Island Biogeography in the 1960s

THEORY AND EXPERIMENT

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Intellectual Origins

When I was still a graduate student, in the early 1950s, an idea was circulating that I found inspirational. It originated with William Diller Matthew, a vertebrate paleontologist at the American Museum of Natural History. In 1915 he had suggested that over long periods of Cenozoic time, the most successful of new mammalia genera and families have been arising from a central headquarters of macroevolution. Matthew concluded that the north temperate zone was that geographic cradle. The new clades were by and large intrinsically dominant over those originating in the southern continents. Radiating into diverse adaptive types, they spread outward into the peripheral land masses respectively of Africa, tropical Asia, Australia, and tropical America. As they expanded, they tended to displace early prominent genera and families that were ecologically similar, first from the north temperate evolutionary headquarters and then the southern land masses. The ruggedness of the species originated from a challenging climate, Matthew thought.

For example, rhinocerotids, once dominant elements of the north temperate regions, have fallen back before groups such as deer and other cervids, while early dominant carnivores have retreated before the currently dominant canids and felids. What people living in the north temperate zone think of as "typical" mammals are just the dominants presiding at macroevolutionary headquarters at the present time.

In 1948 and later, in 1957, Philip J. Darlington, then Curator of Entomology at Harvard's Museum of Comparative Zoology, pressed on with Matthew's idea. But he altered it fundamentally, at least for the nonmammalian land vertebrates. In a study of the cold-blooded land and freshwater vertebrates—reptiles, amphibians, and fish—Darlington identified the headquarters as the Old World tropics.

By the 1980s, with much richer fossil data in hand than available to Matthew and Darlington, researchers had shifted placement of the Cenozoic headquarters to the "World Continent," a biogeographically historical

construct comprising Africa, Eurasia, and North America, and in particular the vast tropical regions within them. Evidence supporting this view came from the phenomenon of the Great American Interchange, the mingling of the independent adaptive radiations of North and South America made possible by the emergence of the Panamanian land bridge about three million years ago. The pattern of the exchange supported the view that competitive displacement among land vertebrates has been a reality. It also suggested that the evolutionary products of the World Continent, represented by North America during the Interchange, were generally superior to those of South America—as revealed by replacement at the levels of genus and family (Simpson 1980, Marshall 1988).

The Taxon Cycle

In 1954–55 the Matthew-Darlington epic view of global territorial biogeography was in the back of my mind, although not to any pressing degree, when I undertook field work on the ant fauna of part of the Melanesian archipelagic chain, from New Guinea to Vanuatu, Fiji, and New Caledonia. I had been elected for a three-year term as a Junior Fellow of Harvard's Society of Fellows, which gave me complete support and freedom to go anywhere to study anything I chose. (I wish this kind of opportunity were available to all new postdoctoral scholars—the world would benefit enormously.) My main goal was to collect and classify the ants of this still poorly known part of the world ant fauna (figure 1.1). Within three years after returning, during which I began an assistant professorship at Harvard, I had managed to publish or put in press monographs on a large minority of the species, many of which were previously undescribed.

While in the field I took as many notes on the natural history of the species as I could. Back home, combining systematics and ecology, I looked for patterns that might shed light on the origins of that classic archipelagic fauna. One day, in a eureka moment consuming only a few minutes, I saw a relation between the spread of species between islands and archipelagoes, on the one hand, to within-island speciation and shifts in habitat preference during evolution, on the other. This was in 1958. I believe I was the first to see such a connection; at least I was not guided by any other work I knew at the time.

