.g., Shermer 2002), with the implications that Darwin's contributions to evolutionary biology were the greater and that Wallace's recognition of the existence and power of natural selection was his primary contribution to our knowledge of the natural world. However independent and insightful was Wallace's contribution in that regard, even Wallace himself politely and steadfastly deferred to Darwin as the greater authority. In textbook accounts of Wallace, he has thus sometimes come to be seen as little more than Darwin's "sidekick."

That view of Wallace is certainly an egregiously misleading caricature. Wallace may well have been quite willing to defer to Darwin on the discovery of natural selection, but I suggest that there is an alternative explanation for Wallace's deference that may be more powerful: Wallace clearly did not define himself solely or primarily as the codiscoverer of natural selection. While he was aware of the importance of that contribution, his writings make it clear that he spent much of his life absorbed in a different set of issues. For Wallace, one of the abiding and most appealing questions was related to natural selection, but not limited to it: Why is the presence of distinct species, and their phylogenetic relationships, so closely tied to geography? and specifically, why are there so many unique species *on islands*?

These questions were foremost in Wallace's mind from a very early point in his life, as evident in one of his first publications, on the distribution of monkeys along the Amazon River (Wallace 1854), that resulted, in part, from his fieldwork along the Amazon and its tributaries from 1848 to 1852. By 1855, while conducting field studies on Borneo, he had clearly developed not only an interest in the mechanism of what we now call speciation and evolution but had also recognized the central role of geography in these processes. In "On the Law Which Has Regulated the Introduction of New Species," which he wrote in Sarawak, Borneo, and published in the *Annals and Magazine of Natural History* in September 1855, Wallace observed that orders and families of organisms tended to be globally widespread, but families and genera were progressively more geographically limited. In species-rich areas, such as the tropics, species tended to occur either in limited overlap with or adjacent to their closest relatives, suggesting a continuity and gradual diversification of species. From this, he deduced a "law": each species came into existence adjacent to its closest relative; no species ever came into existence twice; and areas with seemingly identical climate and soil but geographically isolated from each other almost never had shared species. This law led him to state the crucial importance of several general, interrelated issues that foreshadowed many of the ideas he would develop most fully in *Island Life*: the relationships of families, genera, and species to one another; the geographic distributions of organisms at varying degrees of relatedness; and the current and past distributions of organisms as influenced by past geological and climatic changes. He cited Darwin's observations on the organisms of the Galapagos Islands as a key example, saying that the groups now present had arrived by the action of wind and sea currents, and over an extended but unknown period of time the original colonists were replaced by diversified descendants. This process, Wallace said, had gradually played out all over the surface of the earth over long periods of time. "To discover how the extinct species have from time to time been replaced by new ones down to the very latest geological period is the most difficult, and at the same time the most interesting problem in the natural history of the earth" (Wallace 1855, 190).

Indeed, as this example makes clear, a case can be made that Wallace's recognition of natural selection was made in the pursuit of questions he found compelling about the evolutionary origins of patterns of distribution of organisms, rather than the driving interest in the process of selection (natural, artificial, and sexual) that so strongly influenced Darwin. Perhaps Wallace deferred to Darwin in the area of natural selection because Wallace believed his own primary evolutionary interests and accomplishments lay elsewhere.

I must state clearly at this point that I find *Island Life* to be simply stunning. Its breadth of information about the distributions of plants and animals alone would be worthy of admiration, coming at a time when such information had been summarized in only limited fashion. But Wallace also fully integrated a wealth of data from recent geological, paleontological, bathymetric, and astronomical studies that hugely expanded the context of his interpretations, allowing him to develop insights and understand processes that had only barely been imagined by biologists previously. We know that Charles Darwin, Joseph Hooker, Thomas Huxley, and other British scientific luminaries of his day responded similarly, causing Darwin to write to Wallace that *Island Life* "is quite excellent, and seems to be the best book which you have ever published" (quoted in Slotten 2004, 360). Indeed, it was the publication of this volume that led them to obtain for him a lifetime pension from the British government in 1881 (Raby 2001, 222–26). When, late in his life, Wallace himself listed his ten most important ideas, he included his creation of the science of island biogeography, his identification of the causes of glacial epochs and the geographic changes that accompanied them, and his recognition of the permanence of continents and deep seas (in contrast to alternative theories of "vanished continents" such as Atlantis and Lemuria, as discussed below), all of which Wallace developed in *Island Life* (Shermer 2002, 290–91).

In writing this overview of *Island Life*, I have taken a specific and deliberate approach. My own research interests focus on island biogeography, a field of study that I view as having its origins in the writings of the earliest biogeographers and evolutionary biologists (as we would define them today), but which had its first thorough conceptual development and exposition in this volume. In other words, I am interested in *Island Life* for its role as constituting the first comprehensive synthesis of data, presentation of hypotheses, and definition of issues in island biogeography. Wallace explicitly intended *Island Life* to be a comprehensive overview of pattern and process in island biogeography, utilizing every source of information available to him; this introduction is intended to identify the patterns and processes that he highlighted and to point out the ways in which he integrated the complexities that he recognized.

I have not attempted to place *Island Life* into a comprehensive historical context in the development of biogeography; that would require a worthy but very different type of effort. Also, I have not attempted to consider *Island Life* in the context of Wallace's work on the many other diverse topics that attracted his attention over his long and complex life; most of the recent biographies of Wallace have done so (e.g., Raby 2001; Shermer 2002; Slotten 2004), with the result that those biographies say rather little about this volume and his research on island biogeography. Rather, I have focused on one primary question: What did Wallace say about island biogeography in this, the first comprehensive effort to understand this field of study?

In doing so, I have relied heavily on Wallace's own words. The language of biogeography, and biodiversity science in general, was quite different in 1880 than it is today. As I began writing, I found that describing Wallace's statements using current terminology sometimes changed his meaning and perspective, often subtly but other times more dramatically. Also, the fact that Wallace wrote—as did Darwin and others of his colleagues—in long, complex, and sometimes ponderous sentences and paragraphs makes it difficult to quote him succinctly. I have done my best in this regard but have been careful to cite the pagination of each quotation, so that the reader can easily find the full text and determine the degree to which my selective quotes convey Wallace's meaning. Having provided these quotation-based summaries, I have then often added some brief commentary that places his perspective into a current context, clearly separating my comments and perspective from those of Wallace.

Geographical Distribution: The Descriptive Foundation

Wallace's 1876 two-volume set of books, *The Geographical Distribution of Animals*, is often described as one of the most influential milestones in the study of what is now called biogeography, the study of the geography of nature. Previous efforts to describe broad patterns in the distribution of living and fossil organisms had been based either on much less complete information or on more limited taxonomic groups (e.g., Sclater 1858). Wallace's compilation and analysis showed him to possess an encyclopedic knowledge of the distributions of all animals, to the extent they were known at that time, including not only birds and mammals but also other vertebrates and many invertebrates, fossil and extant. Indeed, it is often treated as his single greatest contribution to biogeography and is frequently cited as the primary basis for referring to Wallace as a principal founder of biogeography (e.g., Claridge 2009; Cox and Moore 2005; Lomolino, Riddle, and Brown 2006, 26–27).

While there can be no doubt about the impact and importance of this massive compilation of information, inspection of the two volumes of *Geographical Distribution* shows it to be largely descriptive; it was his intent to summarize distribution patterns on a grand scale, and he succeeded. But with only 49 of the 1,110 pages devoted to discussion of processes, and the rest to documentation of patterns, Wallace had taken a crucial first step in establishing the foundation of biogeography but left much undone. In the preface to *Island Life*, he referred to it as the "completion of that work [*Geographical Distribution*]," based on "four years additional thought and research." (p. vii). In spite of the scientific rigor and the volume of detail, Wallace clearly intended *Island Life* for a broad audience, saying that "the present work is . . . addressed to a wider class of readers than my former volumes" (p. 442), and several times in the text of *Island Life* he referred to the additional data and more definitive conclusions than he had presented in *Geographical Distribution*, including the importance of integrating information on plant biogeography to obtain the broadest possible framework and perspective (e.g., pp. 457 and 508). After the publication of *Island Life*, he shifted his primary focus to other issues on a wide range of topics, never again attempting a grand synthesis in biogeography.

Content and Approach of *Island Life*

Throughout *Island Life*, Wallace was generous in giving credit to others, most often to Darwin (in twelve places), but also to less prominent and influential figures, such as T. V. Wollaston, who studied invertebrates on St. Helena (p. 286). Indeed, the index to *Island Life* included ninety-three different authors, far more than the few dozen that Darwin (1859) cited in *The Origin of Species*. Wallace clearly viewed his role as being that of a synthesizer and theorist and saw value in crediting others for their empirical contributions.

Island Life is marked by a powerful flow of logic, each step in the argument thoroughly documented by evidence, and each step is essential to the conclusion. Wallace marshaled strongly supportive data from diverse fields and disciplines, always carefully balanced and any potential weaknesses explicitly identified. Remarkably, given its length and breadth of issues, the book constitutes a single essay, developing an integrated set of principles and leading to a very specific set of conclusions. The data, and the inferences based on them, are clearly stated, and Wallace often explicitly stated how they may be tested (and possibly rejected). The integration of data from many sources allowed complex argumentation and understanding; as detailed below, Wallace explicitly argued strongly against simplistic explanations for complex phenomena.

While *Island Life* is a book about island biogeography (the study of the evolutionary origins and ecological maintenance of biological diversity on islands and in island-like settings), and indeed recognized and established the core concepts that dominate the field today, Wallace was clear in stating that it was about much more than island biotas alone. According to Wallace, "islands offer the best subjects for the study of distribution" (p. 3); in today's terms, he used islands as a model system for understanding biogeographic patterns in the world at large. This may seem a somewhat obvious statement today, given its repetition by biogeographers for 130 years, but it was in this volume that the case was made for the first time, and Wallace was entirely correct in saying that synthesis "was almost impossible till quite recently" (p. 7) due to (1) the absence of a theory of "descent with modification"; (2) prior acceptance of "special creation"; and (3) the insufficiency of crucial information about (a) the distributions of many organisms, (b) the fossil record, (c) stratigraphic geology, (d) ocean-floor bathymetry; and (e) orbitally forced climatic cycles (pp. 7–9). These topics are acknowledged and accepted today as crucial components of biogeographic analysis, but in 1880, Wallace's recognition of the need to incorporate such diverse topics, and to develop them into a broad synthesis, was genuinely novel.

According to Wallace, his purpose with *Island Life* was "the development of a clear and definite theory, and its application to the solution of a number of biological problems" (p. 499); "my object in this volume being more especially to illustrate the mode of solving distributional problems by means of the most suitable examples" (p. 399). Wallace clearly enjoyed the challenge of discovering solutions, saying, for example, that Borneo "offers us some problems of great interest and considerable difficulty" (p. 348). His method was to "accept the results of . . . science, and the ascertained facts . . . ; to take full account of the laws of evolution as affecting distribution, . . . and the result is [that] wherever we possess a sufficient knowledge of these various classes of evidence, we find it possible to give a connected and intelligible explanation of all the most striking peculiarities of the organic world" (p. 419). Throughout the volume, he often used strong inference to determine the likelihood of a possible explanation; for example, in discussing the evidence that the British Isles were recently connected with the adjacent continent, he stated that if this were so, then the British Isles should be expected "to show an almost perfect community with the adjacent parts of the continent in its natural productions [i.e., its fauna and flora]; and such is found to be the case" (p. 318).

Part 1: The Determinants of Biogeographic Patterns

Island Life is divided into two parts, the first being an extensive investigation of the processes that influence the distribution patterns of life on earth. At 229 pages, it is nearly as long as the second portion (282 pages) that describes illustrative insular faunas and floras of the world as an exercise in further investigating the processes and contributing factors developed in part 1.

Wallace began part 1, entitled "The Dispersal of Organisms: Its Phenomena, Laws, and Causes," with a brief introduction in which he described an imaginary journey (by an Englishman) from England to Japan, a distance of 13,000 miles, at the end of which the traveler finds that most of the birds, butterflies, and beetles are closely related to those that live where his journey began. Let that same Englishman travel from Australia to New Zealand, a distance of 1,300 miles, and he would find species "totally unlike those" where he began. Saying that "there are some more striking cases even than this," Wallace then compared the great difference in biotas between Bali and Lombok, a distance of 15 miles, and between Florida and the Bahamas, a distance of 50 miles, with virtually no change in climate or soil (pp. 3–4); "some [faunas] exactly resemble the nearest continents, others are widely different." For these perplexing observations, "there is no short and easy method of dealing with them," but "the time has now arrived when their solution may be attempted with some prospect of success" (p. 6). The complexity arises because the patterns are the "outcome and . . . product of the whole past history of the earth" (p. 6), influenced by climate, changes in sea and land, persistence, migration, and extinction.

Wallace then pointed out that "so long as the belief in 'special creations' of each species prevailed, no explanation of the complex facts of distribution *could* [italics Wallace's] be arrived at or even conceived; for if each species was created where it is now found, no further inquiry can take us beyond that fact" (p. 8). Instead, use of new information from the fossil record, stratigraphy, ocean-floor bathymetry, alterations in climate, geological change, and the diversification of organisms "give us a command of the more important facts and principles on which the solution of [biogeographic] problems depends" (p. 11).

In the second chapter, Wallace proceeded to lay out some essential "elementary facts." Every species has a certain area of distribution, with some limited fluctuations, often continuous but also sometimes confined to one habitat within that area (such as the chamois, which occurs only in high mountains but is widespread over much of Europe; pp. 13–14). The distribution may be quite large or rather small, and this may be the case for birds as well as for less vagile groups. The species of a genus often show little or no overlap but frequently occur in an area near their closest relatives. Higher taxonomic levels (genera, families, etc.) tend to have broader distributions than lower levels, though some are quite restricted, and some occur in widely disjunct areas. In the third (and largely descriptive) chapter, Wallace returned to the primary subject of *Geographical Distribution*, making the point at length that political boundaries bear little resemblance to natural biogeographical units and acknowledging the great utility of Sclater's (1858) system of global biogeographic regions, which had been based solely on the distribution of passerine birds.

