Meetings

Adaptive Aspects of Insular Evolution

Explosive evolution, adaptive radiation, gigantism, dwarfism, flightlessness, and development of unusual diets or habits—these are but a few of the lures which islands have long extended to the biologist. Visibly discrete, simpler than continents or oceans, numerous enough to provide natural replications for testing hypotheses, islands have contributed to evolutionary theory much of its clearest documentation and to biogeography comprehensible views into some of the principles behind the seemingly infinite complexity of mainland distributional systems.

Most past research on insular biotas has been taxonomically and historically oriented. In recent years, however, ecological questions have moved into the forefront, and it is beginning to appear that islands may prove to have the same decisive influence in the development of ecological theory as they have had in evolutionary theory. They are extraordinarily suitable for studies of environmental aspects of evolutionary processes: dispersal, colonization, adaptation, competition, and extinction. Aspects of these processes are currently being studied by botanists, zoologists, geneticists, ecologists, and evolutionists throughout the world.

The theme "Adaptive Aspects of Insular Evolution" thus seemed particularly fitting for the Third International Symposium sponsored by the Association for Tropical Biology, Inc. (ATB). With the assistance of a grant from the National Science Foundation the meeting was held on a tropical island, Puerto Rico, at the University of Puerto Rico at Mayagüez, 15–19 June 1969. For the symposium program, Ernst Mayr (Harvard University's Museum of Comparative Zoology) assembled participants representing a wide spectrum of disciplines.

The contributions of nearly every speaker related, in one way or another, to MacArthur and Wilson's island equilibrium model or other aspects of their *Theory of Island Biogeography* (1967). However, as Mayr pointed out, a strategy integrating predictive mathematical theories with traditional comparative field studies appears most likely to yield new insights into the complex phenomena underlying insular evolutionary processes. In addition, the problem of comparing phenomena in one taxon to those in another was recurrent throughout the symposium and generated much discussion.

Sherwin Carlquist (Rancho Santa Ana Botanic Garden) and Terrell H. Hamilton (University of Texas) first broadly outlined factors responsible for characteristics of island floras and faunas, respectively, effectively setting the tone for the conference. Carlquist compared floral components of the Canary and Hawaiian islands, both of whose endemic elements reveal a marked shift toward long-lived and arborescent forms. He also noted several other tendencies exhibited by island floras, including fruit gigantism (paralleling flightlessness in birds and insects), lack of sterility barriers, and hybridization. Hamilton discussed the relative importance of area, elevation, and isolation in predicting the number of bird species occurring on an island; island size (area) was found to account for about 75 percent of the variation.

G. Ledyard Stebbins (University of California, Davis) discussed the use of polyploidy in determining phylogenetic relations of insular floral elements and in estimating the relative age of insular groups as compared to their continental relatives. His data suggest that polyploidy probably facilitates island colonization (polyploids tend to be pioneer species) rather than island conditions favoring production of polyploidy subsequent to arrival and colonization.

The remarkable radiation of *Drosophila* on the Hawaiian Islands was subject of an interesting presentation by Hampton L. Carson (Washington University, St. Louis). The present 650 to 700 species—most morphologically very distinctive and often strongly sexually dimorphic—exhibit extremely high endemicity, with only 3 percent of the examined species occurring on more than one island. Although all Hawaiian *Drosophila* have the same chromosome number, comparative studies of chromosome banding patterns by Carson and his co-workers have yielded detailed chromosome phylogenies of the Hawaiian fauna. A reconstruction of the history of *Drosophila* speciation shows multiple colonization and recolonization; his data also indicate that successful founders of new species populations are likely to be chromosomally monomorphic. Although morphologically distinct, some closely related sympatric species have identical chromosomal banding patterns. This is unusual in *Drosophila*, where speciation normally coincides with a considerable amount of chromosomal repatterning.

Dispersal and colonization studies on plants were the central topics of four speakers. Olov Hedberg (University of Uppsala, Sweden) reported on the alpine flora of African mountains, which exhibits striking adaptations to the extreme daily temperature fluctuations, with "summer every day and winter every night." By contrast, "alpine" plants of the dwarf "elfin forest" on the highest elevations of Puerto Rico are exposed to an almost constant environment of high rainfall and nearly continual cloud cover; this unusual floristic community was discussed by Richard A. Howard (Harvard University). The constant cloud cover and the high density of epiphytes apparently reduce the photosynthetic capacity of the plants by about 50 percent. Additional unusual characteristics include much damage by insects, very low annual increment of new leaves, and low reproductive success. For example, over a 3-year study period, *Tabebuia* plants produced flowers every day of the year, but mature fruit never appeared. Apparently, reduction division in meiosis fails to occur in this species unless flowers are exposed to at least five straight hours of sunshine—a rare occurrence in the elfin forest.

Bassett Maguire (New York Botanical Garden) discussed the composition, endemicity, and adaptation of the isolated mountain floras of the Venezuelan Guayanan highlands. The flora of these summits was apparently derived from the broader lowland flora at a very early time and maintained its integrity to the present, with very little intermountain transfer of floristic elements. Following Maguire's talk, discussion

centered about the question, "Why does a flora stay more or less intact over long periods while faunas in the same area often show a complete turnover?" Several speculations were advanced, and parallels from other regions were noted. Mayr observed that plants normally disperse as "babies," while most terrestrial animals disperse as "adults," an important difference in biogeographic studies.

