BOOKS: ECOLOGY

Island Biogeography Redux, with a Speciation Twist

Bruce M. Beehler

On my first ornithological sojourn in the Southwest Pacific, in the mid-1970s, two books served as intellectual beacons: Ernst Mayr's *Population, Species, and Evolution* (*1*) and Jared Diamond's *Avifauna of the Eastern Highlands of New Guinea* (*2*). Mayr's work provided brilliant insight into the phenomenon of geographic speciation and presented many trenchant examples from birds of the southwest Pacific. Diamond's monograph offered a bold MacArthurian synthesis of how a rich tropical avifauna evolved into a series of ecologically complex communities. To a young field biologist, these books were theoretical treasure troves, enhanced with empirical support drawn from the rainforests of the Pacific.

The Birds of Northern Melanesia Speciation, Ecology, and Biogeography
by Ernst Mayr and Jared M. Diamond
Oxford University Press, New York. 2001. 528 pp. $55. ISBN 0-19-514170-9

Now, in *The Birds of Northern Melanesia*, Mayr and Diamond present their most recent thoughts on the evolution and distributional ecology of the avifauna of their favorite ornithological region. The book is the culmination of the authors' long-term interest in these topics. Mayr first visited the region in 1929 and has written more about it than any other ornithologist. Diamond has gathered data during 19 expeditions since 1964. The volume itself has a long history; I read of it as a work-in-progress more than 20 years ago.

Northern Melanesia comprises a breathtaking range of islands: large (up to 35,742 km^2) and small (down to 0.002 km^2); high (with mountains reaching 2951 m) and low (near sea level); and of volcanic, metamorphic, and coralline compositions. It includes the Bismarck Archipelago (dominated by the great "oceanic high islands" of New Britain and New Ireland), the Admiralty Islands (of which Manus and St. Matthias are the largest), and the Solomon Islands (perhaps the most complex island assemblage on Earth). Despite this variation, the islands share similar climates and habitats. Ornithological surveys of approximately 200 islands (with most of the important ones surveyed repeatedly) have determined the birds' altitudinal and ecological distributions. The avifauna is diverse but not so rich as to be overwhelming, and it has remained relatively unchanged in modern times (with few extinctions and only one widespread introduction). Thus the region is, to Mayr and Diamond, a nearly perfect natural laboratory of allopatric differentiation and adaptive radiation. In their book, the authors attempt to resolve some of the unanswered mysteries of vertebrate speciation through an exhaustive investigation of the current distributional patterns exhibited by Northern Melanesia bird populations.

The foundation for the treatise is a finely honed systematic analysis of the 195 species of land and freshwater birds of Northern Melanesia. The taxonomic appraisal, presented in Appendix 1, is based on Mayr's biological species concept (*3*) and uses "zoogeographic species" as the organizing unit of geographic speciation (*4*). Mayr and Diamond recognize a hierarchy of geographic forms: subspecies (distinguishable populations that are observed or inferred to interbreed), megasubspecies ("exceptionally distinctive subspecies"), allospecies (for populations that are inferred to be reproductively isolated although their distributions do not overlap), and superspecies (for groups of allospecies). The authors determine relationships among taxa from plumage, behavioral, and vocal similarities that they interpret as shared derived traits, although they use Mayrian rather than cladistic methodologies. The approach is much in the spirit of their earlier publications on the systematics of birds of the Southwest Pacific. The distributions of the various species-groups are shown in 52 maps, and 9 color plates illustrate geographic variation and speciation in selected groups as well as the region's endemic genera and most of its endemic species and allospecies.

The 36 brief chapters that make up the main body of the book collectively carry along an orderly disquisition on the origin, dispersal, and geographic differentiation of this rich insular bird fauna. The first few chapters summarize the islands' physical and biological environment and the human impacts on them. The authors examine the effects of the species-area relation and isolation on the number of bird species on islands. They discuss the overwater dispersal ability of individual species and the geographic sources of the avifauna. They analyze current distributional patterns as indicators of speciation mechanisms. And they consider the effects of barriers and endemism on differences among the islands. Other key analyses address the taxon cycle (with its evolutionary sequence of habitat shifts during and after colonization) and the biological species concept. In sum, the book is a treatise on Mayrian geographic speciation as interpreted through the lens of Diamond's significant work on ecological island biogeography.

