Interactions in Evolution

Coevolution. DOUGLAS J. FUTUYMA and MONTGOMERY SLATKIN, Eds., with Bruce R. Levin and Jonathan Roughgarden. Sinauer, Sunderland, Mass., 1983. xii, 556 pp., illus. Cloth, $46.50; paper, $24.95.

Coevolution occurs when two or more species influence the rate or direction of each other's evolution. The subject is knotty because it integrates two nearly immiscible traditions: the theory of evolution concerns the variation within populations that permits or retards change, whereas the theory of community ecology tacitly regards each species as an invariant piece in a mathematical game. Until recently, these traditions relied on the models of allele variation at one or two loci and of pairwise interactions between species, respectively. But such conceptual tools are hard put to predict the outcome of competition, parasitism, predation, or mutualism between genetically complex organisms that vary in abundance in time and space. Progress stalled for decades on an indigestible mix of simplistic theory and observation showing that the vast majority of interactions between organisms are diffuse and that the characters being selected are influenced by several or many interacting loci rather than one or two. A synergism of theory and practice requires that the two confront the same world.

Futuyma and Slatkin provide a well-edited catalyst for this synergism. *Coevolution* has 19 chapters by 23 authors, including sections that extend or criticize theory as well as reviews ranging in subject from reciprocal evolution of plasmids and bacteria to fossil evidence of coevolution between predators and prey. The volume is neither an exposé of new phenomena nor a grand synthesis of all facets of coevolutionary biology. But it provides critical review of a huge literature (over 1800 references are listed) and has the breadth and depth of treatment of both theory and phenomena that will be necessary to chart the next steps.

One role of theory is to guide the intuition of the empiricist; another is to follow a thread of logic far enough to establish its soundness or expose its frailty. *Coevolution* does both. Theorists frequently assume simple reciprocating selection on alternative alleles in each of two species, so Montgomery Slatkin does a service in emphasizing the constraints on selection by genes with multiple effects. Because selection scrutinizes the total phenotype, not just the isolated trait of interest to a specialist, an effective theory must accommodate genetic correlations. Jonathan Roughgarden pieces together the mathematical superstructure of a coevolutionary community equilibrium. The edifice may not appeal to a field ecologist, but it does lay bare the equilibrial assumptions of predictable resource use and stationary age distributions that underlie existing models of pairwise and multiple species interactions. Robert May and Roy Anderson explore the theory of parasite-host evolution. Even where we expect simple evolutionary reciprocity, we find an uncomfortable mix of population theory without genetics, genetical theory without population dynamics, and natural history in which hosts contend with many parasites at a time. The models predict either increased or decreased parasite virulence, and the evidence reveals generalized immune systems rather than specific genetic polymorphisms among hosts (also see the chapter by John Holmes). These authors close off unproductive alleyways, show what must be accomplished to achieve a coherent general theory of coevolution, and emphasize a critical approach to theory. If similar capacity for self-criticism and the courage to grapple with complexity were more common, the discipline would be far more refined than it is.

The substance of *Coevolution* is a penetrating review of empirical work. Distillation from substantial literatures provides the clearest answers to the questions how specific and how symmetric is coevolution. Bruce Levin and Richard Lenski show those of us who tease order out of natural communities what can be done with experimental bacterial and plasmid systems. With noise deadened by larger samples than most of us can possibly observe in nature, we find clear evidence of pairwise coevolution between bacterial hosts and plasmids that tread the fine line between parasitism and mutualism (they confer resistance to antibiotics). Exhaustive ecological, systematic, and genetic evidence also leads Lawrence Gilbert to conclude that coevolutionary convergence occurs in some instances of Müllerian mimicry among butterflies, but other cases of mimicry involve asymmetric convergence of one species with another rather than coevolution of both. Other papers cannot be as definitive. John Barrett warns that mycorrhizal associations include both narrow and wide host ranges, and even that algae and fungi that form lichens often have more than one "mycobiont" or "phycobiont." Douglas Futuyma finds that insects often have specific adaptations to the chemical defenses of host plants but finds little indication that such defenses evolved in response to those particular insects. Peter Feinsinger reports that most pollinators visit many flowers and most flowers are visited by many pollinators. Ironically, the best evidence of coevolution is from flowers that share pollinators through convergence. With few exceptions, discriminating reviews of well-trodden avenues of research show that diffuse relations between organisms are the rule and that asymmetrical interactions make the "co" in coevolution difficult to demonstrate. Such interpretations are not new, but they hardly dominate in the literature. They should.

Coevolution attempts to be comprehensive, and to its credit includes topics well out of the mainstream. A master of rich imagery, Daniel Janzen provides a stimulating exploration of seed dispersal by vertebrates, living and extinct. Some caveats are warranted. The reader should not be so lost in visions of seed-ridden mastodon dung as to dismiss, with Janzen, Hubbell's model of seed dispersal. No such model was offered. The cited paper gave concrete evidence that tropical trees with fruits dispersed by birds and bats are less clumped than those with fruits dispersed by gravity or terrestrial mammals. Similar inaccuracies abound. Janzen points the way to a new frontier, but the adventurer must examine both the maps and the lay of the land carefully. Robert Bakker and Steven Stanley and his colleagues find evidence of coevolution in the fossil record, but also of "sub-optimal" stasis in which one or more species fails to keep pace with adaptations of competitors, or prey. The arguments are both stimulating and aggravating. Competition is maddeningly difficult to demonstrate in nature, and vertebrate predators rarely regulate vertebrate prey. One hopes that the "sub-optimal" limbs of Oligocene predators were of animals that actually "wanted" to eat their more fleet presumptive prey, rather than to eat other animals or berries. Increased tooth wear in ungulates during this adaptive gap implies greater survival to old age and appears to clinch Bakker's argument. But one hopes that the silica content of food plants was constant over millions of years. Nonetheless, these authors dare to tread where others do not, and their papers may consequently prove to be among the most influential in this volume.

