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## REVIEWS

**Coevolution**, edited by D.J. Futuyma and M. Slatkin. Sinauer Associates, Sunderland, Mass. 555 p. (1983)

Coevolution refers to the general phenomenon of one organism's evolution being affected by another. Pairwise coevolution is said to occur when two organisms affect each other reciprocally; diffuse coevolution occurs when several species affect each other's evolution at the same time. This book represents the first attempt to put together whatever is known about coevolution from many different fields in one place.

Chapter 1 provides a broad introduction to the subject. A study of coevolution is of direct applicability to human self-interest, especially in understanding the development of resistance in bacteria, and in combatting agricultural pests. This is followed by a readily understandable summary of the genetic mechanisms that might influence coevolutionary processes by Slatkin.

The going starts to become rough in Chapter 3. Here Roughgarden provides a population genetic treatment of coevolution. It is highly mathematical and assumes familiarity with population genetics. Unfortunately for the theorists, real life is not governed by equations, and I gave up the struggle after trying to visualise situations where the complex equations developed here might actually apply. The examples given later on in the chapter seem to relate only very superficially to all the elegant math that precedes it. Next, Mitter and Brooks discuss the pylogenetic aspects of coevolution, and discuss a useful methodology of determining whether a situation has arisen from coevolution, or whether it is a chance association. Many parasites show exactly the same taxonomic relationships among themselves as their hosts do, and this seems convincing evidence of coevolution.

The next few chapters will be of interest to microbiologists and medical researchers. First, bacteria and their phages are dealt with, followed by a consideration of bacteria that are symbiotic with their hosts. A chapter on plant-fungus associations follows, with one on helminths and their hosts after this.

May and Anderson then follow with a treatment of host-parasite relationships, again from a theoretical viewpoint. The 'conventional wisdom' is that parasites will evolve to limit damage to their hosts, since longer-living hosts mean more successful parasites. This need not necessarily be the case, and the authors show that several other evolutionary pathways are possible.

Futuyma then examines plant-insect interactions. Plants evolve toxic substances to protect themselves against insect attack. Insects then develope means to overcome these defences, and there is often great specificity about which insect can attack which plant. On the other hand, it is also possible that plants have the toxins in their leaves for entirely different purposes and resistance against insect attack is a secondary consequence. Obviously, coevolution cannot have occurred in the latter case, at least in the early stages.

In Chapter 11, Janzen considers the dispersal of fruit by vertebrates, an issue of great importance in conservation. The problem is succintly stated by him : 'The function of a ripe vertebrate-eaten fruit is to get the seeds into the right animal and keep them out of the wrong animal'. Fruits are generally indigestible when unripe; they suddenly become edible to some animals and not to others, over a very short period. Relevant considerations include the schedule to which the fruits ripen, who eats them, where the seeds land, and what subsequently happens to them. This is easily the most well-written chapter in the book, though the number of references cited do amount to a slight overkill.

Mimicry is then discussed by Gilbert. There are two main types of mimicry : Mullerian and Batesian. Batesian mimicry was first described in 1862, and describes the phenomenon of an edible species evolving to look like an inedible, distasteful one, thus fooling predators into leaving it alone. Any butterfly book will provide many examples of this. Mullerian mimicry, also first described over a hundred years ago, occurs when two distasteful or nasty species converge to look like one another. The reasoning here is that after a bird eats an individual of one species, it will then avoid eating individuals of the other, leading to fewer deaths all around.

Coevolution is also implicated in pollination (Feinsinger, Ch. 13). Flower shape and colour evolve to attract the right insect or bird to pollinate it. It is worth noting that in Thailand, durian pollination is largely dependent on the cave-dwelling nectar-eating bat, *Eonycteris*. As this bat is getting rare now, durian farmers are having to resort to pollination by hand–a tedious process, and also an example of the many costs of destroying wildlife.

Marine animals also coevolve with each other (Vermeij). The use of gastropod shells by hermit crabs is well known. Many prey species associate with a 'host' that protects them against predators. Cleaner fish actually swim inside the mouths of predatory fish to remove parasites. Any other fish trying this risks immediate death.

Some of the arguments in the next chapter ('Coevolution and the fossil record') seem to be based on a too facile interpretation of the data. I learned for the first time

that leopards are arboreal. A comparison is made of predators in different places in similar habitats and with similar food preferences eating prey of different sizes. This seems to be violated in at least one of the figures: *Hoplophoneus occidentalis* and *Eusmilis dakotensis* in the fossil guild illustrated seem to be remarkably similar. Also, the eating of 'meat', 'meat and bone' and 'meat and fiber' cannot be considered to be different ecological niches–after all the predator has to kill the prey first in any case.

The next chapter ('The deer flees; the wolf pursues') is an anatomists' delight. Prey species evolve to run faster; predators then also have to run faster to be able to catch them. Bakker examines the fossil record for evidence of this and concludes that many predators were just not able to make the grade.

Now Roughgarden again, discussing coevolution among competitors. He describes two case studies, one of mudsnails in Denmark, and the other of *Anolis* lizards in the Carribean. In both, the phenomenon of character displacement seems to be operating. Simberloff (Chapter 19) then proceeds to demolish these examples. There appear to be serious methodological flaws in the mudsnail study. As for the lizards, Simberloff's null models provide a reasonable alternative hypothesis. Other case studies on character displacement are also shown to be based on misidentifications or flawed data. The argument on whether competition occurs or not is one of the bitterest in the biological sciences today, and the two principal antagonists take it no nearer a solution in this book.

Finally, Orians and Paine examine whether convergent evolution at the community level has occurred or not. For plants, patterns of productivity and growth form show similarities in similar communities. These could however be responses to physical factors and not due to coevolution. For faunas, both terrestrial and aquatic, the answer appears to be no.

In an epilogue, Futuyma and Slatkin attempt to summarise. Very few firm conclusions emerge, but there are a lot of research opportunities. Diffuse coevolution is more likely than pairwise coevolution, but the theory for it has not been developed yet.

In general, there is not enough discussion of the testing of coevolutionary hypotheses against alternatives, though Mitter & Brooks, and Simberloff have some interesting ideas in this direction. Rambutans are liked by gibbons, who eat them. They then disperse the seed. Now, have they coevolved, or does the gibbon just eat rambutans because they happen to be there? Again, is competition really a widespread phenomenon, or does it appear to be so because researchers have selected pairs of species for study, that might be expected to demonstrate it?

The book as a whole will interest very few people, since it is written by specialists in their own fields, few of whom have made an attempt to simplify at all for those outside their own immediate interests. The concept of coevolution is of fundamental importance to tropical ecology, and a consideration of coevolutionary phenomena will ultimately, one hopes, lead to placing the subject on a more rigorous footing. The very concept of coevolution implies a valuable and long overdue perspective which has been missing from the study of 'symbioses' and the study of community organisation in ecology. Naturalists should be aware of this field, even if there is as yet no text that provides an easy introduction. Therefore, parts of it are recommended browsing for all those interested in the biological sciences.

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