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THE RETICULATING PHYLOGENY OF ISLAND BIOGEOGRAPHY THEORY

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Abstract

Biogeographers study all patterns in the geographic variation of life, from the spatial variation in genetic and physiological characteristics of cells and individuals, to the diversity and dynamics of biological communities among continental biotas or across oceanic archipelagoes. The field of island biogeography, in particular, has provided some genuinely transformative insights for the biological sciences, especially ecology and evolutionary biology. Our purpose here is to review the historical development of island biogeography theory during the 20th century by identifying the common threads that run through four sets of contributions made during this period, including those by Eugene Gordon Munroe (1948, 1953), Edward O. Wilson (1959, 1961), Frank W. Preston (1962a,b), and the seminal collaborations between Wilson and Robert H. MacArthur (1963, 1967), which revolutionized the field and served as its paradigm for nearly four decades. This epistemological account not only reviews the intriguing history of island theory, but it also includes fundamental lessons for advancing science through transformative integrations. Indeed, as is likely the case with many disciplines, island theory advanced not as a simple accumulation of facts and an orderly succession of theories and paradigms, but rather in fits and starts through a reticulating phylogeny of ideas and alternating periods of specialization and reintegration. We conclude this review with a summary of the salient features of this scientific revolution in the context of Kuhn's structure, which strongly influenced theoretical advances during this period, and we then describe some of the fundamental assumptions and tenets of an emerging reintegration of island biogeography theory.

Keywords

biogeography; equilibrium theory; island biogeography; islands; scientific revolutions; taxon cycle

Throughout the past two centuries, from Johann Reinhold Forster's (1778) early descriptions of patterns in diversity among islands, through the seminal contributions of Darwin and Wallace in the 19th century, to those of David Lack, Edward O. Wilson, Robert MacArthur, and Peter and Rosemary Grant in the 20th century, island theory has been at the heart of revolutionary insights into the fields of ecology, evolution, and biogeography (see Losos and Ricklefs 2009).

Among the most influential theories in these fields was MacArthur and Wilson's equilibrium theory of island biogeography. The ultimate goal of their theory, which was first articulated in a paper published in *Evolution* in 1963, followed by a monograph published in 1967, was to develop a general theory of biogeography based upon the dynamics of its fundamental processes—immigration, extinction, evolution, and ecological interactions. This theory would explain a variety of insular phenomena ranging from patterns in richness to those in colonizing

abilities, niche shifts, and evolutionary divergence of isolated biotas. Despite the many and sometimes well-founded criticisms that have been levied over the years (e.g., see Sauer 1969; Lack 1970; Gilbert 1980; Haila 1986; Williamson 1989; Sismondo 2000; see also special feature of *Global Ecology and Biogeography*, Volume 9: Island Biogeography [Lomolino and Heaney 2000]), MacArthur and Wilson's equilibrium theory quickly achieved paradigmatic status, transforming the science of biogeography and its related disciplines, including ecology and conservation biology, and indeed spawning new sub-disciplines and research programs, such as metapopulation biology (Hanski and Gilpin 1997; Hanski 1999; Hanski and Gaggiotti 2004). Beyond its paradigmatic influence on these fields, the development of MacArthur and Wilson's theory serves as a compelling case study in how science advances, not just as a simple accumulation of facts and an orderly succession of theories and paradigms, but oftentimes in fits and starts through a reticulating phylogeny of ideas and alternating periods of specialization and reintegration.

Our purpose here is to review and reassess the historical development of island biogeography theory during the 20th century by identifying the common threads that run through four sets of contributions that illustrate some of the features described by Thomas Samuel Kuhn (1996) as the "structure of scientific revolutions." While developments in historical or evolutionary biogeography (sensu Morrone 2009) also transformed island theory during this period, our focus here is on ecological biogeography and what eventually came to be recognized as the paradigm of island biogeography theory. Featured contributions include Eugene Gordon Munroe's (1948, 1953) early development of an equilibrium theory of island biogeography, Edward O. Wilson's (1959, 1961) theory of taxon cycles and his important but largely overlooked concept of "a biogeography of the species," Frank W. Preston's (1962a, 1962b) papers on "The canonical relationship between island area and abundance and richness of insular biotas," and the seminal collaborations between E. O. Wilson and Robert H. MacArthur (1963, 1967). Our epistemological account is far more than just a review of the intriguing history of island theory, but one with fundamental lessons for advancing science through transformative integrations. We conclude this review with a summary of the salient features of this scientific revolution in the context of Kuhn's structure, which provided a framework for understanding theoretical advances during this period, and we then describe some of the fundamental assumptions and tenets of an emerging, integrative theory of island biogeography.

A RETICULATING PHYLOGENY: ANTECEDENTS OF THE EQUILIBRIUM THEORY

EUGENE GORDON MUNROE (1948, 1953)

Ironically, the first in the series of works that we discuss here is both the most extensive and the least appreciated. Eugene Gordon Munroe's 555 page dissertation completed his graduate program under W. T. M. Forbes at Cornell University in 1948. However, save for his dissertation, an abstract published in the *Proceedings of the Seventh Pacific Science Congress* in 1953, and a brief summary of his theory included in a paper presented at various symposia and published in 1963 (Munroe 1963: 304–305), his equilibrium theory had little if any discernible influence on island biogeography and the scientific revolution that would follow MacArthur and Wilson's contributions some two decades later. Yet we have chosen to feature Munroe's dissertation in our discussion of the development of island biogeography theory for three important reasons. First, as we have described elsewhere (Brown and Lomolino 1989), Munroe's insights were nothing short of remarkable and certainly deserve acknowledgment from the scientific community. Second, Munroe's comprehensive review characterizes the status of biogeography theory during a tumultuous stage in its history, when its practitioners were being challenged to integrate into its very broad domain the emerging revelations on the dynamics of the earth and its species. Finally, by identifying factors that all

too often impede scientific revolutions, our summary of Munroe's dissertation and his subsequent unsuccessful attempts to publish a new theory on the historical development of insular biotas serves as an exemplary case study of the challenges that fundamental advances in science often face.

A Passion for the Diversity and Geography of Nature—From his early childhood and throughout his professional career, Eugene Gordon Munroe was driven by an innate and irresistible passion for the natural world—particularly for butterflies and moths. He “collected” his first moth at the age of four and, before reaching his twenties, his field collections of Lepidoptera included those from an impressive array of locations, including New Jersey (USA), Trinidad, Ireland, Scotland, South Africa, East Africa, Guyana, and the West Indies (Solis 2003). He began his college studies at McGill University in 1936, receiving a Bachelor of Science degree with first class honors in 1940, and a Master of Science in Entomology *cum laude* in 1941. That same year, he started his dissertation studies in Systematic Entomology at Cornell University, later serving in the Royal Canadian Air Force from 1942 to 1945 (first as a radar mechanic and then as a medical associate/entomologist) before returning to Cornell in 1945 and completing his dissertation studies in 1948 (Solis 2003).

Throughout his early professional career, Munroe was an ardent student of the classic works in biogeography, including those by legendary naturalists Linnaeus, Buffon, Darwin, Wallace, Huxley, Mayr, and Darlington—visionary scientists who, as very young men, turned their passion for the natural world into what would become a life-long dedication to understanding its variation over space and time. Each of their collecting trips would not just add to lists of a given region's biological diversity, but would simultaneously provide both clues and challenges for understanding the geographic and evolutionary development of nature. As with most pioneering biogeographers and evolutionary biologists, Munroe was a student of science in the broadest sense. His studies as a young scientist included an eclectic selection of related disciplines—such as geology, geography, and meteorology; genetics, systematics, and evolutionary biology; and population biology and ecology—that were themselves experiencing scientific revolutions. In fact, Munroe's dissertation constitutes an early integration of the confluent streams of the emerging disciplines that would later go on to form the foundations of modern biogeographic theory—complementary lines of research on the geological dynamics of the earth and the ecological and evolutionary responses of its biotas.

Accordingly, Munroe's preparation as a young scientist included studying theories of vertical fluctuations in the earth's crust, hypothesized to be responsible for creating and later submerging transoceanic land-bridges and immigration routes. Munroe (1948:48–50) cited Schuchert (1932, 1935), Von Ihering (1931), and Willis (1932), among others, and discussed Wegener's (1912) theory of continental drift as well as the works of Matthew (1915), Simpson (1940, 1943), and other researchers who described how these geological changes influenced both climate and the evolution of regional biotas. Munroe characterized the tumultuous, if not crisis, state of earth science at that time as being largely “divided between the adherents of continental drift, and those who believe that the present oceanic basins are essentially permanent structures, which have not been modified except in *detail* since the beginning of the geological record” (1948:49, emphasis ours). He correctly rejected the extensionists' theories of transoceanic landbridges, while adeptly sidestepping debates over the validity of Wegener's theory, which he would leave up to those “more competent [to] judge of the relative merits” (Munroe 1948:49–50). These debates over the fixity of the continents and ocean basins would not be resolved, of course, for another two decades, ultimately from insights provided by marine geologists during the 1940s and 1950s (see summaries of the historical development of biogeography in Briggs 1987 and Lomolino et al. 2006).

Munroe's dissertation was written long before champions of the plate tectonics theory achieved the scientific revolution that finally embraced and greatly expanded on Wegener's model, which had first been proposed some five decades earlier. Thus, at the time of his dissertation studies, Munroe held fast to a belief in the fixity of the continents and ocean basins, at least at a global scale. However, he did believe that the earth was dynamic at much more local scales, hence the "detail" that Munroe alluded to in the above quote. Of paramount importance to his explanation of the historical development of the butterfly fauna of the West Indies was his concept of geological dynamics from the regional scale down to the archipelagic scale. According to Munroe, such detail included the vertical shifts of local landmasses and portions of the seafloor, which created alternating periods of emergence and submergence of regional landbridges, with concurrent periods of isolation and exchange among otherwise isolated biotas.

Munroe's incipient theory of historical biogeography was also strongly influenced by the concurrent revolutions in evolutionary biology. His views of the dynamics of species were strongly influenced by the works of Sir Ronald Fisher (1930), Julian Huxley (1938), Ernst Mayr (1942), and Sewall Wright, all prominently discussed in his dissertation (e.g., Munroe 1948:10–21). Perhaps most notably, Munroe singled out Theodosius Dobzhansky (1937) as the scientist most responsible for the new synthesis in evolutionary biology, which resulted "from the combination of the methods of genetics with those of the older discipline of taxonomy" (Munroe 1948:7). He described Dobzhansky's book, *Genetics and the Origin of Species* (1937), as "the most important work which has appeared in the field of biology in the last forty years" (Munroe 1948:7).

With his own interests centering on dynamic processes rather than simple descriptions of traits and static patterns, Munroe asserted that species should be "seen as a level in the evolutionary process, rather than as a static grouping of similar organisms" (1948:7). "With the rise of evolutionary theory, however, it became obvious that species were not fixed and immutable categories, as they had been classically considered" (Munroe 1948:6). Especially germane to Munroe's development of an equilibrium theory of island biogeography were the theoretical and mathematical models of early evolutionary biologists. Godfrey Hardy (1908), Wilhelm Weinberg (1908), and other pioneers of their field used such models to demonstrate how gene frequencies of species populations could remain relatively stable in the face of the recurrent turnover of individuals resulting from births, deaths, and dispersal. It is also noteworthy that Munroe (1948:22–27) held an analogous view of the geographic range, which, rather than constituting an invariant characteristic of each immutable species, should instead be viewed as a transient phase in a series of recurrent expansions and contractions of the areas occupied by mutable species. Thus, Munroe may also have been drawing on the earlier ideas of Willis (1915, 1922) that, although marred with some radical and erroneous notions on natural selection, extinction, and other fundamental processes, viewed geographic ranges across continents and oceanic archipelagoes as dynamic and as reflecting the relationship between time, geographic area, and local population density.