Finally, *Coevolution* is unusual in providing both predictive and critical overviews from both the community and phylogenetic perspectives. Geerat Vermeij notes that marine mutualisms are most frequent where nutrients are chronically limited, pointing the way toward productive tests of cost-benefit models of coevolution. Gordon Orians and Robert Paine find remarkably little evidence of community-wide coevolution. Terrestrial plants do show parallel morphological and physiological adaptations to the physical environment, but species diversities in similar environments in Chile and the United States are not convergent. Convergence of form and function is also independent of taxonomic representation in the marine realm; the closest Chilean equivalent of a dominant mussel of the Pacific Northwest is a tunicate. Nowhere is it more evident that we can predict only the general features of adaptation, not the details. Daniel Simberloff notes that most investigations of competition fail to test alternative hypotheses and consequently amount to confirmation by plausibility argument. This issue is contested (see *Science*, 12 and 19 August 1983), but ominously few competition studies actually do document the limiting shared resources required for competitive exclusion or character displacement. Tests with animals that eat foods that are hard to sample (such as birds that eat insects) are frustratingly equivocal. Perhaps direct tests will be more instructive with measurable resources, such as light, space, or mineral nutrients. Last, Charles Mitter and Daniel Brooks chart parallel evolution with the perspective that only comparative analysis can bring. They find clear evidence that some nematodes undergo parallel speciation with their hosts, but no evidence that insects consistently speciate with their food plants. The general message is that we must find ways of distinguishing diffuse coevolution from facultative adjustments of one organism to another, and more important we must discover how to predict when each will occur.

Overall, the editors and contributors should be proud of *Coevolution*. It lifts the discipline from anecdote and speculation and sets a thoroughly scholarly standard of criticism, explores the common ground of an enormously diverse set of phenomena, maps the path for significant future work, and takes a large step toward forging the synergism between theory and practice that fashions science out of a collection of phenomena and ideas. The book should be read in its entirety. It will mark a turning point in our understanding of some of the most fascinating processes in nature.

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Microfossils

Neogene Planktonic Foraminifera. A Phylogenetic Atlas. JAMES P. KENNETT and M. S. SRINIVASAN. Hutchinson Ross, Stroudsburg, Pa., 1983 (distributor, Van Nostrand Reinhold, New York). xviii, 265 pp., illus. $36.50.

Planktonic foraminifera are the most widely used fossils for paleoclimatic, paleoceanographic, and biostratigraphic interpretation of the last 150 million years of geologic history. They have made possible detailed correlation of marine sedimentary rocks worldwide, so that global climatic and oceanographic syntheses can be attempted for a variety of geologic times. They also have what is most likely the best documented fossil record of any animal group; it has tremendous potential in evolutionary and paleobiological studies. Such studies, however, have come slowly because workers on the group have largely been busy using them in geologic applications and because paleobiologists and evolutionists have been unaware of this potential. All these enterprises will be made much easier with the publication of this book.

Although planktonic foraminifera first evolved in the Jurassic and radiated in the Cretaceous, their evolutionary history is marked by three major extinction episodes—in the mid-Cretaceous, at the Cretaceous-Tertiary boundary, and near the Eocene-Oligocene boundary. This book deals with the genera and species that evolved in the 22 million years following the last extinction. The separation of the Neogene forms is thus quite natural.

The book is divided into two parts: a 15-page biostratigraphic section and a taxonomic section. In the first section are brief discussions of classification and of various biostratigraphic zonations. These are fairly standard treatments, but there is bound to be quibbling over details anyway.

In plankton biostratigraphy, the concept of stratigraphic "datums" has been widely and successfully used. A datum is either the first evolutionary appearance or the extinction of a taxon. The use of datums brings chills to dedicated biostratigraphers practicing on other groups where overlapping geologic ranges of species are regarded as the most, or only, reliable stratigraphic markers. Particularly galling will be the use of the last appearance of a species. How can you ever be sure your particular occurrence represents the last one worldwide? Ordinarily you cannot be sure, but in the very complete deep-sea sections usually dealt with by plankton people other means (paleomagnetism, radiometric dates, isotope stratigraphy, and comparison with other groups of fossil plankton) have empirically shown many datums to be isochronous. Such datums work in plankton biostratigraphy because plankton live in some of the most widespread environments on earth. The tropical water masses, for example, are very uniform compared with benthic environments, and they have been interconnected worldwide for most of the Mesozoic and Cenozoic. Water characteristics do vary, of course, but mostly in a north-south direction. Thus different zonations and datums have been recognized for tropical, transitional, and temperate waters, as shown in this book. Planktonic foraminifera work well in these waters, but because of low species diversity they are not so useful in subpolar and polar seas.

The "Phylogenetic Atlas" makes up the majority of the book. It contains careful diagnoses and nicely done scanning electron micrographs of 150 species in 33 genera and subgenera. These are the important species in the view of Kennett and Srinivasan. Synonyms are listed and cross-referenced in a taxonomic index. Phylogenies, shown for all species, are inferred from morphologic similarities and stratigraphic occurrences, but no reasons are usually given for making such evolutionary connections. Although there will be argument about some of these, the relationships are probably mostly correct, for the authors have been studying the Neogene successions for many years and have a good feel for them.

The atlas is the basis for all other work