The fourth chapter, entitled "Evolution the Key to Distribution" deals with "the origin and development of species and groups by natural selection," a matter that "has been much neglected" (p. 54). Wallace was explicit that he would confine himself to the origin of species and genera and not consider higher taxa, which allowed him to stay within the relatively well-known Tertiary period (from the beginning of the "age of mammals," now defined as ca. 65.5 MYA, extending to the beginning of the Pleistocene "ice ages," ca. 2.6 MYA) and avoid disputed questions about the origins of higher taxa (p. 55). He began by saying that "new species can only be formed when and where there is room for them." He directly disputed the notion that every location is "filled by creatures perfectly adapted to all surrounding conditions . . . such a perfect balance of organisms nowhere exists upon the earth." Some species are better adapted than others, as evidenced by differences in abundance, and when climatic or geological changes take place, some "ill-adapted" species may die out, "and thus leave room for others to increase, or for new forms to occupy their places" (pp. 55–56). Those changes in conditions will affect even the abundant species, with some individuals benefiting, others suffering, and the entire population changing as a result (p. 56). In current terms, Wallace took a dynamic, nonequilibrial view of species and communities, with changes in community composition due to extinction and colonization, and species changing because of ongoing natural selection. He acknowledged the potential for periods of stasis but seemed to view that condition as unusual and ephemeral. In support of this view, he cited the extensive evidence of geographic variation within many species (pp. 56–59).

He then went on to state that when a geological or climatic event cuts a distribution into two parts, divergence is inevitable, resulting in the formation of two allopatric species (pp. 59–60).

Abundant, "dominant" groups will often give rise to new species as they disperse outward into new areas and then become isolated. Eventually, the "component species will dwindle away and become extinct," though sometimes "a few species will continue to maintain themselves in areas where they are removed from the influences that exterminated their fellows" (p. 61). They often survive "in islands which have been long separated from their parent continents" or in unusual habitats on continents (such as caves or tropical forests; p. 62). This view of dispersal by abundant species to islands, followed by speciation, decline, and extinction, bears strong similarity to the "taxon cycle" (Wilson 1961; Ricklefs and Birmingham 2002).

For Wallace, the presence of discontinuous distribution by the species of a genus, or genera within a family, was evidence of the "antiquity" of a group (p. 67). Clearly, he based this on the assumption that distributions were formerly continuous, with little scope for long-distance dispersal (though he modified that view in some cases, as discussed below). He also postulated that when there are obvious morphological gaps between genera within a family, "the theory of evolution absolutely necessitates the former existence of a whole series of extinct genera filling up the gap between the isolated genera," many of which will not have been preserved in the fossil record (p. 68). In all of these respects, Wallace espoused what might now be called a "punctuated gradualist" approach, in which intermediate steps are always present in morphology and in geographic distribution, though he emphasized that the rate of change is likely to vary greatly.

In chapter 5, Wallace presented evidence on the extent and limitations of the dispersal abilities of organisms, saying that "these questions lie at the root of any general solution of the problems of distribution" (p. 71). He cited evidence that pigs are able "to swim over five or six miles of sea," and smaller mammals are able to ride on the floating rafts of vegetation that are sometimes seen at sea, especially after hurricanes, and by this means may be able to rarely colonize new islands (pp. 71–72). However, he emphasized the rarity of such events, and asserted that "whenever we find that a considerable number of the mammals of two countries exhibit distinct marks of relationship, we may be sure that an actual land connection . . . has at one time existed" (p. 72). Where seas separate areas with similar mammals, Wallace asserted, there is evidence of the intervening seas being shallow. This hypothesis is discussed in later chapters and led Wallace to a series of mistaken conclusions; for example, he believed that no native mammals are present on the Galapagos Islands because they are in deep water (p. 268; there are, in fact, five [Dowler, Carroll, and Edwards 2000]), and that all of the Philippine Islands were once continuously connected with mainland Asia because they have many nonvolant mammals (pp. 361–62; current evidence indicates that most of the islands were not [Hall 1998]). He also asserted that "the majority of birds . . . require either continuous land or an island-strewn sea as a means of dispersal" (p. 73). He concluded that reptiles seem to have a great ability to travel on floating trees, to an extent greater than amphibians, and freshwater fishes may travel across saltwater in waterspouts or due to the masses of water created by hurricanes (pp. 73–74). Some insects are able to fly, others lay eggs in logs that may float, and many are members of ancient groups that have thus had time to disperse widely when conditions were favorable. Land snails have limited dispersal ability but are so ancient that rare events "during the almost unimaginable ages of their existence" allowed them to traverse barriers. Plants vary as greatly as animals in their dispersal abilities and may also be helped at times by birds that carry seeds on their feet or feathers or in their guts (pp. 76–79). Overall, Wallace emphasized the abilities of some types of organisms to cross over seas, recognized the limitations of many, and was clear in stating that, given sufficiently long periods of time, rare events are virtually certain to take place. He emphasized that these differences between groups of organisms are consistent and may be used to infer the history of an island or archipelago.

At the time Wallace wrote *Island Life*, it was commonly held that some (or perhaps many) current areas of deep seafloor had once been elevated to the level of continents, and the current continents were once at the depth of the deep seas. Citing Lyell's *Principles of Geology* (1872) and a publication only two years prior by T. M. Reade, president of the Geological Society of Liverpool, as examples, Wallace made the case that this opinion was widespread (pp. 81–82). Saying that "the opposite belief . . . is now rapidly gaining ground among students of earth-history" (p. 83), Wallace launched into presentation of evidence that continental areas have always been continents, and deep-sea areas have always been deep seas. In the course of this, he presented evidence that there have been many incursions of shallow seas onto continents, which leads us "to picture the land of the globe as a flexible area in a state of slow but incessant change" (p. 86). What was not discussed at all was the notion that the continents could break apart and move; continental drift did not emerge as a frequent topic of discussion until advocated by Wegener (1912). Wallace neither accepted nor rejected continental drift but instead simply did not consider the possibility. The closest he came to this topic was his comment that oceanic islands do not contain geological formations that are characteristic of continents, with two exceptions: New Zealand and the Seychelles Islands, "both situated near to continents" (p. 102). Given that it was not until nearly one hundred years later that the evidence for continental drift (a term now set aside in favor of "plate tectonics") became robust and was widely accepted, it is remarkable that Wallace was able to recognize and document so many biogeographic patterns that are still recognized today.

The next two chapters, 7 and 8, dealt with the existence, extent, and causes of glacial epochs. On this topic, Wallace displayed what may have been his greatest insights, arguing for a pattern and cause that was not fully understood and accepted for nearly one hundred years.

It was widely acknowledged by 1880 that parts of the northern continents had been glaciated at some relatively recent time. Wallace was emphatic about the importance of this topic, presenting extensive evidence for the existence of the continental glaciers, arguing for their existence as evidence of major episodic change in the earth's climate, and asserting the likelihood that those changes often took place more rapidly than geological changes.

In the first of these chapters, Wallace discussed glacial moraines and till, erratic boulders, glacial striations, and other evidence of extensive glaciation. These, he asserted, were features not widely known among the public, or "even among scientific men" (p. 113), who at the time of his writing had not accepted the existence of massive, widespread continental glaciers. He also presented evidence that glaciation occurred repeatedly, with at least four alternating periods of glaciation and warmth (pp. 113–15), and cited the presence of hippopotamuses, elephants, and rhinoceros in England as evidence of the existence of the warm periods. Such dramatic changes, he argued, must have resulted in the "extinction of a whole host of the higher animal forms" and "a complete change in types due to extinction and emigration" (p. 119). The repetition of glacial and warm periods created the perfect circumstances to promote the spread and subsequent isolation of populations, and hence to promote speciation. This conceptual model was the origin of what has come to be known as the "Pleistocene pump hypothesis" of speciation, which dominated most discussion of speciation in birds, mammals, and some other groups until the late 1990s (Zink, Klicka, and Barber 2004), but Wallace saw it as crucial to understanding distribution patterns over a much longer period of time.

In chapter 8, one of the longest in the book, Wallace tackled the problem of the cause of these major climatic fluctuations. He quickly set aside a series of suggested possible causes, including a decrease in the heat of the planet or variation in the temperature of space or the sun, changes in the position of the earth's axis of rotation, and changes in the obliquity of the ecliptic, the latter two being astrophysical properties of the planet and its orbit. He focused instead on "the combined effect of the precession of the equinoxes and the excentricity of the earth's orbit" and "changes in the distribution of land and water." He considered these to have been "demonstrated facts, . . . capable of producing *some* [italics Wallace's] effect, . . . the only question being whether . . . they are adequate to produce all of the observed effects" (pp. 121–22).

Wallace first cited a series of publications from 1864 to 1879 by James Croll, a largely self-taught Scottish polymath with no formal training in astrophysics, who described the existence of orbital cycles of about twenty-one thousand and one hundred thousand years that he believed caused the glacial episodes. Wallace enthusiastically accepted this interpretation, stating that this was the cause of the periods of glacial expansion and disappearance that he described in the previous chapter (pp. 122–25).

It is striking that Wallace was largely correct, though Croll's work later was found to contain a variety of errors and misinterpretations, and Croll's description of the orbital cycles as a cause of climatic cycles was rejected until reinvestigated and redescribed by the Serbian astronomer Milutin Milankovitch from 1912 to 1920; it was not until 1976, when ice cores from Greenland were found to show annual layers that varied in thickness with the "Milankovitch cycles," that the impact of these cycles on the earth's climate was widely (and abruptly) accepted (Hays, Imbrie, and Shackleton 1976).

Wallace went on to argue that the snow and ice generated by the cold temperatures produced by Croll's orbital cycles could be built up over a period of time, as water evaporated from the oceans was sometimes carried in the atmosphere to cold regions where it was deposited as snow. Once built into a glacial mass, a massive amount of energy would be required to melt the ice, more than would be available during an ordinary summer (pp. 128–30). The ice would not fully melt until the cycle reached its opposite condition, generating great heat and melting the ice. He postulated continental glaciers reaching a thickness of more than one to one and a half miles (p. 132). He also realized that the development of glaciers, and the increase in polar-tropical temperature differentials, would impact on atmospheric and ocean current circulation (pp. 137–39), and the increased albedo of the earth when partially covered by ice would lower global temperatures (p. 139). Additionally, he described the impact that subsidence of land in certain areas would have in changing crucial ocean currents; for example, he cited the potential change in the Gulf Stream that would be caused by subsidence of the Panama land bridge, causing a great reduction in warm ocean waters reaching northwestern Europe (p. 145). He reasoned that during a gradually warming period, temperatures would not actually increase much as the thickness of the ice decreased, but rather would remain cold until nearly all of the ice had melted, when temperatures should increase abruptly (pp. 153–54).

In all of these respects, Wallace was remarkably prescient; modern biogeography textbooks describe these phenomena as fundamental to understanding current biogeographic patterns (e.g., Cox and Moore 2005; Lomolino, Riddle, and Brown 2006). However, from the perspective of what is known now, he also made some large mistakes. He overestimated the coldness of the maximum glacial periods (36°F colder in England than at present) and the heat of the maximum interglacial periods (60°F above current conditions; p. 126; the currently accepted flux between glacial and interglacial periods is just 7–11°F, or 4–6°C). He incorrectly believed that continental glaciers could only be generated in mountainous regions, because those places receive more precipitation than nearby lowlands (pp. 130–32). Also, he accepted Croll's estimate that the last glacial episode reached its maximum about two hundred thousand years ago and "passed away" about eighty thousand years ago (p. 155), rather than peaking at twenty-one thousand and declining rapidly approximately eleven thousand years ago, as now known.

Wallace recognized that the removal of water from the oceans by evaporation and its deposition on land as snow and ice would result in the lowering of the oceans (pp. 157–58), but he did not estimate the extent to which sea level would have changed. As a result, he rarely referred to sea-level change in *Island Life*, and instead explained the presence of dry land connections across shallow continental shelves as being caused by geological uplift, and evidence of marine incursion solely as the result of subsidence. Given current evidence that sea level dropped repeatedly to about 120 m below the present level during the recent glacial episodes (Bintanja, Van de Wal, and Oerlemans 2005), Wallace clearly failed to recognize a significant process that would have allowed him additional great insights.

In chapter 9, one of the longer chapters at forty pages, Wallace laid out a detailed discussion of the impacts of orbitally driven cycles on global climate and the evidence that could be used to test the predictions made in the prior chapter. Because his understanding of the age of the earth (discussed in his following chapter) and the timing of the glacial events was incorrect, many of his specific conclusions have not been borne out by subsequent studies, but the thrust of his arguments was often quite accurate, and the framework of his perspective has held up well.

Wallace began by arguing that the repeated occurrence of glacial cycles would inevitably have "crowded together" species in nonglaciated areas, leading to "a struggle for existence" causing "the modification or the extinction of many species" while also causing the periods of isolation that promote speciation during glacial periods (pp. 163–64). Again citing Croll's publications, he argued that glacial episodes have taken place over the last three million years (which he incorrectly defined as the early Miocene; see the following discussion on the age of the earth), that changes from glacial to interglacial conditions took place rapidly, and that some were quite recent, with evidence of some glacial episodes during earlier periods, especially the Eocene and Cretaceous (p. 165). He argued that erosion would quickly remove much of the evidence on land of all but the most recent glaciation, and that each glaciation would obliterate much of the remaining evidence (pp. 166–67), so that we must look for other forms of evidence. These would include submarine moraines, glacial erratic boulders, and alternating beds of boulders and soil, all of which were known (pp. 170–73). Wallace clearly was puzzled by the implication of Croll's model of orbitally forced climatic cycles that glacial cycles should have continued throughout the Tertiary (pp. 171–75), but he saw compelling evidence of Cretaceous to Miocene tropical and subtropical vegetation in northern latitudes that supported this (pp. 176–83). His solution to what appeared to be evidence of continuously warm arctic conditions in some places was to point to evidence of changes in land elevation that allowed warm ocean currents to bring heat to the Arctic Ocean (pp. 183–91). This, he thought, would have brought enough heat to the north to offset the development of an arctic ice cap that would periodically have been caused by orbital variation (p. 192). The details of his estimates of the extent and effects of both orbital variation and changes in ocean currents were inaccurate, and he entirely missed the impact of continental drift, but his novel explanations of the processes that he described remain central to our current understanding of climatic variation since the beginning of the Cretaceous period, and the scattered evidence he summarized in building a case for early glacial episodes in the Cambrian, Permian, and Carboniferous (pp. 192–202) is accepted today.