As a young scientist, Munroe's perspective was also strongly influenced by the works of the distinguished population biologists, theoretical ecologists, and biogeographers of his era. Included among his studies were the writings of Vito Volterra and Alfred J. Lotka, whose mathematical models described the dynamics and ecological interactions among local populations and how they could maintain relatively stable numbers, under certain conditions, in the face of varying birth and death rates (Munroe 1948:24). Munroe's views were also strongly influenced by more general works in both ecological and historical biogeography, including such early classics as those by Cain (1944), Campbell (1926), Gleason and Cook (1927), Good (1931), Matthew (1915, 1919, 1930), Simpson (1929), and Wulff (1943). His maturation as a biogeographer was perhaps most strongly and directly influenced by his

readings of and interactions with Philip Darlington, Jr., whom he cited in various sections of his dissertation, as well as thanking him in his acknowledgments (Munroe 1948:5) for his advice and assistance. One can only speculate as to whether discussions with the young Munroe during the 1940s had some influence on Darlington's thinking and the significant works that he would later publish in the years to come—*Zoogeography: The Geographical Distribution of Animals* (1957), *Area, Climate and Evolution* (1959), and *Biogeography of the Southern End of the World* (1965).

Biogeography of the 1940s—Just as the development of Wallace and Darwin's theory of natural selection was strongly influenced by their readings of Lyell, Malthus, von Humboldt, and other visionary scientists of that revolutionary era, Eugene Gordon Munroe's preparation and research as a young scientist would strongly influence his own vision and scientific imagination. Thus, upon returning from a collecting trip to tropical America, rather than just annotating his life list, Munroe committed himself to developing a new theory of historical biogeography using Caribbean butterflies as an exemplary case study. However, his concept of "historical biogeography" was very broad indeed. While he did acknowledge a distinction between ecological biogeography, which "[deals] with the ecological reasons for animal distributions," and historical biogeography, "which seeks to explain present distributions in the terms of both present and past geographic and climatic conditions", he was quick to point out that, as many modern biogeographers have come to realize, "they necessarily go to some extent hand in hand" (Munroe 1948:30). In essence, the development of biotas over space and time incorporates the entire history of interactions among species, as well as between species and their environment, and the phenotypic and genetic responses that accumulate over periods ranging from ecological to geological timescales. Interestingly, Munroe's characterization of the state of historical biogeography during the 1940s may, to some degree, be an unfortunately accurate description of the tenor of the field up to quite recently: "The rashness and dogmatism of many workers are responsible for the confusion and disrepute in which the subject of historical zoogeography lies at the present time" (Munroe 1948:30).

Munroe's observation on the confusing and contentious state of biogeography during the 1940s is far more than just an interesting aside in our account of the historical development of his theory. It is clear evidence that he and at least some of his colleagues realized that biogeography had reached what Kuhn (1996) would later refer to as a "crisis" state. The "normal science" (also Kuhn's term) of historical biogeography and its related fields had progressed to the point that a burgeoning morass of anomalies and novelties could no longer be accounted for by the reigning paradigm, which was, in this case, one that desperately clung to assumptions about the static nature of biotas in evolutionary and ecological time, ranging from regional down to more local (i.e., from archipelago to island) spatial scales as well. Rather than signaling impending dark ages, crises in science are the portent of major advances—of scientific revolutions during which the vision and imagination of a discipline are fundamentally transformed, much like punctuated evolution following a period of evolutionary stasis. The 1940s and 1950s were indeed very propitious times to be a biogeographer, especially given the revolutionary developments in fields that would prove integral to future advances in biogeography.

Similarly and nearly simultaneously with the completion of Munroe's dissertation, Dammerman (1948) published his classic book on the faunal dynamics of the Krakatau Islands, including comparisons of their developing biotas to those of two continental islands (Durian and Berhala) and two oceanic islands (Christmas and Cocos-Keeling) in the same region. Although Dammerman actually used the term "equilibrium," his extensive and meticulous account of the fauna of these islands was purely and exhaustively descriptive, apparently lacking any attempt at a conceptual synthesis. Thus, Dammerman's research, albeit empirically rich with few rivals, was not a precursor to or conceptually convergent with the theory

developed by Munroe and, later, by MacArthur and Wilson (see Lomolino et al. 2009; see also Thornton 1992).

Interestingly, publications and insights from the faunal dynamics of Krakatau had no obvious impact on Munroe's development of his equilibrium theory (Munroe 1948, 1953; E. G. Munroe, personal communication to MVL, 2007), which may be somewhat understandable given that Dammerman's monograph was not yet published and that Munroe's field research focused on another part of the globe (i.e., the Caribbean versus Indonesia and the Pacific). In contrast, the studies of Docters van Leeuwen (1936), Dammerman (1948), and others studying colonization following the 1883 eruption and defaunation of Krakatau strongly influenced future syntheses and reintegrations on the subject, including those by E. O. Wilson and, eventually, Robert H. MacArthur as well.

Munroe's Dissertation—Munroe's choice of a focal system and fauna was not simply by default or by chance. On the contrary, determined to make a major contribution to the historical biogeography of butterflies, he realized that “the Antilles form a particularly favorable field for zoogeographic study, consisting as they do of an old and fragmented land mass ... forming well-defined paths of entry by which immigrants may reach the fauna” (Munroe 1948:1). Munroe also noted that butterflies possess traits that make them ideal subjects for such studies, given that they are “taxonomically, geographically and paleontologically well known, and [their] dispersal is seriously hindered by barriers of a known type” (Munroe 1948:64–65). His approach for developing his theory of historical biogeography was to compare reconstructions of the geological and climatic history of the West Indies to the biogeographic dynamics (immigration, speciation, range contraction, and extinction) of extant species and higher taxa or “superspecies” of butterflies. Thus, Munroe deliberately set out to develop a comprehensive theory of faunal development based upon differences among species in terms of their distributions, ecological interactions, and histories of immigration and evolution—a theory that would ideally explain a variety of patterns including geographic variation in species composition, richness, and endemism.

Munroe's dissertation was comprised of three parts. The first part presented an extensive review of relevant literature in evolutionary biology, ecology, and biogeography, along with some original thoughts on the basic principles of biogeography (Munroe 1948:6–24). His discussion of the theory of area is especially relevant to our understanding of subsequent advances in historical and ecological biogeography. Munroe described geographic ranges (“areas”) and how they vary in response to three types of factors: 1) “[the] distribution of the conditions necessary for life,” 2) “the distribution of competing or inimical species,” and 3) “the accessibility of suitable habitats from the region in which the species originated” (1948:22). In Munroe's view, the geographic range was not a fixed characteristic of each static species, but rather a transient stage in a dynamic process of change. These dynamic ranges were the result of interactions among species and among processes that could result in their growth or decay. Increase of population numbers or the breakdown of barriers would result in range growth, whereas the expansion of areas occupied by enemies or competitors, or the deterioration of climatic conditions, would bring about range decay (Munroe 1948:27). This view of the dynamic nature of ranges and the underlying factors and processes responsible for expansions, contractions, and extinctions would prove foundational to Munroe's early and independent development of an equilibrium theory of island biogeography.

Part II of Munroe's dissertation explored his theory of the historical development of Caribbean butterflies. Although not the most voluminous portion of his dissertation, it was still substantial by any standards, spanning some 189 pages and presenting in both impressive breadth of concepts and depth of detail a creative and comprehensive explanation for the historical development of this fauna. In keeping with his assertion that approaches in historical and

ecological biogeography go hand in hand, Munroe (1948:30) created a theory of the historical development of Caribbean butterflies that explicitly emphasized immigration, evolution, and ecological interactions among species and that also explained patterns in species richness along geographic gradients (i.e., those of elevation, area, and isolation)—processes and patterns often considered by more narrow views to be within the domain of ecological biogeography.

In the opening sections of Part II of his dissertation (Munroe 1948:35–63), Munroe presented a detailed description of the then current geography of the West Indies, as well as the geological and climatic history of the region, including the dynamics of mainland landmasses, archipelagoes, and ocean basins throughout the Mesozoic and Cenozoic Eras. His view of the geological dynamics of this region was premised on the assumption that the earth's crust was frequently subject to uplift and submergence, but not to the horizontal displacements that formed the basis of Wegener's theory, which would not be fully embraced by most of the scientific community for another two decades. Munroe's detailed description and map illustrating the current geography of the region included identification of principal immigration routes, along with a discussion of how migrations of butterflies were affected by vertical shifts in land and seafloor, local and regional climate, and characteristics of the species (1948:35–47).

Citing Darlington's (1938) earlier work on the subject, Munroe (1948) asserted that hurricanes played a particularly important role in the dispersal of organisms. He also cogently observed that barriers are taxon- and species-specific; that is, they are dependent on the habitat affinities of the species relative to characteristics of the potential barriers, whether they be landscapes or seascapes. For example, after comparing endemism among forest- and open-country butterflies, Munroe inferred that the higher endemism of forest-dwelling species "is what we should expect, for forest species are obviously less likely to cross unshaded water barriers than are those accustomed to open spaces" (1948:102). This phenomenon is what Lack (1937) and later Diamond (1975) would describe as psychological barriers to dispersal (see also Grinnell's [1914] discussion of the related phenomenon of "associational barriers"). Munroe appears to have believed that this phenomenon was not only associated with endemism, but that it was also a consequence of the formation of insular endemics. In his analysis of vertical distributions of Caribbean butterflies on particular islands, Munroe observed that "there is a tendency for the proportion of endemics to increase in the higher altitude ranges ... [and that] withdrawal of species range from coastal areas may be the controlling factor responsible for the increased endemism of the strictly upper-level fauna" (1948:110–111). His vision of insular species adapting and forming endemics restricted to higher elevational habitats, and, thus, limiting their opportunities for subsequent dispersal across the lowlands, seems anticipatory of the latter stages of Wilson's taxon cycle for insular ant faunas, as described in his seminal papers of 1959 and 1961 and that we will discuss here later.

Let us return for the moment to Munroe's analyses of elevational clines in butterfly communities. In addition to describing trends in endemism, Munroe noted that "the vertical distribution of the fauna shows considerable regularity" and that "[there appears] to be, then, levels of sharp faunal change, limiting reasonably definite faunal zones [that] ... corresponds remarkably well with the zonation of the flora" (1948: 103). He also observed that species richness of butterflies (endemics and "apodemism," or endemics from other islands, combined), "is richest in the tropical lowlands and becomes impoverished with increasing altitude" (1948:110). Using a chart to illustrate the upper and lower elevational limits of butterflies, Munroe depicted a pattern suggestive of a mid-elevational peak in richness of West Indies butterflies. However, it appears as if Munroe did not take notice of this variant of elevational gradients—i.e., mid-elevational peaks (versus monotonic trends) in diversity, which more recent studies reveal may be the general pattern (see Lomolino et al. 2006:634–638; McCain 2009; Rowe and Lidgard 2009).