Rolla M. Tryon (Harvard University), speaking on oceanic island fern floras, noted that the widespread species (in the source area) colonize most successfully. High dispersability due to self-fertile gametophytes plus production of large numbers of minute spore propagules means that presence or absence of a given fern species in an area more likely reflects a difference in adaptation range than in dispersal ability. Ferns on islands characteristically show only low levels of endemicity, and, where endemics occur, they tend to be related to very localized continental species.

Commenting upon their special advantages in biogeographic studies, Ernst Mayr (Harvard University) spoke about island birds, particularly distributional aspects relating to the equilibrium model. Taking issue with MacArthur and Wilson that "saturation implies equilibrium," Mayr pointed out that the two may well be different. The saturation number of species, defined by Mayr as "the level the species would reach if there were no dispersal bottleneck," appears higher than the equilibrium number. In addition, the reservoir of successful immigrants from the mainland is probably more limited than models tend to assume, and turnover in island faunas may be far more important than previously thought. Other discussants felt that dispersal, even to remote islands, was sufficiently high to assure that saturation was reached.

Colonization and extinction in diatom floras were discussed by Ruth Patrick (Academy of Natural Sciences of Philadelphia). Using sterile glass slides of known areas as "islands" and varying invasion rates (by controlling flow of new water over the slides), Patrick has obtained some of the few experimental data bearing upon F. W. Preston's truncated lognormal species-abundance curves and MacArthur and Wilson's equilibrium model. Field comparison of chemically similar streams on islands and continents revealed diatom floras to have fewer total species, fewer rare species, and greater fluctuations in population size on islands. Island streams (and lakes) tend to be much more rigorous and variable than their continental counterparts, and their flora is less finely adapted. With diatoms, invasion rate is more important than area in predicting number of species, and isolation from the nearest species source area with similar conditions (that is, water chemistry) is more important than absolute distance. One fact clearly illustrated by Patrick's work was that biologists must be careful to relate their concept of "area" to the size and needs of the organism under consideration—a slide with an area of 625 mm^2 can easily support a diatom community of over 100 species!

Selected characteristics of shallow water marine invertebrate faunas and quantitative studies of niche utilization in the carnivorous marine snail *Conus* were the subject of Allen J. Kohn (University of Washington). *Conus* occurring on relatively smooth limestone intertidal benches had less species diversity, higher population densities, and more specialized diets than those found on the patchy coral reef substrates. Niche overlap values based on R. Levins' model revealed that theoretically more species of *Conus* could coexist in both habitats, at least in terms of the food parameter.

Two presentations concerned studies of *Anolis* lizards, which have undergone major and complex radiation in the West Indies and which form an important component of their fauna. In an historical view, Ernest E. Williams (Harvard University) presented highlights of his 10 years of investigation into the evolution and ecology of the West Indian *Anolis*. Of special interest was his review of chromosome analyses which have formed the basis for reconstruction of the various island invasion patterns resulting in the present distribution of this lizard. Thomas Schoener (Harvard University) then discussed his recent quantitative field studies on habitat shifts by *Anolis*. Dealing primarily with the spatial and food habit dimensions of the niche, he summarized data demonstrating the importance of perch height and perch diameter as predictive parameters. Reviewing the occurrence of various combinations of terrestrial and arboreal species on different Caribbean islands, Schoener discussed possible theoretical constraints upon the phenomenon of horizontal release (niche expansion) in *Anolis*. One finding of particular note was that on different islands the same species often shifts in entirely different directions; indeed, even within a species, the two sexes were found to expand differently on different islands.

Island colonization and subsequent ecological shifts were also the subject of three additional interesting talks. Philip J. Darlington, Jr. (Harvard University), characterized carabid beetles reaching the West Indies as typically small (less than 12 mm), winged, and frequently associated with fresh water; following arrival, a high percentage became flightless, particularly those occurring at higher elevations. The differential colonizing success of hydrophilic forms led to discussion of the point that an island may be considered at the same time to be "remote" for some species but very "near" for others, depending upon the ecological requirements of the organisms under consideration. Discussing his recently published work on the origin and evolution of Tasmanian birds, Allen Keast (Queens University, Kingston, Ontario) then addressed himself to the question of what happens when an invading species finds a previously unoccupied adaptive zone. Of 40 Tasmanian species, half show evidence of ecological shift; this is an especially striking result when one considers that this continental island is separated from the Australian mainland by only 130 miles and was rather broadly connected during the Pleistocene. Elwood C. Zimmerman (Bernice P. Bishop Museum, Honolulu), whose *Introduction to the Insects of Hawaii* (1948) has stimulated so much fruitful research on that unique fauna, commented on selected cases of adaptation in Hawaiian insects. He concluded with an urgent plea for more study of delicately adapted species on islands everywhere, especially Hawaii, before it is too late.

At the ATB business meeting, publication of the first issue of the Association's new journal *Biotropica* was rereported, with William L. Stern (University of Maryland) as editor. Plans for the Fourth International ATB Symposium, with Betty J. Meggers (Smithsonian Institution) as program chairman, were announced. To be held in Ghana in early 1971, the symposium will focus on comparative aspects of the evolution of Amazon and Congo tropical forest ecosystems.

The symposium lectures, to be edited by José A. Ramos (University of Puerto Rico at Mayagüez), will be published by the University of Puerto Rico.

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