HISTORY OF INSULAR ECOLOGY AND BIOGEOGRAPHY

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Summary

In ancient times, belief in spontaneous generation and divine creation dominated thinking about insular biotas. Weaknesses in these theories let to questioning of those ideas, first by clergy and later by scientists, culminating in Darwin's and Wallace's postulation of evolution through natural selection. MacArthur and Wilson presented a dynamic equilibrium model of insular ecology and biogeography that represented the number of species on an island as an equilibrium between immigration and extinction rates, as influenced by insular sizes and distances from mainlands. This model has been tested and found generally true but requiring minor modifications, such as accounting for disturbances affecting the equilibrium number. There has been basic controversy as to whether insular biotas reflect deterministic or stochastic processes. It is likely that neither extreme is completely correct but rather the two kinds of processes interact.

1. Ancient and Medieval Concepts: the Birth of Insular Biogeography

Attempts to understand the biodiversity of islands have been central to the elaboration of theory in evolution, ecology, and biogeography. The problems of how animals and plants reached such isolated places and how and why they differed from mainland species have long intrigued biologists. Following is a brief summary of this quest for knowledge.

Greece, containing an archipelago as well as being the birthplace of Western science, was a suitable environment for pondering questions of insular dynamics. Some of the early Ionian and Eleatic natural philosophers concluded that individual organisms were formed spontaneously from generative forces residing in such elemental matter as air, water, fire, or earth (mud, slime). Aristotle (384–322 BC) adhered to this view for some animals although he also understood sexual reproduction as the means of procreation of other kinds. The theory of spontaneous generation was compatible with insular distributions; presumably it would be as easy for organisms to generate from mud on an island as on a mainland. Aristotle's prestige was so great that the theory of the spontaneous generation of life enjoyed wide acceptance for centuries and even found adherents as late as the nineteenth century.

A second ancient view of life, the Judeo-Christian doctrine, considered life to have originated by divine creation. All terrestrial life was purported to have been subsequently destroyed by a worldwide flood except for representative breeding pairs that survived in an ark that settled on Mt. Ararat, from which single locality the entire world, presumably including islands, was repopulated.

Little attention was directed specifically to insular distributions in the nearly two millennia following Aristotle, except for the theories propounded by the Christian theologian St. Augustine in the early third century. He, like many subsequent Western philosophers, subscribed eclectically to an amalgam of Aristotelian and Judeo-Christian views. He did not consider the insular distributions of lower animals to be a problem because, like Aristotle, he believed they could spontaneously generate, as a kind of ongoing response to God's initial command that the earth should bring forth the living soul. He considered human transport of favored hunting species as likely. Those that did not fall into either of these categories he postulated were distributed to islands by angels under divine command.

Little interest in insular biogeography was expressed subsequently until the nature of the world's biota began to be recognized following the voyages of discovery begun by European explorers in the latter part of the fifteenth century. Joseph Acosta in 1590 in his *Historia Natural y Moral de las Indias* questioned traditional interpretations and attempted a refutation of St. Augustine's views on dispersal mechanisms. Milius in his treatise *De Origine Animalium et Migratione Popularum* in 1667 grappled with the riddle of how peculiar kinds of animals dispersing from Mt. Ararat could reach distant continents and islands without leaving descendants of like nature at the starting point or *en route*. He reverted to spontaneous generation for terrestrial animals and birds, with each kind taking their origin from the generative qualities of the particular lands in which they are found, and shored up his argument by quoting Genesis 1:24: "Let the earth bring forth the living creatures after its kind."

Curiously, the idea of evolution seemed to have first occurred to a Benedictine monk, Don Calmut, in the eighteenth century. The limited capacity of the ark, in the face of the great biodiversity that was being discovered, prompted him to suggest that the creation of life was followed by diversification of the original species into various forms. He proposed that similar species of a general kind (perhaps equivalent to a modern genus or family) were represented in the ark by only one original species, thereby reducing the accommodation requirements considerably. He believed that each of these general kinds of animals later gave rise to a number of variants (modern species) after the waters of the flood subsided.

2. Darwin and Wallace: the Dawn of the Modern Era

Although objective scientific investigation had begun to develop during the period of geographic exploration, and some theologians were exploring alternative views, philosophical thought continued to be dominated by Christian dogma. Not only was there militant objection to mechanistic explanations but the very prevalence of ecclesiastic thinking stifled enquiry. Nevertheless, as advances in knowledge accumulated and evidence became overwhelming, bold new theories were proposed and defended, not only against attacks from fellow scientists, who rightly demanded rigorous support for new interpretations, but against the onslaughts of a clergy and a public unwilling to consider alternatives.