These connections were summarized in what I later called the taxon cycle (figure 1.2). The taxon cycle comprises the following steps, at least as displayed by the Melanesian ant fauna. Species enter the Melanesian chain of archipelagoes primarily through New Guinea out of tropical Asia and, less so, out of Australia. Those judged to be in an early stage of expansion possess a continuous distribution and a relatively small amount

Figure 1.1. E. O. Wilson with guard crossing the lower Mongi River, Papua New Guinea, April 1955.
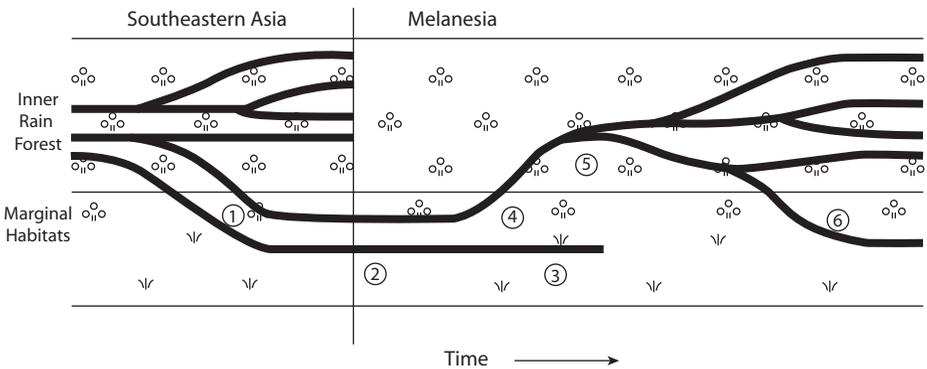

Figure 1.2. The taxon cycle in the Melanesian ant fauna (Wilson 1965, modified from Wilson 1959).

of geographic variation. They turned out to be mostly specialized on marginal habitats, those inhabited by relatively small numbers of species. In Melanesia, the marginal habitats include littoral environments of the coastal shore, river-edge forests, and savannas. Such are places that are happenstance staging areas for between-island dispersal. Local populations

on individual islands are not adapted by natural selection for overseas dispersal. Rather, they are preadapted for overseas dispersal by virtue of the greater probability of an overseas launch followed by survival in the habitats of the islands they reach, which are similar to the marginal habitats from which they departed.

When such a preadapted species colonizes a more distant or smaller island, it encounters smaller ant faunas. The species then often experiences what I have called "ecological release." This means that its populations, in addition to holding the beachhead (so to speak), are able to spread inland and occupy habitats less well filled by potential competitors than in the more species-rich islands from which they came. By moving into central habitats, including lowland and mid-mountain rainforests of the interior, the colonies adapt to new conditions. In time they diverge sufficiently to be called a different race or species. During speciation and adaptive radiation, the colonist clades sometimes also generate new, endemic species adapted to the marginal habitats, and the taxon cycle is set to begin again.

By the time I had finished this first round of research on Melanesia I was a nesiophile, if I may be allowed to coin a term. Nesiophilia, the inordinate fondness and hungering for islands, may be a genetic condition. But, whether hereditary or not, I believe it is shared by many, if not all, who gave lectures at the 2007 island biogeography symposium held at Harvard. Even today, over fifty years following my early visits to Cuba and the South Pacific, I continue sporadic field research on the ants of the West Indies, as much just to visit islands as to conduct scientific research.

The Species Equilibrium

In 1959 I met Robert H. MacArthur, a powerful and charismatic intellect and a naturalist of the first rank. Robert, as he preferred to be called, died of cancer in 1972 at the very premature age of 42, when he was at the height of his productivity. All who know his work will agree it was a huge loss for both ecology and evolutionary biology (see figure 1.3). We became friends, and one of our common concerns was the growing decrepitude of our specialties (as we saw it), in dismaying contrast to the newly triumphant emergence of molecular biology. Ecology and evolutionary biology seemed like the aforementioned rhinos and archaic carnivores, surrendering university chairs and grants to the new wave of biologists coming out of the physical sciences. It was clear in the 1960s that their achievements were to be the hallmark of twentieth-century biology.

Figure 1.3. Robert H. MacArthur (left), with Richard Levins during visit with E. O. Wilson, Dry Tortugas, Florida, 1968.