MUNROE'S EQUILIBRIUM THEORY

Clearly, the most important sections of Munroe's dissertation, in terms of their relevance to island biogeography theory, are those in which he developed a theoretical explanation for the "quite large differences in the numbers of species supported by the various islands" (Munroe 1948:115). As we remarked in our earlier paper, "The independent discovery of the equilibrium theory of island biogeography," Munroe should be acknowledged for much more than just some vague notion of species equilibrium (Brown and Lomolino 1989). Rather, he presented the empirical species-area relationship that stimulated his inductive discovery, while also investigating the generality of this pattern and developing the verbal and mathematical models to explain it (Munroe 1953). Munroe's concept of species equilibrium was equivalent in almost all important respects to that of Robert H. MacArthur and E. O. Wilson, which would follow it some 15 years later. Below we include some representative excerpts from Munroe's dissertation, but we refer the reader to our earlier paper (Lomolino and Brown 1989) for a more extended description of Munroe's independent development of an equilibrium theory of island biogeography (see also excerpts from his dissertation available at the International Biogeography Society web site, <http://www.biogeography.org/html/Resources/index.html>).

A correlation of this kind [number of species and logarithm of area of island] is as interesting as it is unexpected, for it suggests the existence of an equilibrium value for the number of species in a given island, a value which acts as a limit to the size of the fauna. The processes which determine the equilibrium value for an island of given size must be, on the one hand, the extinction of species, and, on the other hand, the formation of new species within the island, and the immigration of new species from outside it. (Munroe 1948:117)

We can, then, think of an equilibrium value for the number of species in a given island fauna, depending on the one hand on the probability of extinction, correlated inversely with island size, and on the other hand on the probability of reinforcement, correlated directly with proximity to an area of richer fauna. Any tendency to differentiation of new species within islands would work in the same direction as reinforcement, i.e., against extinction. It is probable that this tendency is directly correlated with island size, among other factors. (Munroe 1948:118–119)

Later, in papers presented at various symposia and eventually published in *The Canadian Naturalist* in 1963, Munroe summarized his equilibrium theory in narrative form.

How do these differences in biotas arise, and what regulates such similarities as persist? They result from a balance of several processes. In the first place, populations evolve. ... Species not only change, they evolve into groups of species, which diverge and ramify increasingly. ...

A second mechanism is provided by the dropping out of species through extinction, either general or local. Differential extinction acting on initially identical biotas can produce totally different though less varied derivative biotas. ...

A third factor influencing the differentiation of biotas is immigration. This may act as a leveling factor where it represents penetration or circumvention of a barrier. On the other hand differential immigration from different sources may act as an added differentiating factor.

Immigration, like evolution, is a constructive factor, tending to increase the variety of the biota. These two factors are balanced against extinction, which tends to simplify the biota. On the balance that is struck depends not only the nature but also the number of species in the biota. Where evolution and immigration is favoured, the biota will be rich; where more rigorous conditions give the advantage to extinction, the biota

will be poor. On the whole, large, varied and hospitable environments tend to have larger and more progressive biotas than small, uniform or austere ones. (Munroe 1963:304–305)

Thus, Munroe presented a theory that asserted that insular species richness resulted from a balance among the three fundamental processes of biogeography: evolution, immigration, and extinction. This, essentially, represented the narrative form of his mathematical model of species equilibrium, which he presented in a 1953 abstract published in *Proceedings of the Seventh Pacific Science Congress of the Pacific Science Association* (Munroe [personal communication] noted the irony that he submitted two full manuscripts to be published from these proceedings, but only his other paper—on systematics of Caribbean butterflies—was published in full). As is also clear from Munroe's 1963 summary (excerpted above), he viewed the fundamental biogeographic processes as selective and deterministic rather than as stochastic, varying in a predictable manner among islands, among regions, and among species, thus contributing to non-random divergence among insular biotas.

EDWARD O. WILSON (1959, 1961)— TAXON CYCLES AND A “ BIOGEOGRAPHY OF THE SPECIES”

Despite his genuine prescience in developing key elements of a comprehensive and insightful theory of historical and ecological biogeography, Munroe's independent articulation of an equilibrium theory constituted an ancillary, albeit fascinating, branch in the reticulating phylogeny of island biogeography theory. Unsuccessful in his attempts to publish his theory, Munroe turned to his other passions and callings, becoming a distinguished curator and world expert on the systematics and ecology of moths and butterflies.

In great contrast, the next set of contributions we feature here impacted the field in a truly fundamental and transformative manner, perhaps even more so than generally appreciated. In fact, both of Edward O. Wilson's papers on taxon cycles played essential and precursory roles in the scientific revolution that was to culminate in his collaborations with Robert H. MacArthur and their equilibrium theory of island biogeography. Perhaps even more relevant to today's scientists, some four decades after Wilson developed his theory on taxon cycles, his call for what he described as “a biogeography of the species” may well be serving as a template for an incipient scientific revolution in island biogeography (Wilson 1959:122).

Early Experiences as a Naturalist—Like Munroe and the long and distinguished line of biogeographers and evolutionary biologists before him, E. O. Wilson's development as a scientist was driven by an irresistible passion for the natural world, particularly insects. “At twelve years of age, I had arrived with a burning desire to collect and study butterflies. ... I greeted the sights of each new species of butterfly with joy, and when I caught my first specimen I thought myself a big-game hunter with the net” (Wilson 1994:67–68). Most of us, of course, are more familiar with Wilson's fascination with ants, which again began at a very young age. In fact, in 1942, when he was just 13 years old, Wilson's “amateur” collecting yielded the earliest report of a colony of imported fire ants (*Solenopsis invicta*) in the United States.

The similarities in the professional development of Munroe and Wilson also included the perhaps not surprising fact that they both chose to begin their formal careers as naturalists and scientific collectors in the New World tropics. In Wilson's case, this was by virtue of a graduate student fellowship from Harvard University that supported his travels and collections across Cuba and Mexico in 1953, at the age of 23. Also, like Munroe and many other ambitious naturalists of that time, Wilson sought out the advice of the world's leading naturalists and biogeographers. One of his most influential mentors was Philip Darlington—by then a renowned entomologist and zoogeographer and, to Wilson's great fortune, a colleague at Harvard University. Darlington provided valuable counsel to this promising graduate student

who was then preparing for his first collecting trip to the tropics. “Ed, don’t stay on the trails when you collect insects. Most people take it too easy when they go in the field. They follow the trails and work a short distance into the woods. You’ll get only some of the species that way. You should walk in a straight line through the forest. Try to go over any barrier you meet. It’s hard, but that’s the best way to collect” (Wilson 1994: 28–29). During March of the following year, Darlington called Wilson to his office to offer him an opportunity of a lifetime—the chance to explore and collect ants in New Guinea. As Wilson later reflected in his autobiography, “I could work hands on in the very arena where a hundred years before young Alfred Wallace had begun to turn zoogeography, the study of animal distributions, into a scientific discipline. Who knows how the experience might transform my own thinking as a zoogeographer” (1994:164).

An Epiphany: A Biogeography of the Species and Taxon Cycles—Wilson’s travels and scientific studies of ant faunas across New Guinea and Melanesia did indeed fundamentally transform his scientific career from that of a traditional systematist and collector to that of a singularly insightful and eloquent biogeographer, evolutionary biologist, and conservator of nature’s diversity. Most relevant to our discussion here are two of Wilson’s papers that, as we remarked earlier, were precursory to MacArthur and Wilson’s equilibrium theory and perhaps to the ongoing scientific revolution in island biogeography as well. The first of these seminal papers was entitled “Adaptive shift and dispersal in a tropical ant fauna,” and was published in the journal *Evolution* in 1959. Wilson described this paper as presenting a theory and analysis “in very preliminary form” (Wilson 1959:122), while the second paper, “The nature of the taxon cycle in the Melanesian ant fauna,” published in *The American Naturalist* in 1961, succeeded in expanding this into a more comprehensive and integrative theory of the historical and ecological development of insular biotas. Careful examination of each of these papers, however, suggests that Wilson’s humility in characterizing the first paper was unjustified. Indeed, his 1959 paper clearly articulates what we believe to be the central thesis of Wilson’s theory.

There is a need for a ‘biogeography of the species,’ oriented with respect to the broad background of biogeographic theory but drawn at the species level and correlated with studies on ecology, speciation, and genetics. (Wilson 1959:122).

Wilson’s view of the “normal science” (*sensu* Kuhn 1996) of the times was that being advanced by William Diller Matthew, George Gaylord Simpson, and Philip J. Darlington. They postulated that the earth, its land and sea, its climate and its species, were dynamic, expanding from centers of origin and diversity, dispersing across new regions, and then adapting, evolving, and, in most cases, suffering eventual extinction. One key feature of this 20th-century articulation of the Center of Origin-Dispersal-Adaptation (CODA) tradition (developed largely by Darwin and Wallace) was the phenomenon of dominance among species and biotas. Matthew, in his 1915 monograph *Climate and Evolution*, and Darlington, in a 1948 paper “The geographical distribution of cold-blooded vertebrates,” hypothesized that species arising from and dispersing out of centers of origin would then dominate and replace groups occupying peripheral regions. Wilson was “enchanted by the idea of dominant animals and succession of dynasties” (1994: 212), and so he set out to determine the biological nature of biogeographic dominance. In doing so, he would extend the normal science of the CODA tradition from the global and geological scales down to more local scales, such as those of archipelagoes and islands. He recounts this scientific epiphany in his autobiography.

It dawned on me that the whole cycle of evolution, from expansion and invasion to evolution into endemic status and finally into either retreat or renewed expansion, was a microcosm of the worldwide cycle envisioned by Matthew and Darlington. To find the same biogeographic pattern in miniature was a surprise then ... It came within a few minutes one January morning in 1959 as I sat in my first-floor office ... sorting

my newly sketched maps into different possible sequences—early evolution to late evolution. ... Discovery of the cycle of advance and retreat was followed immediately by recognition of another ecological cycle. ... I knew I had a candidate for a new principle of biogeography. (1994:214–215)

And biogeography of the late 1950s was ripe for such revolutionary ideas, experiencing nothing short of a scientific crisis (*sensu* Kuhn 1996) that a growing number of its practitioners, especially the youngest ones including Wilson, were decrying.

The traditional discipline in which I had been steeped throughout my career, was in chaos, Grand chaos, in fact, since the subject matter is the largest in physical scale of all biology, and it spans the entire history of life. ... [B]iogeography was still largely descriptive. Its most interesting theory was the Matthew-Darlington cycle of dominance and replacement. ... Biogeography seemed ripe for the new thinking that was emerging in population biology. (Wilson 1994:244)

Again, in Kuhn's (1996) terms, the normal science of this period had advanced to its conceptual limits, accumulating a burgeoning morass of exceptions and problems, and failing to integrate observed patterns along with relevant phenomena from other disciplines. However, emerging advances in those disciplines, especially in ecology, evolutionary biology, and population biology, now made such a synthesis attainable, at least for those both gifted enough to assimilate these insights and bold enough to acknowledge the crisis and advance a new solution. As Wilson characterized the status of the discipline at the time he formulated his theory, "The nature of general adaptation and the dispersal mechanisms underlying major biotic movement is clearly one of the great problems of modern evolutionary theory. It appears that our knowledge has now reached the stage where finer analyses of these causal processes can and should be undertaken" (1959:122). This is when he sounded his call for "a biogeography of the species."

