Diversity: rain forests versus coral reefs


Coral reefs and tropical rainforests are often compared in the ecological and conservation literature as the most biologically diverse communities on earth. It seems appropriate to assess research on these two systems during the past 30 years with reference to the perennial ecological question: Why are there so many species in the tropics? This question has particular relevance now with the rate of destruction of tropical forest species approaching epidemic proportions and with destruction of coral reefs and tropical coastal ecosystems rapidly increasing. Ironically, their fate is linked, because tropical deforestation causes runoff of forest soils and nutrients, which are suspected to be a major cause of coral reef decline.

This book stems from a meeting at the fourth International Congress of Ecology in Syracuse, New York. So as not to conflict with a planned meeting on insect diversity in the tropics, the editors restricted their attention to the vertebrates, selecting contributors with long experience with community studies of their respective groups (e.g., coral reef fishes, amphibians, reptiles, birds, and mammals), often at more than one site. The editors made an admirable attempt to select contributors who have worked in widely separated geographic areas. If there is to be a general set of hypotheses on the origin and maintenance of species richness in the tropics, long-term data taken by the same methods and the same observers at comparable sites has the best chance of generating useful ideas.

Starting the book with a chapter by P. F. Sale on diversity in reef fishes is not simply an accident of taxonomic order. Largely due to the work of Sale and his colleagues and students, coral reef fishes have been at the center of discussions on the evolution and maintenance of diversity in the sea during the last 20 years. Early on, a stimulating controversy developed turning on whether or not reef fish
communities were equilibrial or non-equilibrial assemblages, whether their diversity was maintained by competition for food and space resources or was a product of chance factors such as predation, disturbance, and recruitment.

Although it is well-organized and interesting, this chapter contains little that is new, the various views having been summarized by the author and others elsewhere. As with so many controversies in ecology, the originally polarized positions of both sides have blended. Nevertheless, Sale clearly aims to keep a lively discussion going by writing, "The patterns of resource partitioning to which we have given so much attention are neither important in permitting coexistence nor likely to be similar from time to time or place to place."

The traditional equilibrium explanations of reef fish diversity grew out of studies of niche theory, niche dimensions, and species packing in bird communities. These concepts assume the importance of competitive interactions in the origin and maintenance of species diversity. The chapters by M. L. Harmelin-Vivien comparing coral reef fish communities at opposite ends of the Indo-Pacific region (Moorea and Madagascar), C. Erhard on rain-forest birds in Africa (Gabon) and South America (French Guiana), and P. V. Driscoll and J. Kikkawa on the birds of lowland forests in Australia and New Guinea are illustrative of the usefulness of long-term comparative data. The authors analyze structural and functional attributes of reef fish and bird communities including reproductive strategies, size class structure, diet, foraging techniques, guild structure, activity rhythms, and species distributions. It is striking how similar methods of analysis may be applied to divergent groups in different regions to reach revealing descriptions of community organization in the sea and on land. Although interesting, such studies are snapshots and do not reveal the underlying dynamics of populations comprising communities nor the role of time-dependent and highly variable processes, such as recruitment in fishes.

The analyses of herpetofaunal and mammalian communities break new ground in directing attention to community structure and organization over broad geographic ranges. W. E. Duellman's chapter on herpetofauna shows remarkable patterns of similarity in habitat use and daily activity of snakes, lizards, and anurans at six sites from Guatemala to Peru. He finds that diversity is related to climatic stability and vegetational diversity, permitting the evolution of specializations that characterize a diverse fauna. Within different groups, however, there appear to be important proximal correlates of species diversity in vegetational heterogeneity (snakes) and amount and seasonality of precipitation (amphibians).

In his analysis of the literature on mammalian communities from a variety of Old World and New World sites, F. Bourlière reviews most of the established hypotheses of species diversity applied to mammals and concludes that the causes of species richness in mammals are obscure. In moist forests, mammalian communities have never been as rich as bird communities, principally because birds have access through flight to the forest canopy, a rich source of insects denied to all but the smallest and longest arboreal mammals. Thus it is not surprising that the most diverse group within the tropical mammalian fauna is bats.

Bourlière and Harmelin-Vivien do not attempt to summarize the points of view expressed by the authors on the causes of high vertebrate species diversity. Rather, in a concluding chapter, they focus on ecosystem-level processes. They briefly compare the physical and biological attributes of coral reefs and rain forests in a table in which the two ecosystems are virtually indistinguishable—perhaps emphasizing our lack of understanding of the similarities and differences.

They conclude that species diversity in the tropics, terrestrial and marine, ultimately depends on a diversity of food resources sustained by high productivity, itself a result of relatively stable climatic conditions and high solar radiation in the tropics. High temperatures can also be invoked as a factor in species diversity for the expanded range of diets, particularly herbivory, found in the tropics and...
even for a hypothetical influence of higher temperature on the rate of organic evolution.