In the next chapter (chap. 10), Wallace addressed the question of the age of the Earth and the time when life originated. He began by saying that biologists and geologists estimated that two hundred million years must have passed since the beginning of the Cambrian, and it would surely seem that life must have originated at least five hundred million years ago. He then noted estimates by physicists that the earth could not be much more than about one hundred million years old, and that they hold this opinion to be "almost indisputable" (p. 206). Wallace noted the incompatibility of these estimates and proceeded to consider the sources and strength of the geological estimates. Summarizing estimates of rates of erosion from land and deposition of marine strata, he showed that repeated cycles of uplift, erosion, and sedimentation must have taken place, so that simply adding up the thickness of current sediments and dividing by the average rate of sedimentation would likely produce an underestimate of the age of the earth, but he went on to estimate that all known erosion and sedimentation could have taken place in as little as twenty-eight million years (pp. 206–18). He then discussed the rates of evolutionary change and diversification, concluding that the repeated rapid changes in climate previously discussed, and the geographic impacts of the glacial cycles operating during the earth's entire history, could have produced all of life's diversity within the one-hundred-million-year period allowed by the physicists (pp. 218–25).

These calculations led Wallace to conclude "that the enormous periods, of hundreds of millions of years, which have sometimes been indicated by geologists are neither necessary nor warranted by the facts at our command" (p. 228). In this, Wallace was badly mistaken, ending with a view of earth history and geological change that operated at a speed in excess of what is now known to be the case, by about an order of magnitude. However, knowledge of the age of the earth, and of the many portions of the earth's history was developing slowly, and it was only after the discovery of radioactivity that realistic estimates were made by anyone. Wallace deserves credit for insisting that it is essential that the evolution of biological diversity be viewed within the context of geological and climatic changes, that astrophysical phenomena (such as cycles in orbital phenomena) must be taken into account, and that explanations of biogeographic patterns must be considered in the context of all of the many complex processes that have operated during the earth's history.

While his estimates of the rates of biological and geological processes were sadly wrong, his determination to state his facts clearly and to base his conclusions only on "the facts at our command" (p. 228), wherever they may lead, was in the best tradition of the scientific method and made it possible for future researchers to test, modify, and improve his model. The example that Wallace set in part 1 of *Island Life* of broad, rigorous synthesis came to some incorrect conclusions, but the questions he raised and the framework he established remain a large part of the foundation of evolutionary biogeography today.

Part 2: Insular Faunas and Floras

In the second part of *Island Life*, Wallace set out to "apply these principles [from part 1] to the solution of numerous problems presented by the distribution of animals" (p. 233). In the initial, brief but crucial, chapter of this section (chap. 11), he was probably the first to explicitly list the "many advantages [of islands] for the study of the laws and phenomena of distribution." Comparing islands to continents, Wallace found that (1) islands have "a restricted area and definite boundaries"; (2) "the number of species and genera they contain is always much smaller than in the case of continents"; (3) "their peculiar [i.e., endemic] species and groups are usually well defined and strictly limited in range"; (4) "their relationships with other lands are often direct and simple, and even when more complex are far easier to comprehend than those of continents"; and (5) "they exhibit . . . certain influences on the forms of life and certain peculiarities of distribution which continents do not present." Based on these attributes, Wallace concluded, "We are therefore able to proceed step by step in the solution of the problems they present . . . and acquire . . . so much command over the general principles which underlie all problems of distribution that . . . we shall find it comparatively easy to deal with the more complex and less clearly defined problems of continental distribution" (pp. 233–34).

Wallace then pointed out that it is essential to recognize that "islands have had two distinct modes of origin: they have either been separated from continents of which they are but detached fragments, or they have originated in the ocean and have never formed part of a continent" (p. 234). He credited Darwin as "the first writer who called attention to . . . oceanic islands, [all of which are] of volcanic or coralline formation, and that none of them contained indigenous mammalia or amphibia . . . , opposed to the opinions of the scientific men of the day, who almost all held the idea of continental extensions . . . and we continually hear of old Atlantic or Pacific continents." To this definition, Wallace added that oceanic islands are "usually far from continents and always separated from them by very deep sea" (p. 235). "All the animals which now inhabit such oceanic islands must either themselves have reached them by crossing the ocean, or be the descendants of ancestors who did so" (pp. 236–37). (This definition applies remarkably well to what are now called "hot-spot islands," such as the Hawaiian, Galapagos, and Azorean Islands, where single plumes of magma create islands [e.g., Wagner and Funk 1995; Borges and Gabriel 2008; Gosliner 2009], as discussed in succeeding chapters of *Island Life*.)

The second type, continental islands, Wallace described as islands that

> are always more varied in their geological formation, containing both ancient and recent stratified rocks. They are rarely very remote from a continent, and they always contain some land mammals and amphibia. . . . They may, however, be divided into two well-marked groups—ancient, and recent, continental islands. . . . Recent continental islands are always situated on submerged banks connecting them with a continent, and the depth of the intervening sea rarely exceeds 100 fathoms. They resemble the continent in their geological structure, while their animal and vegetable productions are either almost identical with those of the continent, or . . . the difference consists in the presence of closely allied species of the same types, with occasionally a very few peculiar genera. . . . Ancient continental islands differ greatly from the preceding. . . . They are not united to the adjacent conti-

> nent by a shallow bank, but are usually separated from it by a depth of sea of a thousand fathoms. . . . In geological structure they agree generally with the more recent islands; like them they posses mammalia and amphibia . . . but these are highly peculiar . . . many forming distinct and peculiar genera or families. They are . . . characterized by the fragmentary nature of their fauna, many of the most characteristic continental orders or families being quite unrepresented. (pp. 235–36)

The one area where Wallace failed to recognize a distinct class of islands is one that has caused some confusion up to today. Islands that form as plate-margin island arcs—such as the Philippines—have a geological origin similar to hot-spot islands, but they are not dependent on a single plume of magma and have a different history. Hot-spot islands typically have a discrete "life history," as clearly seen in the Hawaiian Islands: Eruptions build a given island over a period of a million years or so, rapidly reaching maximum size, then the island moves away from the hot-spot due to movement of the tectonic plate on which it sits. In the absence of new eruptions, each island then gradually erodes, eventually reaching the point of being only an atoll, in which a fringe of coral reef surrounds the flattened top of the former mountain that now resides just below sea level, where areal erosion no longer operates. The entire process, from "birth" to "death" of the island may take only five to eight million years, depending on the speed of movement of the plate and the amount of magma ejected (e.g., Whittaker and Fernandez-Palacios 2007). Plate-margin islands, on the other hand, develop where a plate is subducted beneath another plate, producing many volcanoes over an extended period of time, sometimes for tens of millions of years, causing multiple islands to develop simultaneously, some of which continue to grow for long periods of time while others nearby may erode down. These subduction zones sometimes develop around the edges of continents at a distance of several hundred kilometers, and though separated by deep water, they are near enough for rare colonization phenomena to play a greater role than in most hot-spot islands (Nunn 2009).

In chapter 12, the first to lay out examples of the types of islands, Wallace presented his view of the biotas of oceanic islands using the Azores and Bermuda as examples. Beginning with the Azores, he pointed out that they lie in a region with surrounding depths of more than one thousand fathoms (ca. two thousand meters) in all directions, at a distance of at least three hundred miles to any shallower waters, and noted that they are "wholly volcanic" (pp. 240). These observations contradict "the view of their having formed part of an extensive Atlantis" (p. 240). He cited the presence of some Miocene marine deposits as evidence of their "considerable antiquity, . . . and this fact may be of importance in considering the origin and peculiar features of the fauna and flora" (p. 240). Saying that "we should therefore expect them to be . . . typical" as examples of oceanic islands, he pointed out "the absence of all indigenous land mammalia and amphibia, . . . no snake, lizard, frog, or fresh-water fish" in spite of suitable climate and habitat (p. 240). "On the other hand, flying creatures, as birds and insects, are abundant. . . . When we consider that the nearest part of the group is about 900 miles from Portugal . . . it is not surprising that none of these terrestrial animals can have passed over such a wide expanse of ocean," in spite of the age of the islands (pp. 240–41). Of 53 species of birds known from the islands, none were endemic, and many were uncommon "stragglers." He then noted reports of many species of birds being sighted on the Azores after strong storms but also showed that the number of such species decreases with increased distance from the mainland (p. 242), in clear recognition of the role of isolation on rates of potential colonization. He also cited evidence that "only those species which reach the Azores at very remote intervals will be likely to acquire well-marked distinctive characters" relative to their mainland ancestors (p. 243), an equally clear recognition of the role of gene flow and genetic isolation on the formation of endemic species of island organisms. He labeled the absence of endemic bird genera as evidence that dramatic climatic cycles had taken place and that the current avifauna "had its origin since the date of the last glacial epoch" (p. 244).

Wallace then went on to summarize information about Azorean insects, pointing out that nearly half (101 of 212) had been introduced by humans, but of the 74 native species, 14 were endemic, and 2 represented endemic genera. He attributed the endemism among insects as being the result of the following: “Many of these small insects have, no doubt, survived the glacial epoch, and may . . . represent very ancient forms” and “have many more chances of reaching remote islands than birds, for not only may they be carried by gales of wind, but sometimes . . . may be drifted safely . . . over the ocean, buried in . . . plants” (pp. 245–46). Similarly, land-living mollusks on the Azores were known from 69 species, of which 32 are endemic; he attributed their higher rate of endemism to colonization from the mainland being “a very rare event, and . . . a species once arrived remains for long periods undisturbed by new arrivals . . . and fixed as a distinct type” (p. 247). Of the 480 species of flowering plants known from the Azores, only 40 were considered endemic; Wallace attributed the large number of species shared with Europe to a combination of floating plants, seeds carried by birds (either on their feet and feathers or in their guts), and an uncertain but very large number brought by humans. He concluded that most of the plants (including human introductions, native but shared with Europe, and endemic with closest relatives in Europe) are present “not due so much to ordinary or normal, as to extraordinary and exceptional causes”—that is, not due to “the south-westerly return trade [winds] and . . . the Gulf Stream” that would bring animals and plants from America, but rather to “the violent storms to which the Azores are liable . . . combined with the greater proximity and more favourable situation of the coasts of Europe and North Africa, that the presence of a fauna and flora so decidedly European is to be traced” (p. 253).

Wallace’s description of the biogeography of the Bermuda Islands (pp. 253–57) led him to similar conclusions. He noted that they lie about seven hundred miles from the North American coast (nearest to North Carolina) surrounded by very deep water, and that the “discovery of a layer of earth with remains of cedar trees forty-eight feet below the present high-water mark shows that the islands have once been more extensive.” The fauna includes “no indigenous land mammals, frogs, or snakes,” and “one lizard” that is endemic, related to a species in the southeastern United States. The avifauna, however, is large, made up entirely of shore birds and migratory species, with only ten species, eight land and two water birds, that are permanent residents. Because of the constant flow of "visitors from the mainland, . . . there has been no chance for them to have acquired any distinctive characters through isolation" (p. 258). In comparison to the Azores, there are fewer resident species, which Wallace attributed to "the small area and little-varied surface of these islands, as well as to their limited flora and small supply of insects" and "to the peculiarity of the climate . . . which causes a much larger number of its birds to be migratory than in Europe" (p. 258). Among terrestrial mollusks, Wallace reported that about 4 of 18 species are endemic, which he again attributed to a slow rate of immigration from the mainland (p. 261).

Wallace concluded the chapter with a search for general patterns, stating that the two groups of islands "furnish us with some most instructive facts as to the power of many groups of organisms to pass over from seven hundred to nine hundred miles of open sea," through "violent storms," migration, and "special adaptations for dispersal by wind or water, or through the medium of birds" (p. 263). He reiterated the importance of isolation, area, and island age as factors associated with levels of diversity and again pointed to the absence of "mammals, amphibians, and some groups of reptiles" (p. 264). In doing so, he emphasized the consistency of pattern as the basis for deduction of process and so formed an internally consistent, coherent theory. The complex patterns that he deduced, especially those that influence species richness (area, habitat diversity, resource richness, island age, and the impact of immigration), are strikingly similar to those incorporated into the equilibrium model of MacArthur and Wilson (1967), which dominated studies of island biogeography for three to four decades and remains highly influential today (Whittaker and Fernandez-Palacios 2007; Losos and Ricklefs 2010). His only error in this respect was his conclusion that mammals and amphibians are always absent from oceanic islands; many examples of which were documented subsequently. Despite this error, he built a strong case that the presence of endemic species of some taxa did not require that the island have been part of a former continent but rather resulted from long-distance, overwater colonization, taking place over long periods of time, with the differences in dispersal ability being clearly reflected in species richness and the presence of endemic species within the various groups.

In chapter 13, Wallace turned to the Galapagos Islands, which he characterized as entirely volcanic in origin, surrounded by very deep water that extends over most of the six hundred miles to the coast of South America. He noted the rarity of storms, the presence of strong ocean currents that flow toward the northwest from the coast of Peru, and the usually dry conditions. He noted as well the three-hundred-year history of visits by European sailing vessels and the potential impact of introduced species, including goats, pigs, and cats. He commented on the presence of a mouse, which "we can hardly consider . . . to be indigenous," and asserted that "there can be little doubt . . . that the islands are completely destitute of truly indigenous mammalia; and frogs and toads . . . are equally unknown" (p. 268). (Wallace was correct about the amphibians but wrong about the mammals: five species of endemic rodents are now known, four of which are members of the endemic genus *Nesoryzomys* [Dowler, Carroll, and Edwards 2000; Musser and Carleton 2005]). Among reptiles, he listed the giant tortoises as probably derived from "some ancestral form, carried out to sea by a flood, . . . once or twice safely drifted as far as the Galapagos" (pp. 268–69). Regarding lizards—a gecko and four members of the Iguanidae—he frankly admitted that "how these lizards reached the islands we cannot tell," though surely having come from America "at a remote epoch," but "it is certain that animals of this order have some means of crossing the sea" (p. 269). Snakes, as well, he viewed as unusual on oceanic islands, and he noted that we can tell only that the two on the Galapagos originated on the adjacent continent, probably rather recently due to their similarity to species there. Here, as elsewhere, Wallace inferred that similarity indicates recent divergence.