Wilson's theory was indeed unrivaled in its ability to integrate across fields and to provide a compelling and elegant explanation for a diverse albeit, as he would demonstrate, causally related set of biogeographic patterns and phenomena. Wilson did not use the terms "taxon cycle" or "speciation cycle" until his second paper on the subject (Wilson 1961), but, in his summary of the first paper, he described "[a] cyclical pattern of expansion, diversification, and contraction [that] is hypothesized to account for later evolutionary events following initial dispersal" (Wilson 1959:143). From intuition and inspection of his many maps of ant species distribution in a snapshot of time, Wilson was able to infer dynamic processes of biogeographic expansion, diversification, adaptation, development of insular endemics, and their ultimate extinction over evolutionary time, all driven by processes occurring in ecological time—namely, the dispersal of individuals and interactions between individuals within and among species. Wilson surmised that most groups of the focal taxon (ponerine ants) invaded New Guinea from southeastern Asia, with New Guinea then serving as a source for subsequent colonization of Melanesia (1959:123).

Wilson envisioned colonization across these archipelagoes to follow "the classical filter effect" (1959:123) and, thus, to take on the form of the "immigrant pattern" that Darlington described earlier in his book, *Zoogeography: The Geographical Distribution of Animals* (Darlington 1957:485) (Figure 1). This very regular pattern in the attenuation of species composition across islands and archipelagoes is indeed equivalent to what contemporary scientists now refer to as community "nestedness," and, in the case of Wilson and Darlington's phenomenon, it is a pattern driven by differences in immigration abilities among focal species.

Wilson went on to describe the subsequent sequence of evolutionary and ecological changes as occurring in three stages. Stage I species were those that had relatively continuous geographic ranges across an archipelago or region and that showed little geographic variation

in their traits. Their insular populations were derived from species that had become adapted to habitats along the beachfronts of the source region, thus predisposing them to dispersal and pre-adapting them to colonization of islands fringed with similar habitats. Many if not most of these colonizing populations were then caught in an “evolutionary trap,” as beachfront habitats are not just marginal but also ephemeral, subject to succession, chronic deterioration, or wholesale destruction from storms and other catastrophic events (Wilson 1959:141, acknowledging earlier formulations of the concept of evolutionary traps by Mayr [1942, 1954] and Darlington [1957]).

Some of these colonizing populations, however, might escape the beachfront habitats by adapting and invading the interior rainforest habitats of Melanesia, thus becoming isolated from the colonists and ancestral populations, and setting the stage for evolutionary divergence of populations across archipelagoes. If evolutionary divergence continues to the extent that descendant populations form distinct species, they have then entered Stage II of Wilson’s cycle. Stage II species are those that are endemic to different islands, belong to species groups centered outside of Melanesia, and are restricted to interior habitats within the islands. These insular endemics have experienced character displacement and niche shifts, thereby becoming increasingly more specialized to interior habitats.

If divergence and specialization progress to this stage, the insular endemics are predisposed to extinctions within and across the archipelago. These species have now advanced to the final phase—Stage III—of Wilson’s initial version of the taxon cycle, where geographic ranges of a set of once broadly distributed insular endemics contract, forming relictual species restricted to just one or two islands. Wilson then postulated that the “next and final step for most is extinction [across the entire archipelago], or extreme specialization, perhaps hastened by the inroads of freshly competing Stage-I and Stage-II species” (1959:129). Here then, in very clear yet singularly insightful terms, Wilson described the driving force for this interrelated suite of evolutionary and ecological phenomena: interspecific interactions. Following differential colonization of the beachfront and its marginal and ephemeral habitats, interspecific interactions drive the shifts in behavior, habitat, and geographic distributions within islands, as well as the divergence and extinction of populations and endemic species among them. This also explains why Wilson envisioned this as a cyclical sequence of phenomena: faunal buildup within habitats and across islands is limited because niches have to be vacated (i.e., by emigrations, extirpations, and extinctions) before new colonists can successfully invade the island and its interior habitats.

In his second paper on the subject, Wilson further elaborated and presented a more comprehensive synthesis of his developing theory. While he did not use the term “equilibrium” in either of these papers, in his 1961 paper—“The nature of the taxon cycle in the Melanesian ant fauna”—he did present his conceptualization of species replacement and the balance of nature under what he termed “saturation.” “[I]ndividual insular faunas approach upper limits set by the size of the islands. In other words, they are in a saturated or near saturated condition. It can be inferred that, as a rule, new species can invade an island only if resident species are extinguished to make room for them” (Wilson 1961:172) (Figure 2). Thus, Wilson’s concept of saturation was more similar to Lack’s idea of filling ecological space on islands than to Munroe’s (and later, MacArthur and Wilson’s) concept of faunal equilibrium, which has no upper limit but instead represents a dynamic balance among rates of immigration, extinction, and speciation. It is likely, however, that these earlier concepts of the relatively static ecological saturation of insular biotas were precursory to the eventual development of the dynamic equilibrium that was fundamental to MacArthur and Wilson’s theory of island biogeography.

Unlike MacArthur and Wilson’s theory, however, Wilson’s (1961) updated model retained its emphasis on differences among and interactions between species, and it also added a number

of important developments and innovations to island theory. Here, Wilson further developed the geographic context of taxon cycles by describing how the saturation number of species should vary with island area and isolation. He attributed the species-area relationship, at least in part, to an inverse relationship between island area and extinctions. “Taxa disappear first from the smaller islands and then, apparently progressively, from larger islands” (Wilson 1961:188). His mathematical modeling of the species-area relationship was limited and relatively simple (see Wilson 1961:170), but was based on the same formula that Preston (1962) and MacArthur and Wilson (1963) would later use as the mathematical centerpiece in their much more extensive models of this relationship (i.e., the Arrhenius [1921] power, or log-log model). Wilson (1961) did observe that the exponent of the power model varied among animal groups and faunal regions, and he suggested that residual variation (“scatter in the area-fauna measurements”) results from inter-island differences in habitat related either to anthropogenic disturbance, or simply due to varying completeness in sampling insular faunas (Wilson 1961:170). This, however, was the extent of the mathematical exercises put forth in Wilson’s original theory, and neither here nor in the graph illustrating variation in saturation levels among islands (Figure 2) did he offer a mathematical formula for balance or equilibrium among the recurrent processes he so richly described throughout his two papers on the taxon cycle.

Interspecific interactions and resulting character displacement and ecological release, in both occupied habitats and population densities within those habitats (themes developed by Wilson and William L. Brown in their earlier collaboration on character displacement [Brown and Wilson 1956]), remained the integrating, driving force in Wilson’s model. “The Stage-I species evidently serve an important additional role in displacing, fragmenting, and directing the evolution of older resident species” (Wilson 1961: 189). Like Munroe before him, but, in this case, in a more comprehensive and elegant manner, Wilson developed a theory of faunal development that was both historical and ecological, blurring the unfortunate wedge that is often thrust between what are better viewed as complementary approaches in biogeography. Based on his inspection of maps of species distributions, Wilson inferred that interspecific interactions strongly altered species distributions among islands where “related species tend to exclude one another in an unpredictable manner, forming mosaic patterns” (1961:172). Thus, he anticipated what Diamond (1975) would later term “checkerboard distributions” in his classic paper on assembly rules. Moreover, although Wilson’s conceptualization was deterministic to its very core, his discussion of faunal mosaics introduced a significant stochastic element to the stages and dynamics of the taxon cycle—a phenomenon he termed “faunal drift.” “This expression is used simply to infer that the composition of small local faunas varies in an unpredictable manner, that is, there is a subjective element of randomness. It remains to be seen to what extent faunal drift is really the result of chance phenomena such as accidents of colonization” (Wilson 1961:172). The similarities between Wilson’s faunal drift and the phenomenon of ecological drift—one of the premises of Hubbell’s (2001, 2006; Hu et al. 2006) intriguing neutral theory of biodiversity and biogeography—may be more than semantic.

Other elements that Wilson added to his second conceptualization of the taxon cycle included his prediction that the cycles should vary, albeit in a predictable manner, among functionally different taxa. “Indeed, the entire form of the taxon cycle may be altered in groups with markedly different ecology and population structure. It is one of the tasks of comparative zoogeography to determine the extent of this variation in histories” (Wilson 1961: 190). Wilson also postulated that the taxon cycle “maintains its headquarters in a given land mass indefinitely, expanding and contracting cyclically, or else it declines to extinction,” and that “the headquarters can be shifted from a larger to a smaller land mass (for example, from New Guinea to Fiji) but not in the reverse direction” (1961:191). That is, insular endemics should never colonize in the reverse direction and initiate taxon cycles on the mainland. Only recently have biogeographers been supplied with the tools (from molecular biology, genetics, and

phylogeographic analyses) necessary to reevaluate this assertion, providing a limited but intriguing set of cases that suggest taxon cycles may be reversed (for recently reported cases of this phenomenon, see Dávalos 2007; Heaney 2007; Bellemain and Ricklefs 2008).

Finally, a careful reading of Wilson's second paper reveals that a fundamental catalyst for the scientific revolution away from the traditional, static theory of island biogeography, which assumed unique, one-time immigration and extinction events and was framed within the CODA tradition, was the now well-documented faunal dynamics that followed the cataclysmic explosions of Krakatau in 1883 (Docters van Leeuwen 1936; Dammerman 1948; see more recent syntheses and summaries by Thornton 1996; Whittaker and Fernandez-Palacios 2007). Wilson (1961) recounted the rapid colonization of Krakatau, which, by 1933, was colonized by six widespread species of native ponerine ants. "Together they make a fauna approximately the same size as those found on islands of comparable area in the Moluccas and Melanesia. Similar rapid colonization to near-saturation level occurred on the 'empty' islands of Verlaten and Sebesi, near Krakatau" (Wilson 1961:184). These lessons of Krakatau and the dynamics and resiliency of nature—insular communities that accumulated their faunas through rapid and recurrent colonization to achieve saturation, with extinctions eventually balancing immigrations—would form the central premise of the taxon cycle and, eventually, the equilibrium theory of island biogeography as well.

In summary, Wilson developed a compelling candidate for a new paradigm of island biogeography—a comprehensive yet elegantly simple theoretical construct that could guide a scientific revolution beyond the prevailing static theory, and one that remained primarily descriptive and premised on idiosyncratic explanations for the development of each distinct biota. Wilson's theory, while remaining species-based, demonstrated how ecological and historical processes were dynamic, recurrent, and interrelated, thus resulting in a predictable set of patterns and a sequence of changes in distributions, demography, behavior, morphology, niches, endemism, and extinction of insular biotas.

The promise of this conceptual framework was undeniable, but, given its comprehensive, integrative, and multi-scale nature, the challenges of fleshing out each of the principal components of Wilson's theory must have seemed daunting. Rigorous evaluation and further development of his theory would indeed require some four decades of subsequent contributions from a broad spectrum of natural sciences, including molecular biology, genetics, evolutionary biology, geology, population biology, and theoretical ecology (for recent contributions relevant to taxon cycle theory, see Bellemain and Ricklefs 2008; Gillespie and Baldwin 2009; Ricklefs 2009).

When Wilson was developing his theory, theoretical ecology was, in fact, experiencing its own revolutionary advances, largely through the efforts and analytical prowess of mathematical biologists such as Vito Volterra, Alfred J. Lotka, and G. Evelyn Hutchinson. These and other visionary scientists realized that, although controlled experiments can be invaluable tools for evaluating hypotheses and advancing theories in many disciplines, the complexity and scale of natural sciences such as biogeography typically render manipulative experiments unrealistic, infeasible, or unethical. If, however, the salient patterns and underlying processes could be translated into mathematical models, then the theory's underlying assumptions, deductions, and predictions could be subjected to rigorous logical evaluation. Just as Godfrey H. Hardy, Wilhelm Weinberg, Sewall Wright, Sir Ronald Fisher, and their colleagues advanced the New Synthesis in genetics and evolution decades earlier, theoretical ecologists and population biologists were now using mathematical models to fuel revolutionary advances in these disciplines. Of course, none of this was lost on Edward O. Wilson, who possessed a rare combination of intuitive powers and scientific humility. At the age of 32, he realized that "the future principles of evolutionary biology would be written in equations, with the deepest

insights expressed by quantitative models. I set out to remedy my deficiency by teaching myself calculus, probability theory, and statistics from textbooks I read on verandas and beach cupolas in Trinidad and Tobago” (Wilson 1994:242).