Mayr and Diamond find that the most prolific speciation has occurred among lineages that support abundant populations of moderately vagile birds; small or nondispersing populations do not speciate. There is a temporal component to this pattern, in that old endemics (species late in the taxon cycle), commonly confined to highland forests, tend to be sedentary and thus have "finished" speciating. Peripheral populations show a tendency toward greater differentiation, but these peripheral isolates rarely speciate back "upstream" into the main range of the lineage. Invasion and speciation tends to radiate out from the species-rich zones into the species-poor zones. Other than these conclusions, overarching generalizations prove elusive, and no new biogeographic rules arise from this exhaustive exercise.

Distinctive denizens. Two monotypic genera are endemic to Northern Melanesia: the large owl *Nesasio solomonensis* **(left)** and the crowned ground pigeon *Microgoura meeki* **(bottom center)**, which was exterminated by cats in the 20th century.

Although Mayr and Diamond do not highlight the point, it must be noted that Northern Melanesia's endemic biota has recently suffered the ravages of unscrupulous commercial logging. In only a decade, this former wilderness has become a threatened hotspot, and its irreplaceable biodiversity faces extinction if extensive conservation actions are not implemented very soon. This book describes an avifauna worthy of preservation.

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Clearly, *The Birds of Northern Melanesia* represents a labor of love by the authors, who sink their teeth into a rich subject. In doing so, they follow the analytic approach that they have previously shown to be so productive. For those who found their earlier works illuminating, this book will be quite satisfying. For those who desire a comprehensive application of novel tools and new evolutionary perspectives, this work will disappoint. Unencumbered by null models, molecular datasets, or area cladograms, it is, nonetheless, fine natural history.

References and Notes

1. E. Mayr, *Population, Species, and Evolution* (Harvard Univ. Press, Cambridge, MA, 1970). This is an abridgement of Mayr's magistral account in (*3*).
2. J. Diamond, *Avifauna of the Eastern Highlands of New Guinea* (Nuttall Ornithological Club, Cambridge, MA, 1972).
3. E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963).
4. E. Mayr, L. L. Short, *Species Taxa of North American Birds* (Nuttall Ornithological Club, Cambridge, MA, 1970).

BOOKS: PALEOBIOLOGY

Changes in Life Across Many Temporal Scales

Richard Bambach

This symposium volume is a first-rate review of conceptual issues related to evolutionary pattern in both neontology (laboratory and field biology using living organisms) and paleontology. The studies range in scale from laboratory experiments on single polyps up to theoretical modeling of taxon-age distributions over time spans of 100 million years. *Evolutionary Patterns* is a festschrift in honor of Alan Cheetham, a distinguished paleontologist who has provided breakthrough insights on patterns of colony formation in bryozoans, documented that careful morphometrics can reveal true genetic species in bryozoa, and demonstrated that speciation patterns in fossil bryozoa fit the model of punctuated equilibrium.

Evolutionary Patterns
Growth, Form, and Tempo in the Fossil Record
Jeremy B. C. Jackson, Scott Lidgard, and Frank K. McKinney, Eds.
University of Chicago Press, Chicago, 2001. 415 pp. $85, £54. ISBN 0-226-38930-8. Paper, $30, £19. ISBN 0-226-38931-6.