Being both ambitious and purpose-driven, we soon narrowed our conversations down to the following question: How could our seemingly old-fashioned subjects achieve new intellectual rigor and originality compared to molecular biology? What can we learn from molecular biology on how to advance our own science? We agreed that the basic problem was that ecology and evolutionary biology were still mostly unrooted. They needed foundations from which explanations can be developed bottom-up. Theory has to work from lower to higher levels of biological organization. Either alone will not do. Population biology was the discipline we thought could serve as base to reinvigorate the theory of ecology and evolutionary biology. (Such was the line of reasoning by which I later produced the first syntheses of sociobiology, in *The Insect Societies,* in 1971, and *Sociobiology: The New Synthesis,* in 1975.)
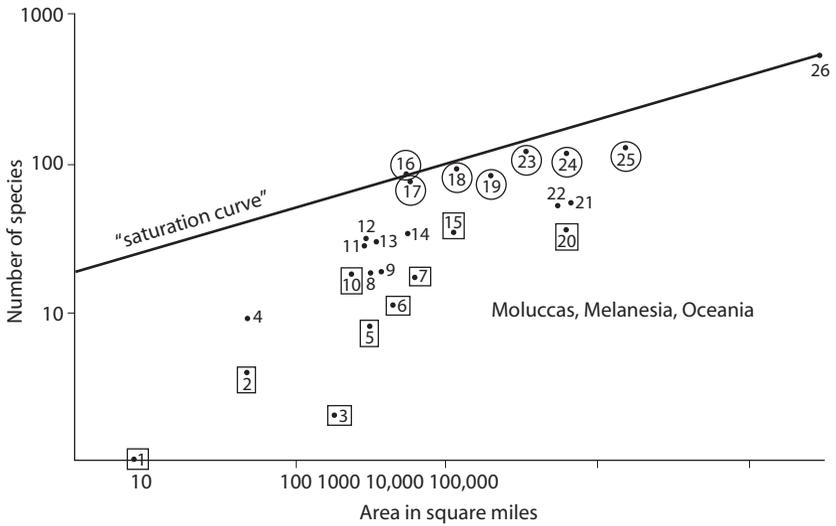
Figure 1.4. Area-species curves, birds, showing areas and distance effects (MacArthur and Wilson 1967).
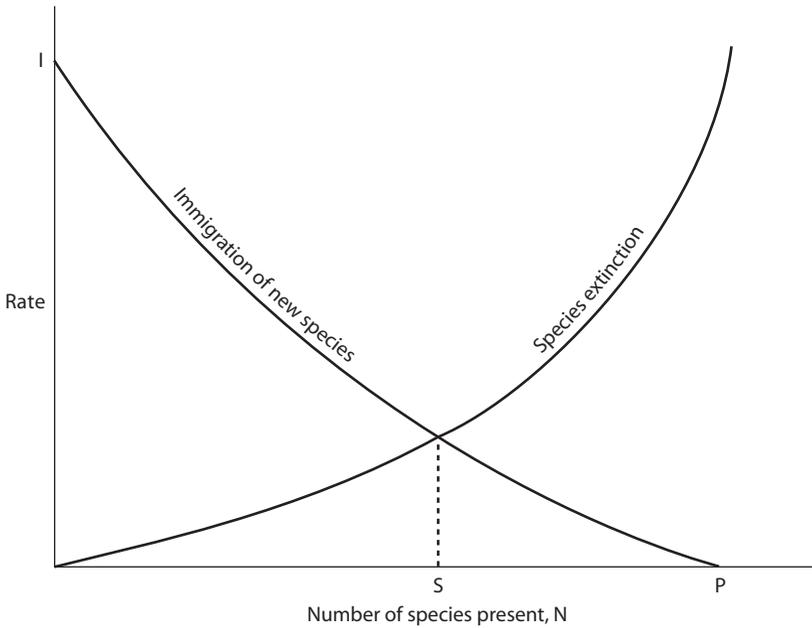
Figure 1.5. Crossed immigration and extinction curves, with the changing intersections (equilibria) predicting the area and distance effects (MacArthur and Wilson 1963).

During our first meeting in early 1960, I urged the prospect of island biogeography on MacArthur. Islands are the logical laboratories of biogeography and evolution, I said. There are thousands of them, for example the Ten Thousand Islands of Florida Bay. There are vast arrays of at least partly isolated faunas and floras living on them. Each is an experiment awaiting the analyses of evolution and ecology.