The next set of contributions that we feature here, those by Frank Preston on the “canonical” nature of the species-area relationship (Preston 1962a,b), epitomize this emerging sophistication in the requisite tools of ecologists and biogeographers during the 1960s. These contributions also form the penultimate link between Wilson’s conceptualization of the taxon cycle and his quintessential collaboration with one of Hutchinson’s most distinguished students, as well as one of the most influential theoretical and mathematical ecologists of the 20th century—Robert Helmer MacArthur.

FRANK W. PRESTON (1962A,B)— THE CANONICAL RELATIONSHIP BETWEEN AREA, ABUNDANCE, AND RICHNESS

Like Wilson and Munroe, Frank W. Preston possessed a passion for the natural world that he pursued from early childhood and throughout his professional career. As a young boy in Leicester, England, he prepared bird skins and collected bird eggs, butterflies, moths, and flowers, and he became the youngest member of the local geological society (Mayfield 1989). In an unfortunate and unlikely coincidence, both he and Wilson suffered from vision and hearing impairments as children, which limited their abilities to observe and identify birds. Wilson adapted by focusing much of his energies on another fauna that fascinated him—insects—whereas Preston persisted as an ornithologist, understandably challenged in field identifications given his myopia, colorblindness, and impaired hearing, but arguably unsurpassed as a quantitative theoretical ecologist of avian communities.

Of all the authors whose works we feature here, Preston was undoubtedly the most diversified in his professional interests. Although most of us know him as a quantitative ecologist, his principal occupation was that of glass technologist; he eventually established his own consulting and research firm (the Meridian Research Center, also known as Preston Laboratories), in addition to publishing technical papers and holding scores of patents on ceramics and glass technology, including revolutionary methods of melting glass using electricity (Mayfield 1989). His research and professional activities also included contributions to glaciology, fluid dynamics of molten rock, and conservation biology.

Preston’s career path was quite distinctive in other ways as well. His brilliance and determination as a young man earned him a scholarship to secondary school, and he qualified by exam for Oxford University. Unfortunately, he lacked the financial means to support a formal education, so, at 16, he began to pursue professional training without attending classes. Through his private studies, published works, and by examinations from London University, Preston received a Bachelor of Science degree, with first class honors, in Civil Engineering in 1916 (at the age of 20), a Ph.D. in 1925, and D.Sc. in 1951 (Mayfield 1989).

Preston’s Canonical Papers—Through his activities in both his principal occupation as a civil engineer and his other calling as a theoretical ecologist, Preston applied the incisive skills of an accomplished mathematician who viewed natural phenomenon as complex and multifactorial, but entirely explicable when subjected to mathematical description and logical scrutiny. Preston’s approach to investigating the mysteries of nature is epitomized by the companion papers he published in 1962 and that we discuss here—“The canonical distribution of commonness and rarity: Parts I and II,” both published in *Ecology*. We chose to feature these papers, in particular, because they also epitomize the growing sophistication of mathematical approaches for advancing ecological and biogeographic theory during the 1960s, when MacArthur and Wilson were developing their equilibrium theory. In fact, MacArthur and Wilson’s (1967) description of the mathematical relationship between area and species number

—a pattern they later described as a “stepping stone” to the development of their equilibrium theory— utilized the same approach Preston developed in his canonical papers.

Preston’s (1962a,b) papers described the mathematical relationships and conceptual linkages among three principal ecological and biogeographic parameters: the area of a region or island, the carrying capacity or total number of individuals it could support, and the total number of species occupying that region or island. In particular, Preston asserted that ecological ensembles of true isolates typically achieve a fixed interrelationship among parameters representative of two types of frequency distribution curves: 1) those describing the number of species in particular abundance classes, and 2) those describing the total number of individuals in each abundance class (Preston 1962a). He discovered a common relationship between statistical parameters of these distributions (the standard deviation, number of species in the modal abundance class, and total number of species in the isolate), and he referred to this as being “canonical,” as it seemed evident of an internal statistical equilibrium among the processes influencing population abundance and diversity within each abundance class, as well as overall.

Preston (1962a:185) then showed how the canonical “interlocking” of these statistical parameters could be used to explain and predict how abundance and diversity should vary with particular factors, including area as well as relative levels of exchange among communities, with the latter varying for true isolates versus samples of a large, contiguous ensemble of communities, where populations frequently exchange individuals via dispersal and immigration. Thus, Preston’s model advanced ecological theory beyond the then prevailing static view to one that holds that community structure results from interactions among recurrent and opposing processes (in this case, births and deaths), which ultimately result in a dynamic, internal equilibrium and Preston’s canonical relationship among statistical parameters.

Whereas Wilson (1959, 1961) referred to “saturation” to describe such a dynamic balance between opposing and recurrent processes, Preston actually used the term “equilibrium.” Yet his concept of an “internal equilibrium” was entirely distinct from that conceptualized earlier by Munroe, as well as that later developed by MacArthur and Wilson in their seminal paper and monograph. What Preston was describing was a statistical equilibrium among processes (birth, death, and emigration) within populations comprising an ecological community or isolate—processes that interact within an island to produce the canonical relationships of lognormal species and individual curves. In fact, Preston (1962a:193; 1962b:423) asserted that the exchange of individuals and species among islands or with the mainland via immigration — one of the fundamental processes in Munroe, Wilson, and MacArthur and Wilson’s models —prevented the internal statistical equilibrium that he described. Thus, richness of samples from highly interconnected patches or samples (e.g., counts of plants or animals in mainland quadrats) deviated substantially, albeit predictably, from internal equilibrium. In such cases, Preston (1962a:190–191; 1962b: 414) predicted that the exponent of the species-area relationship (a in the expression $N \propto A^a$) should be approximately 1.4 for true isolates, but substantially less than this for samples of a large contiguous area subject to frequent exchange of individuals. Whereas Wilson only touched on this subject in his second paper on taxon cycles (Wilson 1961), rigorous mathematical exploration of the species-area relationship was central to Preston’s canonical papers, just as it would be to MacArthur and Wilson’s development of their equilibrium theory.

Preston’s concept of equilibrium was an internal, demographic one and exclusive of the fundamental biogeographic processes of immigration, extinction, and evolution. Despite the important differences among the various concepts of equilibrium, Preston’s contributions significantly influenced the development of ecological theory and, in particular, island biogeography during this period. In fact, although it was not the central focus of his canonical

papers and mathematical models, Preston did discuss possible equilibria among islands—a concept much closer to that of the dynamic equilibrium or saturation envisioned by Munroe, Wilson, and MacArthur and Wilson. “The equilibrium of a sample [non-isolated areas subject to interchange of individuals] is decided by external forces acting beyond the perimeter” (Preston 1962b:412). Later in the same paper, Preston hypothesized that some insular biotas may fail to attain the canonical features of internal equilibrium, but may be “in pretty good equilibrium with one another” (1962b:423). He further postulated that the exchange of species among islands would cause extirpations on recipient islands, thus implying that an external equilibrium may eventually be achieved, but he qualified this with the following caveat. “Presumably the establishment of equilibrium among ... [islands] ... may be a much longer process than establishment of internal equilibrium on a single island” (Preston 1962b: 423). Preston went on to warn that “stability or equilibrium is not instantly, or even promptly attained [largely because] species may indeed be exterminated rapidly, but they can be created only slowly” (1962b:424). Apparently, he may have presaged the belief shared by an increasing number of contemporary biologists that the disparate tempos of immigrations, evolution, and extinctions— natural and especially anthropogenic— render disequilibrium conditions common, if not the norm, for many biotas. Preston (1962b:429) concluded that along with shortfalls in requisite taxonomic, demographic, and biogeographic information, our abilities to evaluate and further develop his theory will be limited by the “transitory” (i.e., disequilibrium) nature of most biotas. “Our theory deals with stable conditions, not transitory ones, and the world is in a very transitory stage at present” (Preston 1962b: 429). Preston attributed this primarily to extinctions and geographic dynamics of the recent ice age (see also Whittaker et al. 2008 for a recent synthesis on long-term dynamics and disequilibria of insular biotas).

Preston also applied his model to other topics, including historical biogeography (e.g., interpreting and quantifying the faunal dynamics of mammals of North and South America following the emergence of the Central American landbridge [1962b: 425]) and conservation biology (e.g., developing quantitative estimates of the “limitations of wildlife preserves” [1962b:427]). Therefore, Preston’s canonical papers fully deserve the special attention they have received here and in other discussions of the historical development of ecology and biogeography (for example, Featured Paper # 8 in *The Foundations of Ecology* [Real and Brown 1991]). Perhaps more so than any of his colleagues, Preston realized that biogeography was primed for the ultimate stage of a scientific revolution—one that built on the earlier insights of visionaries like Matthew, Simpson, and Darlington, and was then advanced to a penultimate stage, albeit almost exclusively in conceptual and qualitative terms, by Munroe and Wilson. Preston’s canonical papers demonstrated the utility, if not the essential role, that rigorous mathematical approaches would play in finally achieving a scientific revolution leading to the establishment of an alternative and more dynamic view of insular communities.

As Preston hypothesized in the introduction to his second canonical paper, rather than being “impoverished or depauperate [islands] really have the number of species that should be expected [and] the agreement is quantitative and not merely broadly qualitative” (1962b:410). However, he acknowledged that while mathematical modeling would provide the final solution, the work was not quite complete, and he concluded his second canonical paper as follows: “It seems to me practically certain that there is a better way of formulating the hypothesis in purely algebraic language, and this might lead to other interesting conclusions and perhaps to a coherent theory embracing many phenomena” (Preston 1962b: 431). Of course, the quest for “a better way of formulating the hypothesis” was already being tackled by another gifted mathematical ecologist, Robert H. MacArthur, who, in collaboration with Edward O. Wilson, would soon publish a comprehensive and revolutionary theory.

MACARTHUR AND WILSON'S COLLABORATIONS

Larry Slobodkin introduced Robert MacArthur (both former graduate students of G. Evelyn Hutchinson) to E. O. Wilson in 1961, during a meeting of the American Association for the Advancement of Science held in New York's Biltmore Hotel in 1961. Slobodkin and Wilson were planning a textbook on population biology, which Slobodkin felt could benefit from MacArthur's theoretical and mathematical abilities. The meeting was brief and inauspicious: MacArthur thought the textbook idea was attractive, but he was suffering from a headache, shook hands, and left (Wilson 1994:239). The three of them met again later that year to flesh out the plans for their textbook, this time at Harvard, but the project was shelved and soon dropped in favor of more pressing issues. In Wilson's case, his passion for field studies in biogeography and his quest for a grand synthesis—taxon cycles and a biogeography of the species—preoccupied his academic and creative energies. The one fortuitous outcome of their abandoned collaboration with Slobodkin was that Wilson and MacArthur discovered they had much in common, including their passions as naturalists and ecologists, and their desire to develop a general explanation for the diversity and geography of nature.