Of the 57 species of birds then known from the Galapagos, Wallace noted 38 as being endemic, all of which are "allied to birds inhabiting tropical America," and all of the species are "consistent with the theory of the peopling of the islands by accidental migrations" over a "long period of time" on islands of "considerable antiquity" (pp. 270–72). The difference in a higher level of endemism compared to the Azores and Bermuda he attributed to the absence of "storms, gales, and hurricanes" (p. 273), and the attendant reduced rate of colonization from the mainland. The insects and land mollusks of the Galapagos were also noted as including mostly endemic species, possibly arriving in "drift-wood, bamboos, canes, and the nuts of a palm [that] are often washed in the south-eastern shores of the islands" (p. 274). He went on to say that "volcanic islands are subject to subsidence as well as elevation . . . and some islands may have intervened between them and the coast, and have served as stepping-stones" (p. 274), thus clearly acknowledging that the development of biogeographic patterns takes place on a timescale that is similar to that of the dynamic geological history of oceanic islands. Of the plants, Wallace knew of about 20 introduced species and 312 native species, of which 174 are endemic to the Galapagos. Most of the endemic species "are allied to the plants of temperate America or to those of the high Andes," while the nonendemic native species are derived from "the hotter regions of the tropics near the level of the sea." (p. 277). "At the time when the two oceans were united [across Central America] a portion of the Gulf Stream may have been diverted into the Pacific, giving rise to a current, some part of which would almost certainly have reached the Galapagos, . . . [helping] to bring about that singular assemblage of West Indian and Mexican plants now found there." (p. 278). Overall, he inferred that the flora shows evidence of "moderately remote origin [i.e., great age], great isolation, . . . changes of condition [i.e., new habitats]," and "long continued isolation" on different islands within the archipelago that would "lead to the differentiation of species, while the varied conditions to be found upon islands differing in size and altitude . . . would often lead to the extinction of a species on one island and its preservation on another" (p. 278). Overall, he concluded that patterns on the Azores and Galapagos are similar, but the Galapagos have a higher percentage of endemic species because they lie "in a calm portion of the ocean," which "demonstrates the preponderating importance of the atmosphere as an agent in the dispersal of insects, birds, and plants," "past conditions of sea and land and past changes of climate," and "the migratory habits of the birds" (p. 279). Stated in current terms, low species richness and high endemism in the Galapagos is the result of reduced colonization rates (influenced not only by distance and ocean currents but also by the infrequency of storms and by the migratory habits of birds in neighboring continental areas) and high survivorship of lineages, with the age of the islands, their specific geological history, changes in ocean currents caused by geological subsidence and/or uplift, changes in climate, and extensive speciation within the archipelago accounting for much of the biodiversity that is present. All of these factors, Wallace noted, were "general principles already adduced" (p. 280).

In chapter 14, Wallace turned to an extreme example of an isolated oceanic island, St. Helena. He began by pointing out that St. Helena is volcanic in origin, mountainous and rugged, lying on a small subsea plateau of shallow water that is surrounded by very deep water. He then described the massive destruction of natural habitats on the island by humans and the animals and plants they introduced, so that only a fraction of the original habitat and biota is likely to remain. Of the surviving native beetles, 128 out of 129 are endemic, 25 of 39 genera are endemic, and "each of these [groups of species and genera] may well be descended from a single species which originally reached the island" with a "great variety of generic and specific forms into which some of them have diverged." He postulated that some arrived as early as the Miocene (p. 290) and may represent persistent relict forms of formerly widespread taxa, originally "conveyed by oceanic currents as well as by winds. . . . Drift-wood might . . . be one of the most important agencies by which these insects reached the island" (pp. 291–92). The flowering plants show nearly equal levels of distinctiveness, without close relatives in continental areas and again showing evidence of being relictual elements from formerly widespread floras; "they no more imply any closer connection between the distant countries the allied forms now inhabit, than does the existence of living Equidae [e.g., horses] in South Africa and extinct Equidae in the Pliocene deposits of the Pampas, imply a continent bridging the South Atlantic to allow of their easy communication" (p. 297). This represents unambiguous acceptance of an essential role for long-distance dispersal, followed by diversification and long-term persistence. It was also an emphatic rejection of deep seafloors uplifting to create transoceanic land bridges or entire continents such as Atlantis—but not, as noted earlier in this commentary, a rejection of continental drift, a concept that he did not consider.

The last set of oceanic islands treated by Wallace, in chapter 15, were the Hawaiian Islands (then called the Sandwich Islands). He began, as usual, by describing the geology of the islands, which he noted as extremely isolated from continental areas (2,350 miles from the American coast), and 600 or more miles from neighboring atolls. He described the islands as entirely volcanic, separated from the continents by enormous ocean depths, so that "we may be quite sure . . . that the Sandwich Islands have, during their whole existence, been as completely severed from the great continents as they are now; but on the west and south there is a possibility of more extensive islands having existed, serving as stepping-stones, but which . . . lowered or destroyed by denudation, and . . . subsidence of the earth's crust, have altogether disappeared, except where their sites are indicated by the upward-growing coral-reefs. If this view is correct we should give up all idea of there ever having been a Pacific continent" (pp. 299–301).

Wallace then commented "that indigenous mammalia are quite unknown" (p. 301). Of the two lizards that are present, Wallace considered the presence of one "hardly likely [to be] . . . due to natural causes," and the other "doubtful" (p. 303).

In great contrast, the "amount of speciality [among birds] is, however, wonderful, far exceeding that of any other islands" (p. 303). Even among "aquatic and wading birds . . . five are peculiar [i.e., endemic]" and two endemic raptors were known (p. 301). Most remarkably, among perching birds, 19 species, all endemic, were known, including 6 species within 4 genera that are endemic, and 5 genera with 12 species that are members of an endemic family, the Drepanididae. Most of the endemic taxa of birds are associated "with Australia and the Pacific Islands," but there are also "slight indications of very rare or very remote communication with America" (p. 303). The high number of species in endemic genera "undoubtedly indicate an immense antiquity for this group of islands, or the vicinity of some very ancient land (now submerged), from which some portion of their peculiar fauna might be derived" (p. 303).

Similarly, land-living mollusks "are very numerous," represented by about 30 genera and 300 to 400 species. All of the species are endemic, as are three-fourths of the genera, and 14 of the genera are members of "the sub-family Achatinellinae, entirely confined to this group of islands" (p. 303). Many of "the species and even the genera are confined to separate islands," and "each valley, and often each side of a valley, and sometimes even every ridge and peak possess its peculiar species," with an average range of "five or six miles, while some are restricted to but one or two square miles, and only very few have the range of a whole island" (p. 304). Citing "the Rev. John T. Gulick," Wallace reported that the number of species on the western islands of Oahu and especially Kaui is especially high, which "would seem to show that the small islets stretching westward, and situated on an extensive bank . . . may indicate the position of a large submerged island whence some portion of the Sandwich Island fauna was derived" (p. 305). These insights anticipated later research that would show that such islands did exist, and may well have been the location of much of the early diversification of the Hawaiian fauna (Sherrod 2009).

Wallace considered the flora of the islands to be "extremely rich," including 554 flowering plants and 135 ferns. A total of 69 plants were believed to have been introduced; of the remaining 620 species, 377 species are endemic, including "no less than 39 peculiar [i.e., endemic] genera out of a total of 253, and these 39 genera comprise 153 species, so that the most isolated forms are those which most abound and thus give a special character to the flora" (p. 306). Included among them, he noted woody shrubs of lobelia, geraniums, violets, plantains, and Compositae (p. 306). He noted that many have their closest relatives elsewhere in Polynesia, but also in Australia, New Zealand, and the Americas, and inferred that ancient islands, long since subsided beneath the sea, "offered facilities for the transmission of plants" from Australia, the Asian mainland, and the Americas (p. 309).

"The great antiquity implied by the peculiarities of the fauna and flora . . . enable us to account for another peculiarity of its flora—the absence of so many families found in other Pacific islands. For the earliest immigrants would soon occupy much of the surface, and become specially modified in accordance with the conditions of the locality, and these would serve as a barrier against the intrusion of many forms which at a later period spread over Polynesia" (p. 309). He inferred that plants typically arrive sooner on oceanic islands than animals, the former exhibiting "the influence of the primitive state of the islands," while animals "passing across the sea with greater difficulty, . . . retain much more of the impress of a recent state of things" (p. 310).

In summary, Wallace noted that oceanic islands

> all agree in the total absence of indigenous mammalia and amphibia, while their reptiles, when they possess any, do not exhibit indications of extreme isolation and antiquity. Their birds and insects present just that amount of specialisation and diversity from continental forms which may be best explained by the known means of dispersal acting through long periods; their land shells [i.e., snails] indicate greater isolation, owing to their . . . less effective means of conveyance . . . ; while their plants show most clearly the effects of those changes of conditions which . . . have occurred during the Tertiary epoch, and preserve . . . some record of the primeval immigration by which the islands were originally clothed with vegetation. But in every case the . . . life in these islands is scanty and imperfect as compared with . . . continental areas, and no one of them presents such an assemblage of animals or plants as we always find in an island which we know has once formed part of a continent. It is still more important to note that none of these oceanic archipelagoes . . . [has] been preserved from Mesozoic times . . . [which] powerfully enforces the conclusion that . . . our continents and oceans have, broadly speaking, been permanent features of our earth's surface." (pp. 310–11)

This conclusion is supported by the "facts that the islands of our great oceans are all volcanic (or coralline built probably upon degraded and submerged volcanic islands), and that their [flora and fauna] are all more or less clearly related to the existing inhabitants of the nearest continents" (p. 311).

Wallace showed remarkable prescience and breadth of vision in thus describing oceanic islands as (1) largely volcanic in origin; (2) populated by organisms with varying levels of dispersal abilities that have influenced their degree of differentiation from mainland relatives; (3) having communities of organisms that have largely evolved in situ and have been persistent over long periods of time; (4) generally being species-poor with biotas that are disharmonic (i.e., with greatly differing proportions of species from the various orders, families, etc., from those on continents); and (5) having biotas that have been influenced by the existence of any past islands either in the archipelago or that served as stepping-stones from continents. Recent in-depth studies of the Azores and Hawaiian Islands, based on vastly greater amounts of information, have come to remarkably similar conclusions (e.g., Borges and Gabriel 2008; Wagner and Funk 1995; Gillespie 2009).

In chapter 16, Wallace turned to continental islands of recent origin, first treating Great Britain, and in the two subsequent chapters taking Borneo plus Java then Japan plus Taiwan as examples. Perhaps not surprisingly, the chapter on Great Britain is rather long (thirty-five pages) and detailed, clearly meant to respond to ideas that were widespread at the time. He began by defining continental islands as

> the very reverse of the "oceanic" class, being fragments of continents or of larger islands from which they have been separated by subsidence of the intervening land at a [recent] period, . . . always still connected . . . by a shallow sea, usually indeed not exceeding a hundred fathoms deep (ca. 180 m); they always possess mammalia and reptiles either wholly or in large proportion identical with those of the mainland . . . [and] the total absence or comparative scarcity of those endemic . . . species and genera which are so striking a feature of all oceanic islands. (p. 312)

He noted that the flora and fauna of continental islands should be expected to differ based on the islands' size, age, distance from the mainland, and species richness. When endemic species are present on a continental island, he posited that they are derived from a formerly widespread species that has become extinct everywhere except the island, where "some modifications . . . may [cause it to] constitute a new species" (p. 313).

Wallace described Great Britain as "perhaps the most typical example of a large and recent continental island now to be found upon the globe" (p. 313), connected to the continent by a broad, shallow continental shelf. Submerged forests offshore "can only be explained by an actual subsidence of the land (or rise of the sea-level) since the trees grew" (p. 315), and the presence of river channels on the ocean floor at depths of 260 feet or more indicated the extent of the change. As noted earlier in this commentary, although Wallace emphasized the vast extent of continental glaciers, he did not clearly recognize the impact of glacial development on sea level and so usually interpreted evidence of change in exposure of shallow seas as evidence of subsidence, rather than changes in sea level.

Wallace then discussed the reasons why Great Britain is "poor in species" (p. 318). In this discussion, his confusion over the age of the earth, actual timing of events, and the nature of events comes to the fore. He was aware that marine deposits existed in Great Britain at heights of about 2,000 feet and inferred that this had happened relatively recently: "During the latter part of the glacial epoch, the subsequent elevation and union with the continent cannot have been of very long duration, . . . cutting off the further influx of purely terrestrial animals, and leaving us without the number of species which our favourable climate and varied surface entitle us to" (p. 319). He thus greatly underestimated the age of the marine deposits and did not recognize that most of Great Britain was covered by glacial ice quite recently (up until ca. 12,000 years ago), and that it was rising seas from melting glaciers that isolated Great Britain from the continent. He also gave a greater role to the effect of isolation on species richness than to the current cool, moist climate, even for reptiles, in which "zoological poverty . . . attains its maximum" (p. 319).

The presence of endemic freshwater fish showed, for Wallace, the impact of genetic isolation and rapid evolution (pp. 323–24), and he predicted that at least some endemic insects (pp. 325–38) and plants (pp. 338–45) would be demonstrated to be present, in spite of the uncertainty over taxonomy and distribution that existed at the time. He concluded by commenting that at least some endemic species occur in Great Britain, and reemphasized that they are largely relictual species that formerly occurred widely but became extinct elsewhere while becoming modified in their refuges (pp. 345–47). It is striking that he chose to emphasize those points, rather than returning to his earlier emphasis on the similarity of continental islands and continents, stating that "our entomologists should, therefore, give up the assumption that all our insects do exist on the continent, . . . as not in accordance with the evidence;

and . . . the study of our native animals and plants, . . . will acquire a new interest" (pp. 346–47).