The book has a distinctly ad hoc flavor arising from its limitation to vertebrate groups, of which only reef fishes and birds have received the concentrated attention of empiricists, experimentalists, and theorists concerned with species diversity. These communities seem to be organized in a similar manner, but one must bear in mind that life histories of coral reef fishes, in contrast to birds, are poorly known, particularly the planktonic larval life characteristic of the majority of species. Although such descriptors as trophic structure, guilds, and niche dimensions may be used for fish and bird communities, their underlying dynamics may be different. To paraphrase Duclmann, fishes are not birds, and the contributions are not integrated sufficiently to resolve the similarities and differences between divergent vertebrate groups or to suggest general hypotheses of the causes of species diversity. This book is not a primer on biological diversity, but it draws together interesting analyses of divergent vertebrate groups that suggest general patterns. At the very least, the book shows that the aim of formulation of general hypotheses of species diversity depends on well-planned, long-term field studies, preferably along gradients of diversity correlates such as temperature or latitude, or in comparable areas in different habitats or regions. Understanding factors influencing species diversity ultimately depends on knowledge of the life-history patterns characteristic of the medium, air or sea water, in which evolution has done its finest work.

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MUDDY EVOLUTIONARY WATERS


One expects that a book on evolution written by a competent specialist will, at least, convey substantial insights involving the author's area of specialization. Niles Eldredge is an invertebrate paleontologist with a thorough background in Devonian trilobites, as well as other groups of unrelated Paleozoic arthropods. The back cover of Macrolelelutionary Dynamics promises the reader that Eldredge will bring macrolelutionary thinking into sharp focus. We found this to be far from the case; there is much confusion in his thinking, and his writing muddles the waters even further.

The book consists of an initial, pedestrian review chiefly addressing the nongenetic aspects of evolution and some lengthy attempts to buttress the now-faltering concept of punctuated equilibrium (see Levinton 1988 for a meaty refutation, emphasizing the genetic deficiencies of the concept), involving among other things a revision that concludes, without any evidence, that all species generation has been cladogenetic, i.e., that phyletic evolution is nonexistent. These are followed by a lengthy, meandering, excessively wordy series of thoughts on varied aspects of evolution. For example, Eldredge takes pains to distinguish between economic and reproductive properties of an individual's phenotype. In his view, these are sufficiently independent that it is possible to treat them as separate entities when considering natural selection, adaptation, and speciation. Ultimately this view leads him to conclude that reproductive properties are not subject to natural selection, a position that may not sit well with more than a few evolutionary biologists.

Eldredge has somehow gotten the misconception that Darwin and many others since have the view that natural selection almost always moves a population in a single direction. Directionality might be expected over a short period of time in response to a particular environmental change, but this response hardly lends necessity to directionality over evolutionary time. As geneticist T. Dobzhansky so elegantly argued, natural selection is totally opportunistic, taking advantage of whatever variation exists in a population at a particular time.

Many population and evolutionary biologists have used the concepts and models developed by geneticist Sewall Wright without really understanding them, and Eldredge is no exception. It is clear that he does not understand Wright's shifting balance theory and, in particular, the sort of population structure Wright envisioned as crucial for evolutionary change. Wright's adaptive landscape analogy is misconstrued far more than once. For example, if the planar coordinates are to be allele frequencies, it is a simple matter to see how a population (or perhaps even a species) could be located at a single point on the fitness surface in multidimensional space and could, through time, change position as a result of the action of various evolutionary forces. The three-dimensional representation of a multilocus landscape is made only for the convenience of our limited brains. The stability of the peaks and valleys of the landscape is the result of an assumption that the environment is constant; Wright would, of course, have been the first to agree that in a temporally unstable environment a population would be continually tracking a moving peak—or even a moving landscape! Peaks do not split. Random genetic drift was envisioned by Wright as both a mechanism for moving a population from one peak, either the slope or the top, into a valley such that it might come under the influence of another peak, and also as a means of fixing gene combinations within demes. These combinations might turn out to be adaptive and could subsequently be spread through a population or species by interdeme selection.

It comes through clearly that Eldredge fails to recognize the basic connection between an organism's ecology ("species are not parts of ecosystems"), in the broadest sense, and its evolution. He still thinks in the old-fashioned way that considers evolution as affecting individual taxa, isolated from any serious consideration of co-occurring organisms. For example, some authors discuss the evolution of dogs in a manner suggesting that varied dog lineages somehow affect each other, rather than recognizing that after initial radiation, each lineage evolves in essentially total isolation from the others, intimately associated with a variety of taxonomically unrelated organisms in