As we mentioned earlier, Wilson felt that the distinguished discipline of biogeography was now in a state of “grand chaos” and was “ripe for new thinking,” so he began to share his ideas on islands, taxon cycles, and a balance of nature with MacArthur (Wilson 1994:244). Like Wilson, MacArthur also shared a fascination for biogeography and the “tapestry of nature” (Wilson 1994: 245), and he quickly agreed to collaborate and complement Wilson's theoretical constructs with his own powers of conceptual synthesis and mathematical abstraction.

MacArthur and Wilson (1963): An Equilibrium Theory of Insular Zoogeography

The purpose of MacArthur and Wilson's first collaboration was not explicitly stated until the final paragraph of their paper: “To deal with the general equilibrium criteria, which might be applied to other faunas, together with some of the biological implications of the equilibrium condition” (MacArthur and Wilson 1963:385). This was indeed a very modest description of a model that would soon revolutionize the fields of ecology and biogeography. Its potential to complete the scientific revolution that had been brewing for decades was certainly not lost on these authors, but they believed it was first necessary to articulate the fundamental premise of their model in a well-measured paper to be published in the highly-respected, peer-reviewed journal, *Evolution*.

Thus, the domain of this revolutionary paper was paradoxically, but strategically, quite limited. While an implicit goal of MacArthur and Wilson's collaborations was to further develop both the qualitative and quantitative aspects of Wilson's theory of taxon cycles, their first collaboration focused on a much more narrow set of topics—principally, patterns in species richness of avian communities and how they resulted from a balance or, as they put it, a “very dynamic equilibrium” among recurrent processes (immigration, extinction, and speciation) (MacArthur and Wilson 1963:384). In fact, while teasing us with hints of more comprehensive works to come, MacArthur and Wilson were so conservative in this first collaboration as to restrict their inferences to one particular taxon—“Indo-Australian insular bird faunas”(1963:385). In addition to its limited taxonomic breadth, clearly beyond the domain of the paper were other relevant and intriguing patterns, including those in species composition within and across archipelagoes (i.e., mosaic distributions and community nestedness), as well as character and niche shifts, ecological release, and patterns in endemism of populations within and among islands. Furthermore, by assuming that speciation was unimportant, except for “the largest, and most isolated archipelagoes, such as Hawaii and the Galapagos” (MacArthur and Wilson 1963:380), MacArthur and Wilson's model was largely restricted to phenomena occurring within ecological timescales. They also assumed that

interspecific interactions and differences in immigration abilities and ecological dominance among species could be ignored when modeling dynamic equilibria and explaining geographic gradients in species richness (i.e., species-area and species-isolation relationships).

Again, the main purpose of their 1963 paper, as they stated in its summary, was “to express the criteria and implications of the equilibrium condition, without extending them for the present beyond the Indo-Australian bird faunas” (MacArthur and Wilson 1963:983). As we discussed in the preceding sections of this review, both Wilson and MacArthur were accomplished naturalists, and their previous studies and publications clearly spoke to the importance of differences among and interactions between species in shaping the patterns they studied. Yet, in the context of their model, species could be treated as “gray boxes” (*sensu* H. T. Odum, personal communication to MVL, 1977); we know that they are different, but those differences presumably are not essential to explaining patterns in species richness under a hypothesis of dynamic equilibrium.

By constructing a species-neutral model and focusing on just one component—albeit a critical and, up till then, nascent component— of Wilson’s original model, MacArthur and Wilson developed a model that was both revolutionary and compelling. Indeed, much of its success derived from MacArthur and Wilson’s abilities to present this ingenious explanation for two very general patterns of species richness in both graphical and complementary mathematical forms. The resultant model was both accessible and readily interpretable to most scientists, and it was amenable to logical scrutiny and a generation of new falsifiable predictions. For example, MacArthur and Wilson were able to demonstrate not only how a dynamic equilibrium would explain species-area and species-isolation relationships, but also why species richness should be relatively stable despite turnover in species composition. Furthermore, they demonstrated how the mathematical form of this species-neutral model could be used to estimate such properties as the mean dispersal distance of the taxon, as well as the degree of saturation of an island whose fauna was displaced from its equilibrial richness (e.g., due to hurricanes or volcanic eruptions), and the resulting time it would take to again achieve equilibrium (MacArthur and Wilson 1963:977–979). Just as important for the evaluation and future development of their theory, the graphical form of MacArthur and Wilson’s model allowed them to develop a set of qualitative and falsifiable predictions regarding biogeographic dynamics of insular communities (e.g., that immigration, extinction, and turnover rates should vary with area, isolation, and climate of the island, and with number of species in the source area [MacArthur and Wilson 1963:974–975]).

The Lessons of Krakatau

Preceding a relatively abbreviated section where they revisited Wilson’s conceptualization of radiation zones, this time within the context of dynamic equilibria, MacArthur and Wilson (1963:980–981) tested important predictions of their theory utilizing Dammerman’s (1948) reports on the biogeographic dynamics of Krakatau’s avifauna following the sterilizing eruptions of 1883 (as defined by MacArthur and Wilson, the radiation zone included those archipelagoes along “the outer limits of the distribution of a taxon, where immigration ... is so rare that speciation and radiation occur easily” [1967: 190]). In addition to providing strong validation for the equilibrium model, the lessons from Krakatau served as a compelling demonstration of the utility of opportunistic experiments in island biogeography. Simultaneously, they planted the creative seeds for some ingenious manipulative field experiments in island biogeography, including the classical mangrove defaunation experiments devised by Wilson and his future graduate student, Daniel S. Simberloff (Wilson and Simberloff 1969; Simberloff and Wilson 1969, 1970).

MacArthur and Wilson’s analysis of the ecological dynamics of Krakatau also serves as an important reminder that the opportunistic surveys of Dammerman (1948), Docters van

Leeuwen (1936), and other naturalists played a key role in the scientific revolution that was to culminate in a dynamic theory of biogeography. Rather than simply cataloguing the local biota at particular points in time, they realized that the 1883 eruption provided what may have been an unrivaled opportunity to advance our understanding of the dynamic nature of insular biotas. They challenged the fundamental assumptions of static biotas, or those that continuously accumulated species but only over evolutionary time, and they exposed the liabilities of premising paradigmatic theory on explanations that are primarily descriptive and idiographic.

MacArthur and Wilson's first collaboration was, in fact, one of a long series of studies benefiting from the lessons of Krakatau and its message to integrate faunal dynamics into modern theories of biogeography. Yet their 1963 paper was, by itself, too limited in scope to complete the scientific revolution whose flames were first kindled in earlier centuries by pioneers of island biogeography including Forster (1778), Darwin (1839, 1859, 1860), and Wallace (1869, 1876, 1881), and then stoked by 20th century biogeographers, ecologists, and evolutionary biologists including Mayr (1965 a, 1965b), Darlington (1938, 1943, 1957), and Preston. As MacArthur and Wilson well understood, the ultimate paradigm shift would require a much more comprehensive development of this revolutionary model.

MacArthur and Wilson's Monograph (1967)—The Theory and a Biogeography of the Species

Following publication of their seminal paper in 1963, MacArthur and Wilson had become close friends and valued colleagues as they continued to develop their equilibrium theory. By December of 1964, they had agreed to "write a full-scale book on island biogeography, with [the] aim of creating new models and extending [their] mode of reasoning into as many domains of ecology as [they] could manage" (Wilson 1994:255). Wilson would later appraise the success of their monograph, with justified candor: "[I]t met with almost unanimous approval ... MacArthur and I accomplished most of what we set out to do. We unified, or at least began to unify, biogeography and ecology upon an internally consistent base of population biology" (Wilson 1994:256).

It is not our purpose here to discuss each of the important insights and implications of MacArthur and Wilson's monograph. Instead, we choose to use this opportunity to complete our account of the scientific revolution in biogeography and, in particular, to discuss how it was and may continue to be guided by the integrative species- and process-based theory first articulated by Wilson in 1959.

A careful review of MacArthur and Wilson's 1967 monograph raises a striking paradox. Although it is most often recognized as an exposé, masterful or misleading, of a model that provided an innovative explanation for a limited set of phenomena (principally, the species-area and species-isolation relationships), their monograph was actually one of the most comprehensive theoretical works in biogeography since those of Darwin and Wallace. In addition to the two introductory chapters and Chapter 3, which developed the equilibrium theory, five other chapters explored a broad range of topics including: r/k selection and its relevance to evolution, as well as the establishment of insular populations (Chapter 4); demography, interspecific interactions, and niche dynamics (Chapter 5); dispersal curves, geometry of archipelagoes, and biotic exchange (Chapter 6); and evolutionary changes following colonization and adaptive radiation (Chapter 7). The equilibrium model was arguably the most revolutionary feature of MacArthur and Wilson's monograph, but their goal was much more ambitious and more comprehensive than this. Prior to its publication, Larry Slobodkin, then at the University of Michigan (UNM), received a draft of the manuscript with annotations by the authors that revealed their ultimate goal of transforming not just island biogeography, but also the field of biogeography in general. The second author of this paper (JHB) was a graduate student at UNM and recalls that the first page included three alternative

titles: *The Theory of Biogeography*, which was crossed out, *The Theory of Biogeography: I. Islands*—also crossed out, and, finally, *The Theory of Island Biogeography*.

The real paradox that we alluded to above is this: The most influential and universally identified feature of MacArthur and Wilson's monograph is their equilibrium model that, as aforementioned, treats species as though they are equivalent with respect to abilities to immigrate, survive, interact, and evolve on islands. Yet such a species-neutral model seems entirely antithetical to the stated purpose of their book, which was the same as that of Wilson's original taxon cycle paper. The following quotes from the introduction to MacArthur and Wilson's (1967) monograph make their ultimate purpose quite clear.

The purpose of this book is to examine the possibility of a theory of biogeography at the species level. We believe that such a development can take place by looking at species distributions and relating them to population concepts, both known and still to be invented.

Certainly, the amount of information on distribution is vast; it has been created by two hundred years of accumulative taxonomy.

A main goal of this book is to identify those kinds of data needed for a further development of a population theory and, ultimately, the full explanation of distribution itself. (MacArthur and Wilson 1967:5–6)

Species distributions were both the foundations for the diversity of patterns that these biogeographers sought to explain, as well as the stimulus for Wilson's original theory of taxon cycles. Species richness gradients were just a select sample of those patterns (derived from cumulative overlap of species distributions), in and of themselves saying little about other phenomena such as colonization strategies, faunal nestedness, radiation zones, patterns of endemism, niche dynamics, and the geography of extinction. As we remarked earlier, Wilson's epiphany came not from inspecting species richness curves, but by poring over distribution maps. He had, of course, been primed for this breakthrough by many years of comparing distributions among species and across biogeographic scales, from local to regional. Thanks to his exhaustive studies of the relevant literature and to his own singular intuitive powers, Wilson was then able to reconstruct the temporal development of distribution patterns and faunal dynamics within and among islands and over ecological to evolutionary timescales.

Yet, in stark contrast to Wilson's original papers on taxon cycles, MacArthur and Wilson's monograph did not include even one map of a species distribution. We assume this was an intentional effort to emphasize the value of general synthesis over the descriptive, idiosyncratic explanations that tended to dominate biogeography prior to this period. But one unfortunate outcome of this was the obfuscation of MacArthur and Wilson's ultimate goal of developing a very general theory that should nonetheless remain species- and process-based; i.e., based on how species differ in, or are differentially affected by, the fundamental processes of biogeography (immigration, evolution, extinction, and interspecific interactions) (see MacArthur and Wilson 1967:4). It is, therefore, noteworthy that MacArthur and Wilson returned to this very general theme in the conclusion of their book, calling for the field of biogeography to "be reformulated in terms of the first principles of population ecology and genetics ... to de-emphasize for the moment traditional problems concerning the distribution of higher taxa and the role of geological change ... and to turn instead to detailed studies of selected species. A 'biogeography of the species' requires both theory and experiments that must be in large part novel" (1967:183).