In chapter 17, Wallace chose to present information on Borneo and nearby islands on what we now call the Sunda Shelf of Southeast Asia, commenting that "nowhere else upon the globe, [is] an island so far from a continent, yet separated from it by so shallow a sea. Recent changes of sea and land must have occurred here on a grand scale" (pp. 348–50). He noted also the absence of volcanoes, and vast beds of coal and alluvial deposits, indicating "great changes of level in recent geological times" (p. 350). Wallace knew of 96 species of mammals on Borneo,

> nearly two thirds identical with those of surrounding countries . . . ; the thirty-four peculiar species . . . do not . . . imply that the separation of the island from the continent is of very ancient date, for the country is so vast . . . that the amount of specialty is hardly, if at all, greater than occurs in many continental areas of equal extent. . . . A more decisive test of the lapse of time since the separation took place is to be found in the presence of a number of representative species closely allied to those of the surrounding countries . . . best seen among the birds, which have been more thoroughly collected and carefully studied than the mammalia. (pp. 351–52)

In current terms, Wallace argued here that the extent of an area must be considered in assessing endemism, and that the degree of differentiation of the endemics from their closest relatives indicates the timing of their separation. His summary of data on the birds led him to state that "one-third peculiar species of mammalia" and "one-fifth peculiar species of land-birds teaches us that the possession of the power of flight only affects the distribution of animals in a limited degree, and gives us confidence . . . to depend on a knowledge of the birds alone. . . . The majority of forest-birds appear to remain confined, by even narrow watery barriers, to almost as great an extent as do the mammalia. . . . The animals of Borneo exhibit an almost perfect identity in general character, and a close similarity in species, with those of Sumatra and the Malay Peninsula" (p. 355).

In contrast, Wallace then went on describe the biota of Java, a "rich and beautiful island" separated from Borneo only by shallow water, but with "certain close resemblances to the Siamese Peninsula, and also to the Himalayas, which Borneo and Sumatra do not exhibit. . . . Its mammalia (ninety species) are nearly as numerous as those of Borneo, . . . only five or six of the species being confined to the island. In land birds it is decidedly less rich, having only 270 species, of which 40 are peculiar. . . . The amount of specialty is less than in Borneo" (p. 357). On the other hand, he noted 13 genera of mammals and 25 genera of birds that are widespread on Borneo, Sumatra, and the Malay Peninsula that are absent from Java, making it "impossible to doubt that Java has had a history of its own, quite distinct from that of the other portions of the Malayan area" (p. 358). Those species that are "peculiar" are related to those of Indochina and/or the Himalayas. Wallace then presented the hypothesis that the faunal differences between Borneo and Java lie in their geological history: he postulated that Java became elevated and connected to the Malay Peninsula and thus the Himalayas at a date subsequent to the Miocene and received some of the northern taxa. Subsequently, he proposed, Java became isolated, and Borneo, Sumatra, and the Malay Peninsula were elevated and received a more recent set of species that retreated from a cold climatic phase in nonequatorial regions (pp. 359–60).

In this, Wallace was correct that climatic shifts produced much of the difference he noted, but the circumstances were not those that he envisioned: instead, during Pleistocene glacial periods, a corridor of relatively dry savannah vegetation developed from Indochina through the center of the exposed Sunda Shelf, allowing rhinoceros, rabbits, and some dry-land birds to reach Java, where they persisted in the relatively dry climate of that island but became extinct elsewhere on the Sunda Shelf (Bird, Taylor, and Hunt 2005; Meijaard 2003). In this case, his intuition led him in the right direction with respect to a role for climate change, the long-term nature of factors that have influenced the presence of various taxa, and the general impact of geological changes, but lack of detailed information caused him to develop a specific hypothesis not supported by current information.

In the final few pages of this chapter, Wallace offered some comments on the biota of the Philippines, a subject of personal interest to me (e.g., Heaney 1986; Heaney and Roberts 2009). He knew of 21 species of mammals, "and no doubt several others remain to be discovered," and 288 species of birds; "about nine-tenths of the mammalia and two-thirds of the land-birds are peculiar species, a very much larger proportion than is found on any other Malay island" (p. 361). On this basis, he concluded that "the Philippines once formed part of the great Malayan extension of Asia, but that they were separated considerably earlier than Java; and having been since greatly isolated and much broken up by volcanic disturbances, their species have for the most part become modified into distinct local species" (p. 361). In this case, Wallace's knowledge of the fauna was woefully inadequate; the current estimate of native land birds is well over 500 species, and where he knew of 21 species of mammals, we now know of 214 species, a great many of which are distinctive members of endemic radiations (Heaney et al. 2011; Jansa, Barker, and Heaney 2006). However, most of the mammals he knew of actually lived on just one distinctive and specific island—Palawan—which may well have had the history that he described—connected with the Asian mainland in the middle Pleistocene, long before Java's most recent connection to mainland Asia (Meijaard 2003; Piper et al. 2011). The rest of the archipelago is oceanic (Hall 1998), and it is there that the level of endemism, and the extent of adaptive radiation, is highest. Thus, while his conclusion about the archipelago as a whole was wrong, that conclusion was essentially correct about the portion of the archipelago from which his data were drawn.

Wallace next turned to Japan and Formosa (i.e., Taiwan; chap. 18). He noted Japan as having shallow-water connections to the Asian continent at both north and south ends, and a climate ameliorated by "a southern warm current flowing . . . much in the same way as the Gulf Stream" (p. 365). He described the animals as representing "two or more lines of migration at different epochs," the majority from "temperate or cold regions," and "a smaller number have a tropical character" with allied species "in Northern India or the Malay Archipelago," and "a slight American element, . . . a relic probably of the period when a land communication existed between the two continents" (p. 365). He reported 40 mammal species, with 25 of 30 land mammals (excluding bats) endemic to the islands but noted that the biota of Korea and Manchuria were too poorly known for comparison. Among birds, 165 species were known, of which 11 were considered to be endemic (plus five subspecies; pp. 368–69). He listed 40 species shared by Britain and Japan, plus many other pairs of closely related species. Several of these birds survive, he thought, due to "favorable conditions which islands afford both for species which elsewhere live farther south . . . and for the preservation in isolated colonies of species which are verging towards extinction . . . surviving in remote islands. . . . Owing to the comparatively easy passage from . . . the main land of Asia, a large number of temperate forms of . . . birds are still able to enter the country, and thus diminish the proportionate number of peculiar species" (pp. 370–71). Wallace claimed that for mammals "this is more difficult; and the large proportion of specific difference in their case is a good indication of the comparatively remote epoch at which Japan was finally separated from the continent . . . probably in the earlier portion of the Pliocene period" (p. 371).

Regarding Formosa, or Taiwan, Wallace stated, "Among recent continental islands, there is probably none that surpasses in interest and instructiveness" (pp. 371–72). With mountains exceeding twelve thousand feet and crossed by "the Tropic of Cancer a little south of its centre," it possesses "an unusual variety of tropical and temperate climates" and "number and variety of . . . higher animals" (pp. 372–73). About 40 percent of the 35 mammal species and 30 percent of the 128 birds known at the time were considered endemic; "the proportion of peculiar species is perhaps (as regards the birds) the highest to be met with in any island which can be classified as both continental and recent" (p. 373). He noted that many of the endemic mammals are more closely related to "Indian or Malayan rather than with Chinese species." Wallace concluded, "It is clear, therefore, that before Formosa was separated from the main land the above named animals or their ancestral types must have ranged over the intervening country as far as the Himalayas on the west, Japan on the north, and Borneo . . . on the south" (p. 375). He described a similar pattern of relationships among the endemic birds, which he then contrasted with the birds of Japan where far fewer endemics are present, and attributed the difference to the large number of migratory species in Japan, which "prevents the formation of special insular races" (p. 379).

Wallace then summarized his observations on the three sets of continental islands (Britain, Borneo/Java, and Japan/Taiwan). He viewed Britain as a place "in which the process of formation of peculiar species has only just commenced," and Formosa as "probably one of the most ancient of the series . . . with a very large proportion of peculiar species, not only in its mammals, which have no means of crossing the wide strait . . . but also in its birds, many of which are quite able to cross over" (p. 380). In other words, the proportion of endemism on continental islands indicates the recency (or antiquity) of isolation. He then observed that

> on a continent, the process of extinction will generally take effect on the circumference of the area of distribution, because it is there that the species comes into contact with . . . adverse conditions or competing forms. . . . A very slight change will . . . cause the species to contract its range, . . . till it is reduced to a very restricted area, and finally becomes extinct. It may . . . happen . . . so as ultimately to divide the specific area into two separate parts. . . . Were it not for the constant intermingling and intercrossing . . . , pairs of allied species [are formed]. . . . When the division . . . leaves one portion . . . in an island, a similar modification . . . occurs. . . . But islands also favour the occasional preservation of the unchanged species, . . . which rarely occurs in continents . . . probably due to the absence of competition. . . . The distribution and affinities of the animals of continental islands thus throw much light on that obscure subject—the decay and extinction of species; while the numerous and delicate gradations . . . to well-defined species and even distinct genera, afford an overwhelming mass of evidence in favor of the theory of "descent with modification." (pp. 380–81)

Wallace thus combined evidence that isolation on a continental island often results in the development of endemic taxa, that the age of isolation is associated with the extent of endemism, that extinction plays an active role both on islands and on adjacent continents, that relictual species often survive on islands, and that reduced levels of competition and mild climates on islands together contribute to the development of general biogeographic patterns resulting from common processes that are the inevitable result of evolution.

In chapter 19, one of his longest (thirty-seven pages) and most complex in presentation, Wallace turned to what he defined as ancient continental islands,

> those which, although once forming part of a continent, have been separated from it at a remote epoch. . . . Such islands preserve to us the record of a bygone world—of a period when many of the higher types had not yet come into existence and when the distribution of others was very different from what prevails at the present day. . . . A partial subsidence [of the island] will have led to the extinction of some of the types . . . and may leave the ancient fauna in a very fragmentary state; while subsequent elevations may have brought it so near to the continent that some immigration even of mammalia may have taken place. (pp. 383–84)

Wallace thus clearly recognized the role of the breaking up of land masses resulting in the evolution of disparate terrestrial lineages from a common ancestor that once lived in both areas, through a combination of long-term persistence and diversification, thus anticipating the development of vicariance biogeography (e.g., Rosen 1978; Humphries and Parenti 1999). He also saw that reduction in area could result in extinction of some lineages, and that a reduction in the degree of isolation of such an island could allow some colonization from the mainland, even by nonflying mammals, which he regarded as very limited in their abilities to cross sea channels.

As his prime example, Wallace made the same choice that many biogeographers would make today: Madagascar, "the most interesting of such islands" (p. 384). He described the island as comprised mostly of a "lofty granitic plateau" surrounded by "plains of a few hundred feet elevation" (p. 384). He described the island as ringed by a narrow strip of shallow water, which in turn is surrounded by deep water, except to the north and east, where a series of isolated shallow-water banks support small islands, including Mauritius, Aldabra, the Seychelles, and the Maldives, "which together would form a line of communication by comparatively easy stages of 400 to 500 miles each between Madagascar and India" (p. 386). He described the biota as "exceedingly rich and beautiful" and "of surpassing interest from the singularity, the isolation, or the beauty of its forms of life" (p. 388). These features conform to his concept of an ancient continental fragment: an island with geology of a continental type (e.g., granitic rather than volcanic), surrounded by deep water, and a fauna with few species closely related to the neighboring continent.

Wallace noted that "Madagascar possesses no less than sixty-six species of mammals—a certain proof in itself that the island has once formed part of a continent; but . . . these animals [are] very extraordinary and very different from the assemblage now found in Africa . . . , and thus our first impression would be that it could never have been united with the African continent." "We must look for their probable allies," Wallace stated. "Most important are the lemurs, consisting of six genera and thirty-three species." Regarding their closest relatives, he pointed out that a "group of lowly organized and very ancient creatures still exists scattered over a wide area . . . from West Africa to India, Ceylon, and the Malay Archipelago . . . which appear to maintain their existence by their nocturnal and arboreal habits, and by haunting dense forests" (p. 388). He then noted "a dozen species of Insectivora," the tenrecs (distantly related to species in Cuba and Haiti), a unique family of cat-like carnivore, and some civets of endemic genera related to those of Africa and Asia. He knew of only four murid rodents and mentioned "a river hog . . . and small subfossil hippopotamus, both of which, being semi-aquatic animals might easily have reached the island from Africa . . . without any actual land-connection" (p. 389). He described the lizards and snakes as a mixed lot with relationships to Africa and to America, often rather distant. In all cases, he greatly underestimated the number of species (e.g., 9 genera and 22 species of endemic murid rodents are known currently [Jansa and Carleton 2003]) but accurately recognized the distinctiveness of the fauna.

To explain the presence of so many highly distinctive and apparently "ancient" taxa with distant relationships to Africa and America (and a few elsewhere), Wallace turned to a hypothesis offered by Thomas Huxley that the southern portion of Africa had been isolated from the northern portion and Europe "by a sea stretching from the Atlantic to the Bay of Bengal" coupled with the inference that "the higher types of mammalia were developed in the great Euro-Asiatic continent . . . and that they only migrated into tropical Africa when the two continents became united . . . in the latter portion of the Miocene or early in the Pliocene period" (p. 390). He concluded that Madagascar had once formed part of Africa but separated from it before Africa formed its recent connection to Europe and Asia (p. 391). Madagascar, he thought, had received its mammalian fauna from an earlier time when it, Africa, and Europe shared a more primitive fauna that was widespread, as shown by fossils of "ancient types" of insectivores, carnivores, and primates in Europe that had "a wide range at the period of their maximum development; but as they decay their area of distribution diminishes or breaks up into detached fragments . . . while those which are absent . . . belong to more recent and more highly developed types" (p. 392).

