Biological Journal of the Linnean Society (1986), *28:* i–iii

Introduction

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Studies of the island biogeography of organisms have played a prominent role in the development and maturation of evolutionary biology since the time of Charles Darwin and Alfred R. Wallace; indeed, scarcely a textbook on general biology or evolution is published that does not comment on the historical importance of these studies. This prominence is based on the fact that island faunas serve as simpler and more tractable models for the more complex interactions among organisms on continents. By studying a world in miniature, we can come to recognize patterns and processes in the world at large.

A second, very striking aspect of island biogeography is that its importance to theoretical biology has not diminished in the 125 years since Darwin and Wallace made their seminal contributions. Early studies by Darwin and Wallace falsified many of the claims of the creationists of that day, paving the way for the tremendous expansion of evolutionary biology that followed. At the turn of the century, island studies helped to document the ubiquity of variation among populations, which ultimately led to the abandonment of typology and the acceptance of polytypic species. In the 1930s and 1940s, studies of insular variation contributed to development of the biological species concept and to the 'Modern Synthesis'. In the 1960s and 1970s, the equilibrium model of MacArthur and Wilson brought about a revolution in the way discontinuously distributed (insular) faunas were viewed, by synthesizing the current ecological theory with island biogeography. Beginning in the 1970s, vicariance biogeography combined plate tectonics with rigorous methodologies for investigating higher-level phylogenetic relationships, thus adding greater resolution to the time component of biogeographic analysis.

Throughout this period, studies of mammals have figured prominently, perhaps because their enormous range in vagility make mammals particularly apt subjects for biogeographic research. Wallace based many of his conclusions

0024-4066/86/050001+03 $03.00/0

on independent and parallel radiations of mammals in different parts of the Malaysian and Australasian regions; Matthew considered only mammals in his classic studies; Simpson wrote extensively on the mammal faunas of island-continents; several very prominent early studies of the equilibrium model utilized mammals; and many of the best examples of vicariance biogeography are based on studies of mammals.

In spite of the continuing contribution of studies of mammals to island biogeography, there has been no attempt at a synthesis of recent research; most symposia and published volumes on island biogeography have focused on given groups of islands (e.g. the California Channel Islands (Power, 1980), the Galápagos (Berry, 1984), and the Gulf of California islands (Case & Cody, 1983)), or have taken a very broad, and often generalized perspective (Williamson, 1982; *Oikos* special issue, 1983). Few recent studies have dealt comprehensively with a limited taxonomic group (but see the classic book on the birds of Jamaica by Lack, 1976).

In 1983, one of us (Heaney) was invited to organize a symposium on island biogeography of mammals for the International Theriological Congress to be held at the University of Alberta in August 1985. This was gladly accepted as a perfect opportunity to assemble a group of people who could provide a broad synthesis of the current state of mammalian island biogeography. Plans began immediately for publication of the papers from the symposium, with Patterson enlisted as co-editor. Astonishingly, we have been able to keep to the schedule we set for ourselves, but only with great assistance from the editors of the *Biological Journal of the Linnean Society* and Academic Press. All but two of the papers in this volume were presented at the symposium; those two were added to round out our coverage. Thus, most of the authors have had many opportunities to discuss and refer to each others' papers, and the result is a volume that is much more fully integrated than is typical for collections of papers.

The organization of the volume follows a flow from papers emphasizing short-term, primarily ecological perspectives to those with long-term, systematic and genetic perspectives. The final paper provides a summary and synthesis for the entire volume, and also includes comments on how the principles developed here can be extended to global phenomena.

In organizing the symposium and this volume, we have encouraged the contributors to combine theoretical and empirical approaches, with an emphasis on thorough documentation and empirical demonstration of patterns and processes. We believe that this has led to new insights by leading us to ask questions that have been previously unrecognized or glossed over. It has also caused us to search for new methods and techniques for measuring phenomena that we have found to be of importance. Examples of these new methods are Lomolino's procedure for determining the influence of interactive effects of extinction and immigration, Patterson and Atmar's procedure for determining 'nestedness' of faunas within archipelagos, and Heaney's use of middle Pleistocene landbridge and oceanic islands to derive quantitative estimates for very long-term rates of colonization, extinction and speciation.

Some of the results of these studies are worthy of emphasis. Demonstrations by Lomolino and Hanski of the frequency of colonization of non-volant mammals to near-shore islands provide dramatic documentation of the

colonization potential of seemingly poor dispersers under ideal conditions. These provide the background for Crowell's unique measures of turnover rates, based on his 20-year studies along the coast of Maine. Patterson and Atmar demonstrate that mammal faunas in landbridge archipelagos are very rarely random assemblages, arguing that constituent faunas are typically nested subsets of the source fauna that are produced by selective extinction. Newmark evaluates area and habitat diversity as correlates of species richness in western North American parks, and concludes that area itself is the best predictor of the success of a reserve in protecting mammal populations. In an important contribution to a long-standing debate, Lawlor demonstrates empirically the biological significance of species–area slopes, correctly predicting variation in slopes among numerous archipelagos and taxa. Heaney's measurements of long-term rates of colonization and extinction are the first such estimates for mammals, and his demonstration of the importance of speciation invites a synthesis of equilibrium and vicariance biogeography. Morgan and Woods use a superb fossil record to demonstrate the fluctuation in the rate of extinction among West Indian mammals that has occurred as a result, first, of changing sea level and climate at the end of the Pleistocene, followed by the arrival of Amerindians, and finally by the arrival of Europeans and *Rattus rattus*. Berry reviews population genetic studies which indicate that founder effects contribute importantly to insular evolution. Finally, in his summary paper, Brown argues for continued use of the equilibrium model as a heuristic tool *because* of its simplicity and limitations, rather than *in spite of* them; he also argues that, on the basis of data presented in this volume, the major processes of island biogeography are highly deterministic, and therefore amenable both to further study and to prediction.

All of the authors recognize that we have raised more questions than we have answered; we take this as evidence of the fertility of the field in which we are working, and the promise of future returns on these research efforts. We expect some of our conclusions to be controversial, and we welcome the increased level of interest and research that we hope will follow.

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