This then leaves us with two intriguing questions. Regardless of how each of us might assess the success or shortcomings of MacArthur and Wilson's monograph, it certainly had a revolutionary effect on the field of island biogeography and on related disciplines in ecology

and evolutionary biology as well. Yet why and how within the context of the structure of scientific revolutions was this achieved? Some understanding of why MacArthur and Wilson succeeded where Munroe and other earlier biogeographers had not will assist us in answering our second question: What is the future of biogeography, and, in particular, what is the likelihood of advancing Wilson's original vision of a biogeography of the species, or replacing it with an equally general reintegration of island theory?

THE STRUCTURE OF SCIENTIFIC REVOLUTIONS

The development of MacArthur and Wilson's equilibrium theory is an intriguing case study in what Kuhn (1996) described as "the structure of scientific revolutions"—also the title of his book, first published in 1962, which strongly influenced scientific thinking during the relevant period of theoretical advance in biogeography, ecology, and evolutionary biology. Fundamental scientific advances are not simply processes of incremental accumulation of facts; rather, they are the development of new perspectives and theories that transform the scientific imagination and the ways in which we interpret and integrate those facts. As Kuhn put it, "Scientific fact and theory are not categorically separable, except perhaps within a single tradition of normal scientific practice" (1996:7).

The epistemological process that Kuhn described was analogous to the evolution of life forms by the process of punctuated equilibrium: "a succession of tradition-bound periods punctuated by non-cumulative breaks" (Kuhn 1994:208). Scientific disciplines and the visions of their scientists develop through a series of prolonged periods of normal science conducted under the rules of a reigning paradigm, alternating with periods of scientific crises and subsequent shifts to revolutionary paradigms—those "universally recognized scientific achievements that for a time provide model problems and solutions to a community of practitioners" (Kuhn 1996:x). That is, paradigms set the rules and agenda for investigations during subsequent periods of normal science. Here we interpret some key features of the development of island biogeography theory during the 20th century within the context of Kuhn's structure for scientific revolutions.

A PRE-PARADIGMATIC MORASS OF ISLAND PATTERNS

As the French mathematician and philosopher Henri Poincaré wrote, "Science is built upon facts much in the same way that a house is built with bricks; but the mere collection of facts is no more a science than a pile of bricks is a house" (1904, 1952). Thus, one invaluable role of a paradigm is to guide scientists in interpreting facts (Poincaré's "bricks") and integrating them into some grand scheme of how nature functions. Lacking such a conceptual structure, the pre-paradigm period of most scientific disciplines is characterized by fact collecting—no doubt essential to genuine advances within a given discipline, but often resulting in a morass of largely disarticulated information. Kuhn's examples of such pre-paradigmatic collections included "Pliny's encyclopedic writings [and] the Baconian natural histories ... of heat, color, wind, mining, and so on [which] are filled with information, some of it recondite" (1996:16).

In some ways, island biogeography theory of the mid-20th century may be characterized in a similar manner. Although the field of biogeography, in general, had experienced a succession of paradigms, ranging from that of unique to multiple periods and sites of creation, as well as those of the extensionists versus the Center of Origin-Dispersal-Adaptation tradition, none of these seemed particularly well-suited unifying paradigms for island biogeography. As a result, explanations for the diversity and development of insular biotas tended to accumulate in an encyclopedic fashion with idiosyncratic, albeit often fascinating and factually correct, explanations for each particular archipelago and its flora or fauna.

ESSENTIAL CRISES

The emergence of a discipline's first paradigm, along with subsequent scientific revolutions and paradigm shifts, typically follows—and indeed may require—a scientific crisis. At such times, scientists become so frustrated with the morass of disarticulated information or the accumulation of anomalies and novelties to a reigning paradigm that they feel compelled to take radical action and advance a new paradigm. These periods are marked by “frequent and deep debates over legitimate methods, problems, and standards of solution ... debates ... almost non-existent during periods of normal science, they recur regularly just before and during scientific revolutions” (Kuhn 1996: 47–48). Kuhn recalled some of the classic cases of confusion and frustration during scientific crises in astronomy and physics: Copernicus complained that astronomers had become so “inconsistent in these [astronomical] investigations ... that they cannot even explain or observe the constant length of the seasonal year”; Einstein felt that “it was as if the ground had been pulled out from under one, with no firm foundation to be seen anywhere, upon which one could have built”; and, in characterizing the crisis in quantum mechanics during the 1920's, Wolfgang Pauli admitted to a friend that “at the moment physics is again terribly confused. In any case, it is too difficult for me, and I wish I had been a movie comedian or something of the sort and had never heard of physics” (Kuhn 1996:83–84).

As we described earlier, the burgeoning but disarticulated morass of information on the diversities, distributions, and dynamics of insular biotas had accumulated well beyond the tensile strength of the CODA tradition. In response, bold and visionary scientists set out to develop a grand synthesis that would ultimately result in Munroe's unpublished but insightful theory, Wilson's taxon cycle, and MacArthur and Wilson's equilibrium theory.

THE YOUNG SHALL LEAD

One of the most remarkable and also humbling features of scientific revolutions is that they are often led by scientists who are either very young or new to the discipline. Some of the most familiar examples include Einstein, who wrote his first scientific work, *The Investigation of the State of Aether in Magnetic Fields*, at the age of 15, experienced his famous thought experiment of traveling alongside a beam of light the next year, and completed his *Annus Mirabilis* collection of papers (featuring his theories of quantized light, Brownian motion, special relativity, and the equivalence of matter and energy) while cloistered away in his corner of the patent office at just 26 years old. Other classic examples of youthful brilliance include that of James Watson, who was only 25 when his collaboration with Francis Crick—then at the relatively august age of 37—led to the discovery of the structure of the DNA molecule.

According to Kuhn, young scientists or those new to the discipline are less habituated to the effects, both positive and negative, of its reigning paradigm. Again, one of the key functions of a paradigm is to focus the energies of scientific communities on a particular set of topics and to provide them with a set of rules and acceptable methods for describing relevant phenomena with greater efficiency and precision. Yet normal science under a long-accepted paradigm also has some serious liabilities, including its tendency to act as blinders and limit the imaginations of scientists, the scope of the questions, and the means by which they can be investigated (see Kuhn 1996:64). As Kuhn observed, “the very young or very new to the field ... are little committed to the traditional rules of normal science, are particularly likely to see that those rules no longer define a playable game and to conceive another set that can replace them” (1996:90).

It may not seem that remarkable, at least in retrospect, that the scientists who were to feature most prominently in the 20th century scientific revolution in island biogeography all did so at very young ages or when they were relatively new to the field. Munroe was just 29 when he

developed his equilibrium theory of island biogeography. Edward Wilson was 30 when he published the first of his two seminal papers on the taxon cycle. Frank Preston, although 52 when he published his first classic paper, “The commonness and rarity of species,” in *Ecology* in 1948, was new to the fields of biogeography and ecology. Robert MacArthur, already widely respected for his previous research, was just 33 when he and Wilson published their first collaboration on the equilibrium theory. Each of these gifted scientists was blessed with a healthy measure of scientific impudence—they were too new to the discipline to be blinded by or habituated to the traditional normal science and its idiosyncratic approaches to studying biotas that were assumed static across ecological time scales. Thus, unencumbered and simultaneously frustrated with the status quo, they boldly strove for a revolutionary grand synthesis.

THE DATING OF DISCOVERIES AND REVOLUTIONS

If genuine advances in science were achieved by the simple accumulation of facts, then each discovery and scientific revolution could be precisely dated by simply noting when the ultimate fact was collected. As Kuhn observed, however, “new theory ... is seldom or never just an increment of what is already known. Its assimilation requires the reconstruction of prior theory and the re-evaluation of prior fact, an intrinsically revolutionary process that is seldom completed by a single man and never overnight” (1996:7). Accordingly, we chose to feature here not just one seminal publication, but a series of works that span some two decades in the developmental history of island biogeography. These comprise just a small subset of the important works in this field whose development was, rather than a predictable or teleological advance to more facts, a reticulating phylogeny of the ideas and imaginations of many scientists. Moreover, as we discuss in the final pages of this paper, the scientific revolution initially attempted by Munroe and then clearly articulated in Wilson’s taxon cycle may have yet to be fully realized.

INEVITABILITY AND REDISCOVERY IN SCIENCE

Given the reticulating nature of “discovery” in science, particular advances in reformulating the cumulative knowledge available to the scientific community may become both inevitable and subject to rediscovery—i.e., the “multiple and independent appearance of the same scientific discovery” (Merton 1961). As Merton observed after reviewing Ogburn and Thomas’s (1922) analysis of well over 100 cases of independent discovery in science, “the innovations became virtually inevitable as certain kinds of knowledge accumulated in the cultural heritage and as social developments directed the attention of investigators to particular problems” (1961:475). Darwin and Wallace’s independent discovery of the theory of natural selection is perhaps the prototypical example of an inevitable and independent discovery in the natural sciences, while Munroe’s (1948, 1953, 1963) early development of an equilibrium theory, equivalent in many respects but much more rudimentary than MacArthur and Wilson’s theory, appears to be a more obscure but still instructive case of the same phenomenon.

LIGHTNING FLASHES

Despite the difficulties in precisely dating the critical days of a paradigm shift, scientists are blessed, albeit not nearly often enough, with moments of inspiration that more than make up for many years of frustration. According to Kuhn, crises are solved “not by deliberation and interpretation, but by a relatively sudden and unstructured event like the gestalt switch. Scientists then often speak of the ‘scales falling from the eyes’ or of the ‘lightning flash’ that ‘inundates’ a previously obscure puzzle” (1996:122).

We have previously recounted Wilson’s epiphany, which came one January morning in 1959 while he sat on the floor of his Harvard office poring over distribution maps. MacArthur likely experienced something similar when he sketched the first graph illustrating an equilibrium

between opposing forces of immigration and extinction (Figure 3). Just as likely, these and other biogeographers of this period experienced similar “lightning flashes” when they first read reports of rapid colonization, recurrent turnover, and dynamics of Krakatau’s biota—accounts that appeared entirely inconsistent with static theories of island biogeography.

THE PARADOX OF PRESCIENCE, AND THE ALLURE OF AESTHETICS

Scientific crises can conclude in one of three ways: 1) the normal science of the reigning paradigm ultimately proves capable of explaining the anomalies, 2) a new paradigm emerges with superior abilities to explain the patterns and problems in question, or 3) the problem cannot be resolved under the existing tools and information available to scientists, so it is then “set aside for a future generation with more developed tools” (Kuhn 1996:84). The triumph of a new theory over an older one or over a rival candidate for the new paradigm is not always arrived at by purely objective criteria. As Kuhn acknowledged, although the decision should be “based less on past achievement than on future promise ... the importance of aesthetic considerations can sometimes be decisive ... [e]ven today Einstein’s general theory attracts men principally on aesthetic grounds” (1996:155–158).