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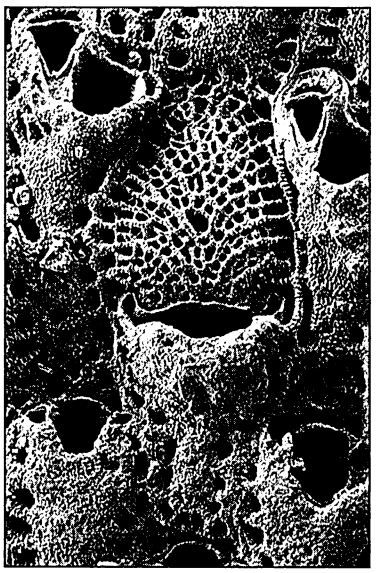
Many of the papers in the volume deal with colonial organisms. The contributions center on three major themes: determinants of colony form; recognition of species and the tempo of speciation and extinction; and macroevolutionary patterns and trends. As is universal with symposium volumes, the writing styles vary (with some papers much more difficult to digest than others). But every chapter contains interesting information, and the book's organization gives more structure to the material than is common for such compilations.

Highlights include the papers by Buss on colony growth in hydroids, Okamura *et al.* on competition versus feeding in determining colony form in bryozoa, Pandolfi *et al.* on the extinction of two Caribbean reef corals, and McKinney *et al.* on differences between diversity and abundance trends in bryozoan evolution. Through a series of clever experimental manipulations, Buss illustrates that some simple hydromechanical conditions influence budding and branching in hydroid colonies. If these signals can be transduced to effect expression of pattern-forming genes, global rules will be responsive to local states. Okamura and colleagues elegantly explain feeding efficiency in bryozoans and predict the distributions of forms under competition for limited space and under various conditions of flow and potential food acquisition. They then test their hypotheses against field data from gradients back into submarine caves. They conclude that the prevalence of spot forms and several zooid types in caves reflects the better adaptation of those forms to low food availability rather than a refuge from spatial competition. Pandolfi and his colleagues document the extinction in the last 80,000 years of two reef coral species formerly common throughout the Caribbean, while the other common Caribbean reef corals persisted. After the disappearance of the "organ-pipe" species of *Montastraea*, one of the dominant modern reef builders (*M. annularis*) developed narrow as well as wide column widths, apparently expanding into the morphospace of its extinct congener. In an expanded version of a study they published with the late Jack Sepkoski [*Science* **281**, 807 (1998)], McKinney, Lidgard, and Taylor review the transition from a predominance of cyclostome bryozoans in the Early Cretaceous to the present-day dominance, in both abundance and diversity, of cheilostomes. Although the shift in taxonomic diversity was nearly monotonic, changes in abundance were not: cyclostomes became more abundant after the end-Cretaceous extinction before declining again. This is an exceptionally elegant demonstration of the need for more complete data in paleontology as well as a warning that one-dimensional analyses may not tell the whole story.



"Punk eek" bryo. The bryozoan genus *Metrarabdotos* shows a pattern of morphological evolution consistent with the punctuated equilibrium model.

CREDIT: ALAN CHEETHAM/DEPARTMENT OF PALEOBIOLOGY, NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION

Two issues that plague communication between neontologists and paleontologists are differences between their approaches in temporal scale and the availability of detailed data. Neontologists generally expect more complete data on organisms than a paleontologist can ever hope to have. For instance, several of the papers in this book discuss cytological features (McShea), experimental manipulation (Buss), and the utility of gene sequencing to identify control genes in development (Buss again) or differences in species (Knowlton and Budd). Paleontologists cannot get such data from fossils. On the other hand, the fossil record provides opportunities for directly observing changes in past life in their historical context on a time scale beyond the few centuries within reach of the neontologist. The 80,000-year gaps between data points in the Pandolfi *et al.* study probably seem huge to most biologists, and clearly they do not let us follow the extinction in detail. But neontologists have never observed the extinction of common reef coral species on any time scale, nor have they been able to see how such an extinction affects the morphology and occurrence of other reef-building corals. The paleontological perspective does both and leaves us with the intriguing question, what could cause such a selective extinction in a complex ecosystem?

With its collection of well-constructed studies of evolutionary issues at all temporal scales, *Evolutionary Patterns* is an excellent example of how neontology and paleontology can and should interface. The book illustrates the point that full understanding of the whole range of evolutionary phenomena requires both neontological and paleontological study.