Wallace then presented a discussion of how best to interpret "anomalous [i.e., disjunct] distributions" in which members of a taxonomic group (especially at the family level) currently occur only in widely separated areas—as do the tenrecs of Madagascar and what Wallace considered to be their closest relatives in the Greater Antilles (including the solenodon of Cuba). He offered camels and tapirs as examples; camels now occur in Asia and nearby northern Africa, and in the Andes of South America; tapirs live in tropical South America and Southeast Asia. Fossils of both camels and tapirs are known from North America and Europe, bridging the geographic gap in the modern distribution, leading him to ask,

> Who could possibly have imagined such migrations, and extinctions, and changes in distribution . . . if we had only the distribution of the existing species to found an opinion upon? . . . We must, on every ground of philosophy and common sense, apply the same method of interpretation to the more numerous instances of anomalous distribution we discover among such groups as reptiles, birds, and insects, where we rarely have any direct evidence of their past migrations through the discovery of fossil remains. . . . In no single case have we any direct evidence that the distribution of land and sea has been radically changed during the whole lapse of the Tertiary and Secondary periods, while . . . the testimony of geology itself . . . upholds the same theory of the stability of our continents and the permanence of our oceans. Yet . . . we still continually meet with suggestions of former continents stretching in every direction across the deepest oceans. (pp. 393–94)

Wallace thus rejected the common practice of the time of hypothesizing now invisible, continuous dry-land areas as always being necessary to explain disjunct distributions, and argued for the use of well-documented cases (e.g., groups of mammals with good fossil records) as models for how to interpret other similar patterns based on current distributions of organisms that lack fossils.

Wallace also argued for the permanence of land and sea, aside from relatively minor changes due to uplift, subsidence, volcanic eruption, and so forth, throughout the Tertiary. He has subsequently been criticized for not seeing evidence of continental drift/plate tectonics, but that was not his point: instead, he argued against speculation about the existence of former continents that have now almost or entirely disappeared and simply did not address the question of possible movements of the existing continents. A clear example of the distinction is present in his next section, in which he argued against the widely accepted former existence "of a hypothetical continent—Lemuria—extending from Madagascar to Ceylon and the Malay Islands," which had been proposed based largely on some distribution patterns among birds, especially "five or six [species] . . . decidedly Oriental" in affinities, and the absence of many typical groups of African birds from Madagascar (p. 394). Wallace argued that "the absence of numerous peculiar groups of African birds is so exactly parallel to the same phenomenon among mammals that we are justified in imputing it to the same cause" (p. 395). Noting further that "the Oriental birds in Madagascar . . . are slightly modified forms of *existing Indian genera*, or . . . *species hardly distinguishable from those of India*" (p. 395; italics Wallace's), he proposed that they must have arrived recently, by way of the extensive set of shoals, coral reefs, and small islands that extend from Madagascar to India that he described earlier, when those islands were somewhat higher and larger, thus anticipating the results of recent DNA-based phylogenetic studies that came to the same conclusion (e.g., Sheldon et al. 2009; Warren et al. 2006). Lemuria, he concluded, was "a provisional hypothesis . . . not affording the true solution" similar to the hypothesized and widely rejected continent of Atlantis (pp. 398–99).

Turning next to the islands that lie near Madagascar in the Indian Ocean (which he refers to collectively as the "Mascarene Islands"), Wallace began by reminding the reader that "my object in this volume being more especially to illustrate the mode of solving distributional problems by means of the most suitable examples" (p. 399). He described the Comoro Islands as volcanic and probably of fairly recent origin, providing "no indication whatever of there having been here a land-connection between Madagascar and Africa" (p. 400). He considered the birds (and a large fruit bat) to have mostly arrived from Madagascar, and the few nonvolant mammals to have arrived through "the occasional transmission . . . by means of floating trees" (p. 400). The Seychelles he described quite differently, noting that the abundance of granite shows that "they form a portion of the great line of upheaval which produced the central granitic mass of Madagascar" (p. 401), and he hypothesized that some intervening islands (the Amirantes, the Providence, and Farquhar Islands) "probably rest on a granitic basis. Deep channels of more than 1,000 fathoms now separate these islands from each other, and if they were ever sufficiently elevated to be united, it was probably at a very remote epoch. . . . The existing flora and fauna of the Seychelles must therefore be looked upon as the remnants which have survived the partial submergence . . . or to its having since undergone so much submergence as to have led to the extinction of such mammals as may once have inhabited it" (p. 401). "The reptiles and amphibia are rather numerous and very interesting, indicating clearly that the islands can hardly be classified as oceanic" (p. 402). A few lizards he regarded as probably introduced on ships or possibly on floating trees, but many species and some genera are endemic, the latter including a frog likely to be "a relic of the indigenous fauna of that more extensive land of which the present islands are the remains" (p. 403). Also present are two species of caecilians, possibly "the oldest land vertebrate now living on the globe—dating back to the early part of the Tertiary period, when the warm climate . . . and the union of Asiatic and American continents, allowed the migration of such types over the whole Northern Hemisphere, from which they subsequently passed into the Southern Hemisphere, maintaining themselves only in certain limited areas" (pp. 404–5). In this, without recognizing the full significance of his comments and descriptions, he foreshadowed the current recognition that these islands were indeed once connected as part of a combined

Madagascar-Indian subcontinent, and left as isolated fragments as India moved northward, "at a very remote epoch."

In the final portion of chapter 19, Wallace turned to Mauritius, Bourbon, and Rodriguez, three volcanic islands surrounded by deep water, with no indigenous mammals or amphibians but incomplete information largely because the original forest was almost wholly destroyed by sugar cultivation (p. 406). With special interest, however, he noted the presence of fossils of extinct flightless birds, including the dodo of Mauritius and the allied "solitaire" of Rodriguez, "rapidly exterminated when man introduced dogs, pigs, and cats into the islands, and himself sought them for food" (p. 407). He ascribed their flightlessness to the effects of natural selection on pigeon-like relatives that reached these predator-free islands, once again rejecting their presence as indicating the existence of the continent of "Lemuria" (pp. 408–9). He noted, however, the presence of an endemic genus of snake, and another of a lizard, which he implied arrived over water at a time in the past when the islands were less isolated (pp. 409–10).

Moving next to the flora of Madagascar, Wallace referred to "its extreme richness and grandeur, its remarkable speciality, and its anomalous external relations," with some taxa allied to Africa, Asia, South America, and Australia (p. 410). Of the plants on the Mascarene Islands, he cites 1,058 species, 840 of which are endemic either to several islands within the group or to a single island. Of the 440 genera represented, he cited "Mr. Baker" as saying that 50 genera are endemic, 22 are Asiatic but not African, and 28 are African but not Asiatic. "This implies that the more ancient connection has been on the side of Africa, while a more recent immigration, shown by identity of species, has come from Asia," with just a few from South America, Australia, and Polynesia (p. 412). He explained this by observing that plants "are undoubtedly more long-lived specifically than animals, especially the more highly organized groups [i.e., mammals], and are less liable to complete extinction," and thus showing evidence of the same past connections as the mammals, with the extinction of geographically intervening species between the islands and the more distant continents (p. 412), though noting also the massive impact of habitat destruction and the attendant erosion and drought in the Seychelles, Mauritius, and Bourbon. He commented that the "great preponderance of ferns" and, to a slightly lesser extent, orchids in these and other oceanic islands is due to the ease with which their minute spores and seeds are carried by the wind (p. 416).

In conclusion, Wallace described Madagascar as "a continental island . . . of immense antiquity," with the Comoros, Aldabra, and the Seychelles as "detached fragments of this island"; Mauritius, Bourbon, and Rodriguez as associated oceanic islands; and numerous coral reefs (including Cargados and the Maldives) as submerged, previously larger islands (p. 417). "The entire group," he said, "contains just that amount of Indian forms which could well have passed from island to island;" the "slightly modified species" having done so during the late Tertiary; while the distinct genera indicate "a more ancient connection. But in no case do we find animals which necessitate an actual land-connection. . . . To suppose . . . a direct land-connection, is really absurd" (p. 418). The patterns, he stated, are all the result of the geological history of the earth, coupled with the rare colonization by some taxa over a long period of time, with survival of archaic forms on some islands, with the long isolation of Madagascar from Africa playing an especially large role. He ended by stating, "Had the numerous suggested continental extensions connecting these remote [islands] . . . been realities, the result would have been that all these interesting archaic forms . . . would long ago have been exterminated, and one comparatively monotonous fauna have reigned over the whole earth. So far from explaining the anomalous facts, the alleged continental extensions, had they existed, would have left no such facts to be explained" (p. 420).

In chapter 20, Wallace turned to the discussion of "anomalous islands" but first made the point that the Greater Antilles are ancient continental islands, as shown in his *Geographical Distribution of Animals*. He also included Iceland as an "ancient continental island," due to its shallow connections to Greenland and Europe, almost certainly "in the early part of the Tertiary, and thus afforded one of the routes by which that intermigration of American and European animals and plants was effected, which we know occurred during some portion of the Eocene and Miocene periods" (pp. 421–22)—a recognition of what has come to be known as the DeGeer Passage (e.g., Lundberg et al. 2007).

Among "anomalous islands," "there remains the great Malay island—Celebes, which, owing to its possession of several large and very peculiar mammalia, must be classed, zoologically, as 'ancient continental;' but whose central position and relations both to Asia and to Australia render it very difficult to decide in which of the primary zoological regions it ought to be placed" (p. 422). He commented that the geology of the island was almost unknown, though data indicated that it is surrounded entirely by deep seas, partially filled by river and volcanic deposits (pp. 422–24). In comparison, he stated that the nearby islands of Java and Bali differ from Borneo primarily by having a smaller fauna that is shared with that of southern Asia, with the Philippines having the same pattern but even fewer species and "a greater amount of speciality" (p. 424). In contrast, on the islands to the east of Celebes ("the Mollucas, New Guinea, and the Timor group"), 23 of the mammalian families found on Borneo are absent, and only 4 are present, but with 4 families of marsupials present: "We have here a radical difference between the two sets of islands not very far removed from each other. . . . The Asiatic or Malayan group . . . bounded strictly by the eastern limits of the great bank [now called the Sunda Shelf]. . . . To the east another bank unites New Guinea and the Papuan islands . . . with Australia [now called the Arafura Shelf] . . . while the Molucca and Timor groups are surrounded by much deeper water" (p. 425).

Of Celebes itself, Wallace knew of only 16 species of terrestrial mammals, an "extreme poverty in this class" (p. 426). Two marsupials and two rats "belong to the Mollucan and Australian fauna"; most of the rest—some squirrels, a deer, a pig, a civet, and a tarsier—are allied to Asian taxa, excepting three species—a "baboonlike ape," the anoa (a small buffalo), and "the strange babirusa. . . . Neither of these three animals last mentioned have any close allies elsewhere, and their presence . . . must give us the clue to the past history of the island." They are "in all probability very ancient forms, which have been preserved to us by isolation in Celebes. . . . And this compels us to look upon the existing island as a fragment of some ancient land, once perhaps forming part of the great northern continent. . . . The exceeding scantiness of the mammalian fauna, however, remains to be accounted for. . . . If the portion of separated land had been anything like as large as Celebes now is, it would certainly have preserved a far more abundant and varied fauna" (pp. 426–28). He presented two alternative theories to account for this paucity of species: either that "the original island has . . . been greatly reduced by submersion, so as to lead to the extinction of most of the higher land animals; or that it . . . was only united with the Asiatic continent for a short period, or perhaps even never united at all, but so connected by intervening islands separated by narrow straits that a few mammals might find their way across. The latter supposition appears best to explain the facts." Wallace concluded, "The question . . . can only be finally determined by geological investigations. If Celebes has once formed part of Asia . . . then some remains of this [rich] fauna must certainly be preserved in caves or late Tertiary deposits, and proofs of the submergence itself will be found when sought for" in the geological record (p. 428).

Wallace then went on to describe the bird fauna, concluding that "Celebes has been receiving immigrants from all sides, many of which have had time to become modified into distinct representative species. These evidently belong to the period during which Borneo on the one side, and the Moluccas on the other, have occupied very much the same relative position as now. There remain the twelve peculiar Celebesian genera" (p. 429). Eight of these he traced to either Asia or Australia, leaving four "which have no near allies at all. . . . These may fairly be associated with the baboon-ape, anoa, and babirusa, as indicating extreme antiquity and some communication with the Asiatic continent" (p. 430). "We are therefore again driven to our former conclusion—that the present land of Celebes has never (in Tertiary times) been united to the Asian continent, but has received its population of Asiatic forms by migration across narrow straits and intervening islands. . . . But facts of a very similar character are equally opposed to the idea of a former land-connection with Australia or New Guinea, or even with the Moluccas" (pp. 431–32). Celebes thus "occupies such an exactly intermediate position between the Oriental and Australian regions that it will perhaps ever remain a mere matter of opinion with which it should properly be associated" (p. 432).

In the next three chapters (chaps. 21–23) of *Island Life*, Wallace turned to "the most remarkable and interesting of insular faunas," the "anomalous" island of New Zealand (p. 442). He described it as having "geological structure of . . . a decidedly continental character,"

> surrounded by moderately deep ocean; but the form of the sea-bottom is peculiar, . . . the 1,000-fathom line . . . extending in a broad mass westward, and then sending out two great arms, one . . . stretches over Norfolk Island to the great barrier reef, thus forming a connection with tropical Australia. . . . Judging by these indications, we should say that the most probable ancient connections of New Zealand were with tropical Australia and New Guinea and . . . a land-connection or near approximation . . . at remote periods will serve to explain many of the remarkable anomalies. . . . We see, then, that both geologically and geographically New Zealand has more of the character of a "continental" than of an "oceanic" island; yet its zoological characteristics are such as almost to bring it within the latter category, and it is this which gives it its anomalous character. It is usually considered to possess no indigenous mammalia; it has no snakes, and only one frog; it possesses . . . an extensive group of birds incapable of flight; and its productions . . . bear no . . . close relation to those of Australia or any other continent. These are the characteristics of an oceanic island. (pp. 443–44)

Wallace briefly noted the presence of a "forest-rat" that the Maoris said had been brought to New Zealand by their ancestors (p. 445). Wallace was skeptical, but the Maoris were correct: the rat was *Rattus exulans*, known as the Polynesian rat, which was carried throughout the Pacific by Polynesians (Matisoo-Smith and Robins 2004). He also commented on (apparently erroneous) reports of a "small otter-like animal" (p. 446); no such animal has been documented on New Zealand, and it is somewhat surprising that he was less cautious in this case than, for example, the evidence of native rodents on the Galapagos Islands.