The development of island biogeography theory seems entirely consistent with Kuhn’s structure. MacArthur and Wilson’s equilibrium theory emerged following a scientific crisis that had exhausted the limits of normal science and the traditional, static theory of island biogeography. But this occurred decades after Munroe’s frustrated attempts to publish and further develop his theory, which came well before the scientific community developed an adequately comprehensive and accurate understanding of the dynamics of the natural world, both geological and biological, and well before they had the tools to fully appreciate and further develop theories of dynamic island biogeography. As with Wegener’s original theory of continental drift, Munroe’s equilibrium theory came well before the scientific community was ready for such revolutionary ideas (alternative 3, above). Similarly, Wilson’s theory was first articulated decades before requisite advances in supporting sciences, including genetics, molecular biology, and phylogeography, would enable a resurgence of research on taxon cycles and related aspects of a species- and process-based biogeography (e.g., Ricklefs and Bermingham 2002; Wiens and Donoghue 2004; Stuessy 2007; Riddle and Hafner 2007; Bellemain and Ricklefs 2008).

By the time MacArthur and Wilson were about to publish the first of their collaborations in 1963, Munroe was far along in his career as a leading systematist of Lepidoptera. Philip Darlington warned Munroe that his Harvard colleague, Ed Wilson, was about to publish a theory very similar to his, but it had been some 10 years since Munroe was stymied in his attempts to publish his equilibrium theory, and he was now just too preoccupied with the demands of his current career to resurrect his manuscript in time to lay claim to its first articulation (Munroe to MVL, personal communication, September 7, 2007).

In contrast to the fates of Munroe and Wilson’s earlier theories, MacArthur and Wilson’s equilibrium theory received rapid and overwhelming—albeit not universal (e.g., see Sauer 1969)—acclaim, owing in large part to three factors: 1) its relative simplicity and resultant aesthetic appeal (as Kuhn [1996:155] put it, new theories often “appeal to the individual’s sense of the appropriate or the aesthetic—the new theory is said to be ‘neater,’ ‘more suitable,’ or ‘simpler’ than the old”); 2) its timeliness (i.e., being advanced when the requisite scientific tools were available); and 3) its genuine, collaborative nature (the subject of the next section, below). As we remarked earlier, MacArthur and Wilson’s monograph called for a very general theory—a new paradigm based on Wilson’s concept of a biogeography of the species. Clearly, that call was unattainable at the time it was made. The result was the subsequent distillation of their very general theory to its most tractable and compelling components—the equilibrium model of species richness. Their original theory, in contrast, required a much more thorough

understanding of fundamental biogeographic processes, which, at that time, MacArthur and Wilson viewed as “among the most difficult in biology to study and to understand” (1967:4). The advanced genetic, molecular, geological, systematic, and statistical analyses required for evolutionary and phylogeographic reconstructions (i.e., for constructing histories of place and of biotas) were simply unavailable, if at all imagined, at the time.

This then is the “paradox of prescience”: We strive for theories that are ahead of their time, but then are often forced to set them aside or let them languish in developmental diapause until our tool kits catch up to our scientific imaginations. Over time, MacArthur and Wilson’s very general theory underwent domain contraction (*sensu* Pickett et al. 2007), to the point that it eventually became viewed by some as a “numbers game” (*sensu* Whittaker 1998; Whittaker and Fernandez-Palacios 2007) explaining variation in richness of equivalent and nonevolving species among islands differing almost exclusively in their area and isolation.

TOWARD A REINTEGRATION OF ISLAND BIOGEOGRAPHY

This is, indeed, a very exciting time to be a biogeographer. By nearly all measures, including the accelerating number of peer-reviewed publications as well as entire journals and books focusing on biogeography, along with establishment of the International Biogeography Society in 2000 (www.biogeography.org), with its current membership of well over 700 scientists from 35 countries, the discipline is becoming increasingly recognized as one of the most integrative fields of science. Accordingly, biogeography is also viewed as one with perhaps unrivaled promise for understanding the complexities of nature and for developing effective tools and strategies for conserving the rarest and most geographically restricted life forms. We believe that this renaissance in biogeography is founded, not just on the continual advancements in our ability to collect and catalog facts, but on some truly fundamental advances in our capacities to integrate those facts into more comprehensive and insightful theories of the geography of nature.

Although scientific revolutions are typically “invisible” while underway (Kuhn 1996: 136–143; see also Pickett et al. 2007), there are some very clear signs that biogeography is experiencing a wave of paradigm shifts, or perhaps better put, paradigm expansions and reintegrations. For example, historical biogeography, which had long suffered from contentious and fractionizing debates between feuding research programs (e.g., dispersalists vs. extentionists, vicariance vs. dispersal camps, panbiogeographers vs. phylogeographers vs. cladists), is now enjoying a rapprochement and reintegration of these long-divergent but now complementary approaches (see Brooks 2004; Parenti 2007; Riddle and Hafner 2007; Sanmartín 2007). Along with other biogeographers such as John Wiens and Michael Donoghue (2004), we are calling for a reintegration of biogeography, reuniting historical and ecological divisions of the discipline for perhaps the first time since Darwin and Wallace.

The perceived crisis in the inabilities of equilibrial and species-neutral theories, or other equally restrictive paradigms, to account for the marvelous diversity of insular patterns and phenomena will likely become the flashpoint for the next, perhaps ongoing, scientific revolution. That revolution will likely be achieved, not through a shift to an equally specialized alternative to the equilibrium theory, but by a re-expansion of conceptual domains toward a more integrative theory of island biogeography. We do not anticipate nor recommend an actual reemergence of Wilson’s taxon cycle theory *sensu stricto*, and we acknowledge that the number of publications focusing on taxon cycles per se, or advancing more integrative theories of island biogeography, is limited. We do, however, find good reason to remain optimistic that the tide is turning and a grand synthesis rivaling Wilson’s theory in scope and promise, but now enlightened by some four decades of technological and theoretical advances for studying complex, scale-dependent processes, is on the horizon (e.g., see notable studies on taxon cycles by Roughgarden and

Pacala 1989; Losos 1992; Ricklefs and Bermingham 2002; for some recent and relatively integrative theories of island biogeography, see Heaney 2000; Lomolino 2000; Ovaskainen and Hanski 2003; Hanski 2004; Whittaker 2004; Whittaker et al. 2001, 2008; Stuessy 2007; Lomolino et al. 2009).

While we hesitate to predict which of the alternative theories will prevail, we strongly recommend that the new paradigm should share some properties fundamental to Wilson's original theory. That is, a genuinely integrative theory of island biogeography should be:

- **multi-scale**—benefiting from some four decades of insights into the importance of and strategies for modeling scale-dependent processes in nature (e.g., O'Neill et al. 1986; Tillman and Karieva 1997; Allen and Hoekstra 1992; Edwards et al. 1994; Brown 1995; Rosenzweig 1995; Brown and West 2000; Whittaker et al. 2001);
- **species- and process-based**—inclusive of species as well as system (island and archipelago) properties affecting the fundamental processes of immigration, extinction, and evolution;
- **inclusive of system feedback** in the form of interspecific interactions, evolutionary divergence, and speciation, which can affect each of the fundamental processes and capacities of focal species (i.e., modifying their abilities to immigrate and survive, evolve, and dominate other species in ecological interactions on islands).

Species are not identical, immutable, equivalent, or independent particles, although modeling them as such often yields some intriguing patterns that often appear convergent with those in nature (see Bell 2001; Hubbell 2001, 2006; Bell et al. 2006; Holt 2006; Hu et al. 2006). Just as islands and archipelagoes differ in characteristics influencing the fundamental biogeographic processes (e.g., in area, isolation, and characteristics of intervening seas or immigration filters), so too do species, and we assert that many of the most intriguing patterns in island biogeography emerge because of, not despite, this variation. Again, MacArthur and Wilson and, later, Hubbell and others have elegantly demonstrated that interspecific differences can be ignored to some degree when developing models to explain patterns such as variation in species richness among islands or patches of habitats. Yet a truly integrative, general model of island biogeography should include deterministic as well as stochastic (neutral) components in order to explain a much broader spectrum of intriguing and interdependent patterns, including species distributions; nestedness and ecological assembly of communities; gradients in endemism, richness, and rarity; niche shifts and character release; increased woodiness in typically herbaceous plants; evolution of flightlessness in birds and insects, and dwarfism and gigantism in insular vertebrates; and range contraction and extinction of island endemics.

Over the past four decades, biogeographers, ecologists, and evolutionary biologists have made great strides in their abilities to investigate the fundamental biogeographic processes. We anticipate that continued expansion of relevant research programs will reveal that these processes are not only interdependent in terms of their influence on biogeographic patterns, but that the fundamental processes themselves exhibit predictable patterns of covariation among islands and among species. For example, along a gradient from the equator to the poles, insular ecosystems can be characterized by interdependent and parallel trends of decreasing ambient temperatures, primary productivity, and carrying capacity. Patterns of covariation in traits among species should also be significant and predictable. In many groups of vertebrate animals, for instance, physiological scaling laws indicate that larger species should be better immigrants and more likely to dominate interspecific interactions (i.e., prey on or out-compete smaller species); they should require more resources and, therefore, be more prone to extinction; and they should have longer generation times and, thus, exhibit slower rates of evolutionary change. However, just as Wilson (1961: 90) predicted that the nature of taxon cycles should differ among faunal groups, we certainly do not expect these particular patterns

of covariation to hold for all insular biotas. Instead, we use these examples to emphasize that such patterns of variation among insular systems and among species are highly non-random and interdependent, thus contributing to the generality of patterns in geographic variation among insular biotas.

We now have the means to study these fundamental processes, including their scale dependence and patterns of variation and covariation among systems and species. Research directed at further exploring these processes and patterns will make great strides toward reintegrating the long-divergent but complementary conceptual branches of island theory, and will achieve genuinely transformative advancements in our understanding of the geography of life in general.

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B)

FIGURE 1. DARLINGTON'S THEORY OF SELECTIVE IMMIGRATION

According to Darlington's (1957) model, (A) species populations are distributed in a nested fashion among islands of increasing isolation from their mainland source. Publication of this model was soon followed by Wilson's (1959) empirical demonstration of the nested pattern for four species of ponerine ants (B). In part (A), immigration abilities of species $A > B > C > D$; in part (B), distribution patterns suggest that immigration abilities of species $4 > 3 > 2 > 1$. (Illustrations redrawn by Lomolino et al. 2006; reproduced with permission from Sinauer.)

FIGURE 2. WILSON'S CONCEPT OF SPECIES SATURATION AND ISLAND AREA

According to Wilson, the relationship between the number of ponerine and cerapachyine ant species and island area resulted from the tendency for insular faunas to be in "saturated or near-saturated conditions," approaching an upper limit "set by the size of the islands" (1961:170–171).

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FIGURE 3. ROBERT MACARTHUR'S FIRST GRAPHICAL MODEL OF DYNAMIC EQUILIBRIUM ON ISLANDS

Using data supplied by Ruth Patrick from her then unpublished studies on the colonization of glass slides by freshwater diatoms (see Patrick 1968), Robert H. MacArthur sketched the first graphical equilibrium model illustrating how species richness should vary with island area (second column, labeled "is. small (or) is. large" (i.e., small or large islands, respectively), affecting extinction rates, and two curves labeled "ext.") and isolation (simulated by enclosures with small or large openings; first column, affecting immigration rates, two curves labeled "immigr. of new sp."). Illustration from a scan by Swanson (2000) of a note from MacArthur to E. O. Wilson dated 27 April 1962, which included the following: "But I did want to tell you

my ideas about a model of number of species so that you can improve it while I am away. ... Basically, unless immigration and local species extinctions are much rarer than I guess, they must about balance” (see Wilson 1994:250; Swanson 2000:89–90). (From the Robert Helmer MacArthur [1930–1972] Papers, Department of Ecology and Evolutionary Biology, Princeton University.)