The geologists and biologists of the nineteenth century forged the modern basis of insular biogeography, especially those two great, traveling naturalists Charles Darwin and Alfred Wallace. Their studies of insular life played a pivotal role in their elaboration of natural selection as the agent of biological evolution.

Although Darwin and Wallace presented an initial synopsis of the theory of evolution in a joint, brief essay, the main exposition occurred in Darwin's definitive sixth edition of *The Origin of Species* in 1872. In that treatise, Darwin drew a number of conclusions that serve as the foundation of modern insular biogeography. Some of these were Darwin's original ideas, others he gleaned from other sources, but the synthesis is his. They can be summarized and paraphrased as follows:

1. Insular biotas are depauperate (islands have fewer taxa than an equivalent area of mainland).
2. The composition of insular and mainland biotas is often different.
3. Endemism is high among insular biotas.
4. Overwater dispersal is an important consideration in insular biology.
5. Certain taxa are absent from islands because of their inability to disperse across seawater barriers.
6. A population isolated on an island may diverge under the pressures of natural selection from mainland populations and eventually speciate: the changes that occur on islands are adaptive.
7. Insular taxa are often more closely related to those of a nearby island or mainland than to those from more distant regions. The degree of divergence varies among taxa.
8. Competitive interactions may influence the evolution of insular faunas.

Wallace's views, as expressed in the 1895 revised edition of *Island Life*, were similar to those of Darwin. Indeed, one could illustrate the above list of conclusions almost equally well by quotations from *Island Life* as from *The Origin of Species*. In summary, both naturalists believed that insular biotas resulted from evolutionary divergence of species isolated on islands after some dispersal event, with the degree of divergence related to distance from the source, and speciation ultimately leading to endemism; the number of species present and the nature of the biota were believed to reflect interspecific differences in dispersal ability and competitive interactions. All these ideas have a modern flavor, and indeed, they are all still part of current insular biogeographic theory, albeit some of them controversially so (see below).

Both Darwin and Wallace realized that there were minor geological changes in the configuration of land and water. However, they both discounted continental drift and were firmly convinced that the major outlines of the continents and oceans were permanent. Consequently, they considered dispersal to be either across sea barriers, or via temporary land connections. Most biogeographers in the century following the appearance of Darwin's and Wallace's books shared an opposition to continental drift, and argued among themselves as to whether land bridges or dispersal over water best explained particular distributions. Only when the mechanism of continental drift was elucidated by geologists in the latter half of the twentieth century was that theory widely accepted by biologists and included in their repertory of explanations for distributional patterns.

3. Genetics and Insular Biogeography

The nature of heredity was not understood in Darwin's and Wallace's day and although they knew that traits were inherited, they did not know how. Consequently, they were unable to couch evolution in general, and speciation on islands in particular, in genetic terms. A significant later advance in the understanding of insular biotas has been identification of the mechanisms of divergence in populations on islands. It is beyond the scope of the present treatise to present a detailed account of this broad topic. However, two important processes enhancing divergence of insular populations from their parent, mainland one should be mentioned. One is genetic drift. In small populations, such as those occurring on small islands or during the early colonization of bigger ones, random changes in gene frequencies can become established that would be swamped in larger populations. These may or may not be adaptive and such small populations can diverge in ways that would not necessarily be predicted in adaptive terms.

Another important feature, known as the "founder effect," is that those few colonists reaching an island do not carry the full range of genetic potential of the entire parent population, but rather only a subset of it. There is thus a genetic bottleneck and immediately the founder population differs genetically from the parent one.

Genetic drift and the founder effect both can enhance divergence of small, isolated populations. They both result in altered genetic constitutions upon which insular selective forces can then operate in leading to local adaptation.

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Biographical Sketch

Harold Heatwole received a Ph.D. in zoology from the University of Michigan in 1960, based on a thesis dealing with herpetology. His first academic appointment was at the University of Puerto Rico where he carried out a study of the herpetofauna of the islands of the Puerto Rican-Virgin Island archipelago. This stimulated an interest in insular biogeography and community ecology generally and he broadened his studies accordingly. Upon immigrating to Australia in 1966, he transferred his research interests to the islands of the Great Barrier Reef. He earned a second Ph.D., this time in botany, and from the University of Queensland with a dissertation on “Some Aspects of Phytogeography and Vegetation Dynamics of Islands of the Great Barrier Reef.” His study of islands has also taken him to various Pacific localities, Indonesia, the small offshore islands of New Guinea and to most of the subantarctic islands. Of his total of 290 scientific publications, 52 deal with islands, including two books: *A Coral Island* and *Community Ecology of a Coral Cay*, the latter co-authored with T. Done and E. Cameron. He is currently a professor at North Carolina State University.