However, once again, Wallace's use of geological information, coupled with the rather new bathymetric charts produced by the British Royal Navy, provided a major source of insight into the origin of biogeographic patterns. The kiwis and subfossil moas, he said, are most closely related to the emus and cassowaries of

Australia and New Guinea, with the presence of "no less than fifteen species . . . in the small area of New Zealand . . . is at once [suggestive] of great geographical changes"—specifically, a land connection at an "ancient time" that allowed some species to enter, then subsequently subsided, leaving only a deep submarine ridge as evidence (pp. 449–50).

Notably, he went on to explicitly reject the "speculations" (of Captain Hutton) that New Zealand, Australia, Antarctica, South America, and South Africa were once united into a continuous continent, with the distribution of large flightless birds related to ostriches and emus as prime evidence (p. 450). Wallace argued that proposing such a continent was unnecessary and "utterly opposed to all sound principles of reasoning in questions of geographic distribution; for it depends on two assumptions, both of which are at least doubtful, if not certainly false—the first, that [the distribution of ostriches, rheas, emus, and their relatives] over the globe has never in past ages been very different from what it is now; and the second, that the ancestral forms of these birds never had the power of flight" (pp. 450–51). The first assumption he countered with examples of formerly more widespread groups, including fossil marsupials in North America and Europe, camels in North America, trogons in Europe, ostriches in North India, and tentative evidence of "Struthious" birds (i.e., relatives of ostriches, rheas, and emus) in Eocene deposits of England (p. 451). The second assumption he countered with the observation that all of these flightless birds have the rudiments of wings and a broad sternum, which became reduced due to "retrograde development" associated with the loss of flight, as seen in the dodo and other flightless, insular birds (pp. 451–52).

Among "winged" birds, Wallace noted the presence of many species allied to those of tropical Australia and New Guinea and virtually none allied to those of temperate Australia. Similarly, Wallace reported that the few lizards are related to species that occur in the Australian tropics and elsewhere, and the tuatara is "a distinct order of reptiles . . . having therefore no affinity with any living animal." The single frog represents an endemic genus related to species in Europe and South America (pp. 453–54).

From all of these data, Wallace deduced that "the total absence (or extreme scarcity) of mammals in New Zealand obliges us to place its union with North Australia and New Guinea at a very remote epoch" (p. 454), before monotremes and marsupials arrived in Australia, and cited the absence of species of birds and lizards shared among New Zealand and Australia as supporting this. To maintain complete isolation, the separation must have occurred in "the earlier portion of the Tertiary period at least," with submergence of the connecting ridge to the current depth of 1,500 fathoms (pp. 454–55). This, he said, might have been followed by development of a dry-land "southern extension towards the antarctic continent at a somewhat later period . . . , affording an easy passage for the numerous species of South American and antarctic plants" and some freshwater fishes (p. 455). He then proposed the "pure hypothesis" that the land that now makes up New Zealand broke up into separate islands, causing the development of distinct species, followed by reunion into a large landmass with many species, and then followed by a final stage of subsidence (pp. 455–56). Wallace ended the chapter by stating that "it would be well to see how far these conclusions [based on New Zealand's fauna] are supported by the facts of plant-distribution" (p. 456), the subject of the next chapter.

Wallace's discussion of the "affinities and probable origin" of the flora of New Zealand (chap. 22) began with the observations that "plants have means of dispersal far exceeding those possessed by animals," though "comparatively few species are carried for very great distances," and that "plants . . . are more numerous in species than the higher animals, and are almost always better known" (p. 457). He argued strongly for taking an integrated view of biogeographic patterns, stating that "no explanation of the origin of the fauna of a country can be sound which does not also explain, or at least harmonize with, the distribution and relations of its flora" (p. 457). He then quoted Joseph Hooker as saying in reference to the plants of Australia and New Zealand, "I find all attempts to theorize on the possible causes of their community of feature frustrated by anomalies in distribution, such as . . . no two other similarly situated countries" (pp. 457–58), including both the absence from New Zealand of some common Australian tree genera, and the presence in New Zealand of many "broad features of resemblance" with the flora of Australia (pp. 458–59). Wallace described the flora of New Zealand as being species-poor relative to that of Great Britain, but about two-thirds of the 935 species are endemic. On the other hand, of the 258 species not endemic, about 85 percent are shared with Australia, and most of them are also shared with the antarctic and South America (and some with Europe); only about 9 percent of the flora is shared only by New Zealand and Australia (p. 450). At the generic level, a higher proportion is shared with Australia (ca. 83 percent of 303 genera), though most of the species are distinct. Wallace then emphasized the many Australian taxa that are absent from New Zealand (pp. 459–60).

Wallace next argued that the presence of a rather species-poor tropical flora in Australia, and the low percentage of endemic species or genera, is evidence that it is "recent and derivative," largely drawn from Indian and Malay regions (p. 462). The temperate flora of Australia, on the other hand, occurs widely over "enormous areas covered with Cretaceous and other Secondary deposits," which "support . . . the view, that during very long epochs temperate Australia was cut off from all close connection with the tropical and northern lands by a wide extent of sea" (p. 462), with southwestern Australia being "the remnant of the more extensive and more isolated portion of the continent" on a "very large area of granite" (p. 464). He inferred that "the eastern portion of the continent must either have been widely separated from the western, or had perhaps not yet risen from the ocean," with the presence of widespread sedimentary deposits of the "Secondary period" supporting the latter view (p. 464), which he illustrated with a map of Australia during the Cretaceous period that shows a large shallow sea between eastern and western Australia (p. 466). New Zealand, he proposed, had its geological connection with eastern Australia during its period of isolation, when its flora was limited and when few plants had established themselves in the northern part of the island, where the land bridge developed (as discussed in the prior chapter). Thus, he said, "It is therefore no matter of surprise, but exactly what we should expect, that the great mass of pre-eminently temperate Australian genera should be absent from New Zealand," especially those genera which were at the time confined to the island of western Australia (p. 468). The temperate-zone genera that are shared, he further noted, have "special features . . . that would facilitate transmission across the sea . . . and the fact that in several of them the species are absolutely identical shows that such transmission has occurred in geologically recent times" (p. 471). Of the species shared by New Zealand and Australia, "the larger portion . . . must have reached New Zealand . . . by transmission across the sea, because we know there has been no land-connection during the Tertiary period, as proved by the absence of all the Australian mammalia and almost all the most characteristic Australian birds, insects, and plants" (p. 471). The bulk of these, he argued, have "exceptional powers of dispersal" (including sedges and grasses) or are arctic species that arrived "from some now submerged antarctic island" (p. 472). He also argued that once some of the species with high vagility became established on New Zealand, they became "adapted to the climate" and "modified in accordance with the new conditions" and "soon took possession of all suitable stations. Henceforth immigrants from Australia had to compete with these indigenous and well-established plants, and only in a few cases were able to obtain a footing" (p. 473).

In summary, Wallace sought to investigate a case that Joseph Hooker, the mostly widely known and respected plant biogeographer of his day, had declared to be especially difficult to understand. He combined information from newly available bathymetric charts and deep-historical geological information with details regarding the presence of plant species with differing climatic requirements, dispersal abilities, and histories of distribution; he also posited the impact of rapid local adaptation in producing island taxa that are resistant to invasive species (an idea he cited as originating with Darwin; pp. 475–76). This allowed him to propose a plausible hypothesis, based on observed patterns, which incorporated elements that formed an integrated set of biogeographic processes and could be tested subsequently by determining whether similar patterns existed in other "anomalous" parts of the world.

In his third chapter (chap. 23) on New Zealand, Wallace turned to the "difficulty" of the presence in New Zealand of a large number of arctic plants, as previously noted by Joseph Hooker. Wallace noted that more than one-third of the genera of plants in New Zealand are also found in Europe, and many of these are also shared with South America, Tasmania, and southern Australia, some being of the same species in all of these areas, and others having different but closely related species. He noted that "many north temperate genera also occur in the mountains of South Africa" (p. 478). In a long quote, he cited Hooker as seeing a virtual "continuous current of vegetation . . . from Scandinavia to Tasmania . . . in rapidly diminishing numbers, it is true, but in vigorous development throughout," wherever high mountains provide a suitable climate, regardless of the type of vegetation lower on a given mountain (pp. 478–79). After expressing his admiration of Hooker for describing the patterns succinctly, Wallace proceeded to offer an explanation for the processes behind the pattern.

Wallace began by describing "the wonderful aggressive and colonizing power of the Scandinavian flora, as shown by the way in which it established itself in any temperate country to which it may gain access. About 150 species have thus established themselves in New Zealand," with similar numbers in Australia and "the Atlantic states of America, where they form the commonest weeds. Whether or not we accept Mr. Darwin's explanation of this power as due to development in the most extensive land area of the globe where competition has been most severe and long-continued, the fact of the existence of this [competitive] power remains"(p. 479). He then cited the existence in the Azores (roughly nine hundred miles west of the coast of Portugal) of 400 out of 478 flowering plants as being identical to European species, and the "most interesting and suggestive fact that more than half of the European genera which occur in the Australian flora occur also in the Azores. . . . It affords a demonstration of the power of the very plants in question to pass over wide areas of sea," by wind, floating on water, or attachment to birds. "We have in such facts as these a complete disproof of the necessity for those great changes of sea and land which are continually appealed to by those who think land-connection the only efficient means of accounting for the migration of animals or plants; but at the same time we do not neglect to make the fullest use of such moderate changes as all the evidence at our command leads us to believe have actually occurred, and especially of the existence of intermediate islands, so often indicated by shoals in the midst of the deepest oceans" (pp. 479–80).

How, then, might arctic plants have moved such great distances over continents and oceans? Wallace suggested that landslips, debris from torrents, and other events in mountainous terrain often provide fresh soil surfaces where aggressively colonizing species may gain a foothold, even if only temporarily, with each acting "as a fresh centre of dispersal; and thus a plant might pass on step by step . . . till it reached a district where . . . it was able to establish itself as a permanent member of the flora. Such, generally speaking, was probably the process by which the Scandinavian flora has made its way to the southern hemisphere" (pp. 482–83). He added that the existence of repeated global changes in climate, including glacial periods due to shifts in the earth's orbit, would have further promoted this spread of arctic plants by opening up bare soil where glaciers retreated, and lowering the elevation of the snow line and the arctic habitat immediately below the snow line, thereby reducing distances between areas of arctic habitat, facilitating dispersal (pp. 484–85). He noted as well that "the depression of the ocean which must have arisen from such a vast bulk of water being locked up in land-ice" (pp. 485–86), thereby lessening the distances to be traversed over water. These processes, he said, have continued for a long time, providing many opportunities for arctic plants to disperse and to develop the pattern in which some species occur over wide areas, and others are locally limited but allied to groups of species that are widespread. Further, mountain ranges themselves have been dynamic, being uplifted and then eroding, providing stepping-stones of arctic habitat over the passage of time (pp. 487–88). He specifically pointed to the Andes as providing "the only unbroken chain of highlands and mountains connecting the arctic and north temperate with the antarctic lands . . . , the only break of importance being the comparatively low Isthmus of Panama, where there is a distance of about 300 miles. . . . Such distances are, as we have already seen, no barrier to the diffusion of plants" (pp. 488–89). And during alternations of climate, "the southern extremity of America being considerably the nearest [to the antarctic islands], and also the best stocked with those northern types which have such great powers of migration and colonization, such plants would form the bulk of the antarctic vegetation" (p. 490).

Wallace then argued that Australia has received European plants by two routes. The first arrived by way of South America and the antarctic islands, and the second "by way of the mountains of Southern Asia, Borneo, the Moluccas, and New Guinea at a somewhat remote period when loftier ranges and some intermediate peaks may have existed, sufficient to carry on the migration by the aid of the alternate climatal changes which are known to have occurred. . . . So far as I can judge of the facts, there is no general phenomenon—that is, nothing in the distribution of genera and other groups of plants . . . that is not fairly accounted for by such an origin" (p. 492). As to the similarity of the vegetation of Australia and South Africa,

> this resemblance has been supposed to imply some former land-connection of all the great southern lands, but it appears to me that any such supposition is wholly unnecessary. The differences between the faunas and floras of these countries are too great and too radical to render it possible that any such connection should have existed except at a very remote period. . . . We should prefer to consider the few genera common to Australia and South Africa as remnants of an ancient vegetation, once spread over the northern hemisphere, driven southward by the pressure of more specialized types. . . . It is suggestive of such an explanation that these genera are either of very ancient groups—as Conifers and Cycads—or plants of low organization, as the Restiaceae, or of world-wide distribution, as Melanthaceae. (pp. 493–94)

Wallace concluded the chapter by observing,

> Our inquiry . . . has thus led us to a general theory . . . rendered possible solely by the knowledge very recently obtained of the form of the sea-bottom in the southern Ocean, and of the geological structure of the Australian continent. Without this knowledge we should have nothing but a series of guesses or probabilities on which to found our hypothetical explanation. . . . I have shown what an important aid to any such explanation is the theory of repeated changes of climate . . . while the whole discussion justifies the importance attached to the theory of the general permanence of continents and oceans. . . . The whole inquiry into the phenomenon presented by islands . . . has, I think, shown that this theory does afford a firm foundation for the discussion of questions of distribution and dispersal; and that by its aid, combined with a clear perception of the wonderful powers

of dispersion and modification in the organic world when long periods are considered, the most difficult problems connected with this subject cease to be insoluble. (pp. 496–98)

In the final chapter of *Island Life* (chap. 24), Wallace presented a succinct and powerful summary of the main points of the volume. It is, he said, "the development of a clear and definite theory" (p. 499), with the following essential components (the numbering of points is mine, not Wallace's):

1. "The distribution of . . . living things over the earth's surface, and their aggregation in definite assemblages in certain areas, [are] the direct result and outcome of a complex set of causes, which may be grouped as 'biological' and 'physical'" (p. 499).

2. The first biological cause is "the constant tendency of all organisms to increase in numbers and to occupy wider area, and their various powers of dispersion and migration which . . . enable [them] to spread widely over the globe" (p. 500).