I showed MacArthur a set of area-species curves I had collected, including one for the ants of Melanesia. With echoes of Matthew, Darlington, and the taxon cycle in my head, I conjured up images of competition, geographic displacement, and equilibrium—in those days we spoke of equilibrated faunas as being "saturated" (equilibrial) or unsaturated (below equilibrium) (figure 1.4). In short time, MacArthur came back with the crossed curves of immigration and extinction rates of species on an island as functions of numbers of species already on the island. Where they crossed was our equilibrium (figure 1.5)!

We were both very pleased with this abstract representation. It seemed the logical portal to the real and complex world of islands and archipelagoes. It invited ideas from population biology, including the demography of growth and decline, the response of populations to density-dependent or -independent factors, and the way species fit together in configurations that allowed more or fewer to coexist. We published the main outlines of what we had found in 1963. Then we began a series of more extensive discussions, mostly by correspondence, about how to tie the processes of immigration and extinction to the data and derivable principles of population ecology and genetic evolution. The result of the back-and-forth was *The Theory of Island Biogeography* in 1967. It was published as the first book of the still flourishing Princeton University Press monograph series on population biology and evolutionary theory.

Experimental Island Biogeography

That was all well and good for the goals we had set, but it was all book work, and talk. Waves of nesiophilia still washed over me. I yearned to keep up what I enjoyed in Melanesia, by physically exploring faunas, especially ant faunas, from island to island. But I couldn't go back to Melanesia due to the long visits required. I was now married with a teaching job at Harvard. So I conceived the idea of a natural laboratory of island biology, close to home, where experiments in biogeography and ecology could be performed and then monitored during frequent but relatively brief periods. I had an advantage in choosing that option: I studied insects. Insects and other arthropods are relatively very small and live in large populations that inhabit very small places. Therefore the

islands could be relatively small, and the generation times of the inhabitants could be expected to be conveniently short.

Beguiled by this dream, I pored over maps of islands, particularly very small islands forming micro-archipelagoes, that lie all around the Atlantic and Gulf coasts of the United States. Soon I hit upon the Florida Keys as the logical place to go. That choice was made easier by the fact that much of my childhood had been spent on or close to the coasts of South Alabama and the panhandle of Florida. It would be like going home.

The best approach to experimental island biogeography, I thought, would be to start with many islets that are ecologically similar but vary in area and distance, then turn them into miniature Krakatoas. That is, find a way to eliminate the faunas and then follow the process of recolonization. If the islands were small enough, they would have resident breeding populations of insects and other arthropods, but constitute no more than a small part of the home ranges of birds and mammals. And if the islands were numerous enough, or at least if their natural environments were sufficiently transient, the experiment would have no significant effect on the island system as a whole. In other words, it should not scandalize my fellow conservationists.

The site I first picked was the Dry Tortugas, at the very tip of the Florida Keys. In the summer of 1965, with a small group of graduate students, I visited all of the smallest of these islands and identified the meager array of plants and arthropods on them. The idea was to continue the process until a hurricane wiped the islands clean, then observe their subsequent recolonization by plants and arthropods. I knew that we might have to wait for several years for such a storm to pass over. Providentially, in the 1965 season not one but two hurricanes swept the Dry Tortugas. When we returned in 1966, we found the smallest islands bare of the terrestrial life we had observed just months earlier. Our study could then begin.

However, by this time I had grown dissatisfied with the prospects for these particular miniature Krakatoas. There were too few such islands, the faunas and floras seemed too small, hurricanes were too few and unpredictable, and there was no way to run controls.

So I next turned to the red mangrove islets of Florida Bay. They had none of the shortcomings of the Dry Tortugas. But they did have one large disadvantage: hurricanes would not be able to strip away all the arthropods from the dense mangrove foliage. That had to be done as part of the experimental procedure. At this point Daniel S. Simberloff, who had begun his doctoral studies under my direction, joined me in the enterprise. The year was 1965.

Figure 1.6. Mangrove islet covered by rubberized nylon tent for fumigation (1968).

Dan and I quickly became colleagues more than student and teacher (after all, we were trying something completely new). We chose the islands that seemed most favorably located and visited them to be sure of their suitability. Next we set out to meet two daunting goals: first, locate a professional exterminator who would undertake the admittedly bizarre job of eliminating all the arthropods without harming the vegetation; and second, line up the help of the few systematists able to identify, to the species level, the beetles, bark lice, moths, spiders, mites, and other arthropods of the Florida Keys.

After a lengthy search in the Miami area, we turned up one professional exterminator, Steve Tendrich, who was intrigued by the eccentricity of the project and willing to take the job. After Dan and I had surveyed the arthropods on one of the islands ("E1"), Tendrich sprayed it with a short-lived insecticide. Our follow-up survey revealed that all of the arthropods on the surface had been eliminated, but a few still survived in the beetle burrows of the branches and stems. Tendrich then turned to fumigation with methyl bromide, a gas that dissipates rapidly after application. He experimented with cockroach egg cases and red mangrove saplings to determine the dosage strong enough to kill resistant arthropods but not so strong it would harm the mangrove (figure 1.6). We then proceeded to census four more islands, "defaunate" them, and begin the

Figure 1.7. E. O. Wilson, in red mangrove tree with osprey nest, Florida Keys, 1968.
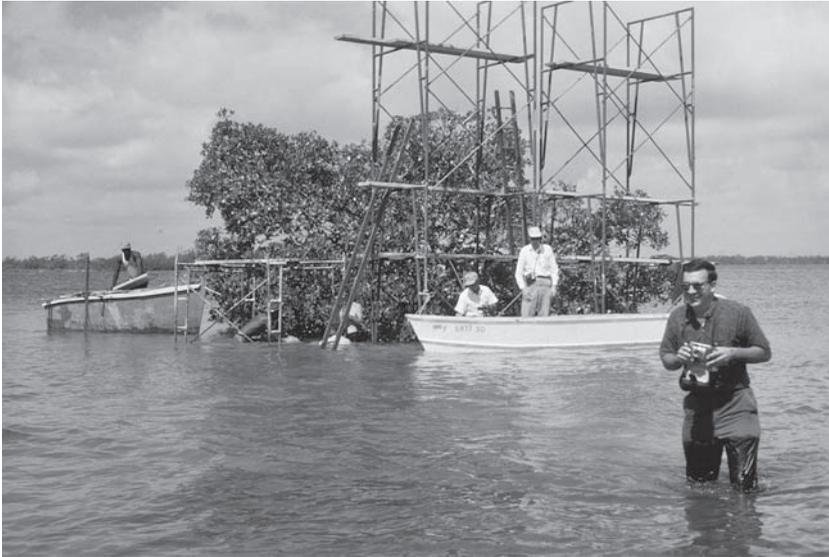
Figure 1.8. Daniel Simberloff, near E7, October 10, 1966.

monitoring process (figures 1.7 and 1.8). After a successful start, Dan began the grueling process of monthly centimeter-by-centimeter inspection of each island, while I managed the process of consulting the taxonomic experts who could identify the arthropod species (Simberloff and Wilson 1969).

Within two years, the numbers of species on all the islands had returned to their preextermination levels. The most distant island (E1), which began with a low number as expected, returned to its same low level. Thus the existence of species equilibria was demonstrated. To an amazing degree, however, the composition of the species differed from island to island, and on the same island before and after defaunation (Simberloff and Wilson 1971). Also, the rapidity of the recolonization and the extensive and frequent turnover of most species, were consistent with the basic MacArthur-Wilson equilibrium model applied to small islands. Finally, the protocols for individual species and groups of species revealed important details of the natural history of colonization. For example, spiders arrived early, in many cases almost certainly by ballooning with silken threads, but suffered rapid turnover. In contrast, mites generally arrived later and persisted with less turnover.

Epilogue

I am very pleased that the research I have recalled here has not become entirely obsolete, yet it has been greatly exceeded during the ensuing four decades in ways I could not have imagined. What we found and said in the 1960s appears to be generally true, and that is the best for which any scientist can ever hope.

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