3. The second biological cause is "those laws of evolution and extinction which determine the manner in which groups of organisms arise and grow, reach their maximum, and then dwindle . . . in very remote regions" (p. 500).

4. The two physical causes are "the geographical changes which . . . isolate a whole fauna and flora" or "lead to their dispersal and intermixture with adjacent faunas and floras" (p. 500) and

5. "the exact nature, extent, and frequency of the changes of climate . . . , because such changes are among the most powerful agents in causing the dispersal and extinction of plants and animals" (p. 500).

6. These "facts thus far established are then shown to be necessary results of the 'law of evolution' . . . and are shown to follow as logical consequences" (p. 501).

7. "The grand features of our globe—the position of the great oceans and the chief land-areas—have remained, on the whole, unchanged throughout geological time. . . . The general stability of the continents has, however, been accompanied by constant changes of form, and insular conditions have prevailed over every part in succession" (pp. 501–2).

8. "The occurrence of a recent glacial epoch of great severity

in the Northern Hemisphere is now universally admitted but the causes . . . are matter of dispute" (p. 502).

9. "While generally adopting Mr. Croll's views as to the causes of the 'glacial epoch,'" these being variations in the earth's orbit around the sun and precession of the equinoxes, Wallace also believed that "without high land there can be no permanent snow and ice" (p. 502), and

10. that uninterrupted warm climates in the far north during long portions of geological time were caused by geological changes that allowed "warm tropical waters freely to penetrate . . . the arctic sea by several channels" (p. 503).

11. Because "the sun is ever losing heat far more rapidly than it can be renewed from any known or conceivable source," and "the earth is a cooling body, . . . a limit is therefore placed to the age of the habitable earth" (p. 505).

12. A review of available evidence regarding the time required to produce the known sedimentary rocks showed that "the time required is very much less than has hitherto been supposed" (p. 506).

13. Further, the high rate of evolution caused by frequent changes in climate show "that the periods allowed by physicists are . . . far in excess of such as are required for geological and organic change" (p. 507)

14. Study of the flora and fauna of oceanic islands demonstrates "how important an agent in the dispersal of most animals and plants is a stormy atmosphere," such that islands in calm areas have many species "of immense antiquity" because of the rarity of colonization (p. 507).

15. Continental islands share most of their species with adjacent continents but have fewer, often far fewer, species than the continent, often with "a considerable amount of speciality" (p. 508). Climate impacts the richness of such islands, with tropical islands having greater species richness and "a large proportion of peculiar species, . . . in general very closely allied to those of the adjacent parts" of the nearby continent (p. 508).

16. Successfully understanding ancient continental islands, such as Madagascar, requires knowledge of the geology and seafloor bathymetry, "without recourse to the hypothesis of a now-submerged Lemurian continent" (p. 509). Celebes is "an outlying portion of

the great Asiatic continent of Miocene times, which either by submergence or some other cause has lost the greater portion of its animal inhabitants, and since then has remained more or less completely isolated" and "has thus preserved a fragment of a very ancient fauna along with a number of later types which have reached it . . . by the ordinary means of dispersal" (p. 509).

17. New Zealand is "completely continental in its geological structure" with "the former connection . . . with Australia" when that island was itself "divided into an eastern and a western island," allowing some plants and animals to enter New Zealand and survive (p. 510), while other plants of arctic origin entered by way of islands to the south (p. 511).

In conclusion, Wallace commented, "I trust that the reader . . . will be imbued with the conviction . . . of the complete interdependence of organic and inorganic nature . . . dependent on the long series of past geological changes—on those marvellous astronomical revolutions which cause a periodic variation of terrestrial climates—on the apparently fortuitous action of storms and currents in the conveyance of germs—and on the endlessly varied actions and reactions of organized beings on each other. . . . Their broad results are clearly recognizable" (p. 511–12).

I conclude that Wallace's core perspective on biogeography, and on island biogeography in particular, may be summarized as the following fundamental points (see also Lomolino, Riddle, and Brown 2006, 26–27):

1. The earth has had a long and complex history of geological and climatic change, and the current distribution and diversity of life is intimately interwoven with both of those factors. Attempted explanations of distribution patterns that involve single factors are likely to fail. Climatic changes have been influenced by both astrophysical (e.g., orbital) and geological processes (e.g., land uplift or subsidence that influences both elevational zonation and ocean currents).

2. Organisms differ greatly in their ability to disperse; some have mechanisms that allow them to move long distances relatively quickly, and others are extremely limited by hostile habitats, including seawater. These differences, which fundamentally influence the effective degree of isolation, have profound effects on their patterns of diversification.

3. Explanations of distribution and diversity patterns should be made on the basis of observable or strongly inferred processes and should not invoke processes that are beyond the realm of demonstrably factually based science. Most processes relevant to biogeography occur in a gradualistic fashion, not catastrophically, but some are dramatic and fairly rapid (e.g., those related to climate and glaciation).

4. Rates of evolution vary among taxa and over time, influenced by climatic and geological changes and by local circumstances (e.g., the presence or absence of competitors, isolation from or connection with closest relatives).

5. Diversification or extinction are the possible ultimate fates of any given lineage; archaic lineages often survive in isolated places.

6. Islands are key to understanding the diversity of life on earth.

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LITERATURE CITED

Bintanja, R., R. S. W. Van de Wal, and J. Oerlemans. 2005. "Modelled Atmospheric Temperatures and Global Sea Levels over the Past Million Years." *Nature* 437:125–28.

Bird, M., D. Taylor, and C. Hunt. 2005. "Palaeoenvironments of Insular

Southeast Asia during the Last Glacial Period: A Savanna Corridor in Sundaland." *Quaternary Science Reviews* 24:2228–42.

Borges, P., and R. Gabriel. 2008. *Predicting Extinctions on Oceanic Islands: Arthropods and Bryophytes*. Terceira: Universidade dos Açores.

Claridge, E. 2009. "Wallace, Alfred Russel." In Gillespie and Clague 2009, 962–67.

Cox, C., and P. D. Moore. 2005. *Biogeography: An Ecological and Evolutionary Approach*. 7th ed. Oxford: Blackwell Publishing.

Croll, J. 1864. "On the Physical Cause of the Change of Climate during Geological Epochs." *Philosophical Magazine* 28:121–37.

———. 1875. *Climate and Time in Their Geological Relations, A Theory of Secular Changes of the Earth's Climate*. New York: D. Appleton.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Dowler, R., D. S. Carroll, and C. W. Edwards. 2000. "Rediscovery of Rodents (Genus *Nesoryzomys*) Considered Extinct in the Galapagos Islands." *Oryx* 34:109–17.

Gillespie, R. G. 2009. "The Ecology and Evolution of Hawaiian Spider Communities." *American Scientist* 93:122–31.

Gillespie, R. G., and D. A. Clague, eds. 2009. *Encyclopedia of Islands*. Berkeley: University of California Press.

Gosliner, T. M. 2009. "Galapagos Islands: Biology." In Gillespie and Clague 2009, 357–67.

Hall, R. 1998. "The Plate Tectonics of Cenozoic SE Asia." In *Biogeography and Geological Evolution of SE Asia*, edited by R. Hall and J. D. Holloway, 99–132. Leiden, Neth.: Backhuys.

Hays, J. D., J. Imbrie, and N. J. Shackleton 1976. "Variations in the Earth's Orbit: Pacemaker of the Ice Ages." *Science* 194 (4270): 1121–32.

Heaney, L. R. 1986. "Biogeography of Mammals in SE Asia: Estimates of Rates of Colonization, Extinction, and Speciation." *Biological Journal of the Linnean Society* 28:127–65.

Heaney, L. R., E. A. Rickart, D. S. Balete, M. V. Duya, M. R. Duya, and S. Steppan. 2011. "Seven New Species and a New Subgenus of Forest Mice (Rodentia: Muridae: *Apomys*) from Luzon Island." *Fieldiana Life and Earth Sciences* 2:1–60.

Heaney, L. R., and T. E. Roberts. 2009. "New Perspectives on the Long-Term Biogeographic Dynamics and Conservation of Philippine Fruit Bats." In *Ecology, Evolution, and Conservation of Island Bats*, edited by T. H. Fleming and P. Racey, 17–58. Chicago: University of Chicago Press.

Humphries, C. J., and L. R. Parenti. 1999. *Cladistic Biogeography: Interpreting Patterns of Plant and Animal Distributions*. 2nd ed. Oxford: Oxford University Press.

Jansa, S. A., K. Barker, and L. R. Heaney. 2006. "The Pattern and Timing of Diversification of Philippine Endemic Rodents: Evidence from Mitochondrial and Nuclear Gene Sequences." *Systematic Biology* 55:73–88.

Jansa, S. A., and M. D. Carleton. 2003. “Systematics and Phylogenetics of Madagascar’s Native Rodents.” In *The Natural History of Madagascar*, edited by S. M. Goodman and J. P. Benstead, 1257–65. Chicago: University of Chicago Press.

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. *Biogeography*. 3rd ed. Sunderland, MA: Sinauer Press.

Losos, J. B., and R. E. Ricklefs, eds. 2010. *The Theory of Island Biogeography Revisited*. Princeton, NJ: Princeton University Press.

Lundberg, J. G., J. P. Sullivan, R. Rodiles-Hernández, and D. A. Hendrickson. 2007. “Discovery of African Roots for the Mesoamerican Chiapas Catfish, *Lacantunia enigmatica*, Requires an Ancient Intercontinental Passage.” *Proceedings of the Academy of Natural Sciences of Philadelphia* 156:39–53.

Lyell, C. 1872. *Principles of Geology, or the Modern Changes of the Earth and Its Inhabitants*. 11th ed. New York: Appleton,.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press,.

Matisoo-Smith, E., and J. H. Robins. 2004. “Origins and Dispersals of Pacific Peoples: Evidence from mtDNA Phylogenies of the Pacific Rat.” *Proceedings of the National Academy of Sciences* 101 (24): 9167–72.

Meijaard, E. 2003. “Mammals of South-East Asia and Their Late Pleistocene Environments.” *Journal of Biogeography* 30:1245–57.

Musser, G. G., and M. J. Carleton. 2005. “Superfamily Muroidea.” In *Mammal Species of the World: A Taxonomic and Geographic Reference*, edited by D. E. Wilson and D. M. Reeder, 894–1531. Baltimore, MD: Johns Hopkins University Press.

Nunn, P. D. 2009. “Oceanic Islands.” In Gillespie and Clague 2009, 689–92.

Piper, P. J., J. Ochoa, E. C. Robles, H. Lewis, and V. Paz. 2011. “Palaeozoology of Palawan Island, Philippines.” *Quaternary International* 233:142–58.

Raby, P. 2001. *Alfred Russel Wallace: A Life*. Princeton, NJ: Princeton University Press.

Ricklefs, R. E., and E. Birmingham. 2002. “The Concept of the Taxon Cycle in Biogeography.” *Global Ecology and Biogeography* 10:77–100.

Rosen, D. 1978. “Vicariant Patterns and Historical Explanations in Biogeography.” *Systematic Zoology* 27:159–88.

Sclater, P. L. 1858. “On the General Geographical Distribution of the Members of the Class Aves.” *Journal of the Linnean Society: Zoology* 2:130–45.

Sheldon, F. H., D. J. Lohman, H. C. Lim, F. Zou, S. M. Goodman, D. M. Prawiradilaga, K. Winker, T. M. Braile, and R. G. Moyle. 2009. “Phylogeography of the Magpie-Robin Species Complex (Aves: Turdidae: *Copsychus*) Reveals a Philippine Species, an Interesting Isolating Barrier and Unusual Dispersal Patterns in the Indian Ocean and Southeast Asia.” *Journal of Biogeography* 36:1070–83.

Shermer, M. 2002. *In Darwin’s Shadow: The Life and Science of Alfred Russel Wallace*. Oxford: Oxford University Press.

Sherrod, D. R. 2009. "Hawaiian Islands: Geology." In Gillespie and Clague 2009, 404–10.

Slotten, R. A. 2004. *The Heretic in Darwin's Court*. New York: Columbia University Press.

Wagner, W. L. and V. A. Funk. 1995. *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*. Washington: Smithsonian Institution Press.

Wallace, A. R. 1854 . "On the Monkeys of the Amazon." *Annals and Magazine of Natural History*, 2nd ser., 14 (84): 451–54.

———. 1855. "On the Law Which Has Regulated the Introduction of New Species." *Annals and Magazine of Natural History*, 2nd ser., 16 (93): 184–96.

———. 1876. *The Geographical Distribution of Animals*. 2 vols. London: Macmillan.

———. 1880. *Island Life: Or the Phenomena and Causes of Insular Faunas and Floras*. London: MacMillan.

Warren, B. H., E. Bermingham, R. P. Prys-Jones, and C. Thebaud. 2006. "Immigration, Species Radiation and Extinction in a Highly Diverse Songbird Lineage: White-Eyes on Indian Ocean Islands." *Molecular Ecology* 15:3769–86.

Wegener, A. 1912. "Die Entstehung der Kontinente." *Geol. Rundsch.* 3:276–92.

Whittaker, R. J., and J. M. Fernandez-Palacios. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford: Oxford University Press.

Wilson, E. O. 1961. "The Nature of the Taxon Cycle in the Melanesian Ant Fauna." *American Naturalist* 95:169–93.

Zink, R. M., J. Klicka, and B. R. Barber. 2004. "The Tempo of Avian Diversification during the Quaternary." *Philosophical Transactions of the Royal Society of London*, Series B-Biological Sciences, 359:215–19.

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BY

ALFRED RUSSEL WALLACE,

AUTHOR OF "THE MALAY ARCHIPELAGO," "TROPICAL NATURE," "THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS," &C.

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TO

SIR JOSEPH DALTON HOOKER,

K.C.S.I., C.B., F.R.S., &c., &c.,

WHO, MORE THAN ANY OTHER WRITER,

HAS ADVANCED OUR KNOWLEDGE OF THE GEOGRAPHICAL

DISTRIBUTION OF PLANTS, AND ESPECIALLY

OF INSULAR FLORAS,

I Dedicate this Volume,

ON A KINDRED SUBJECT,

AS A TOKEN OF ADMIRATION AND REGARD.