Book-Reviews

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John N. Thompson. 1994. *The Coevolutionary Process.* The University of Chicago Press, Chicago and London. p. xi+376. Price US $ 19.95; UK & 15.95. (ISBN 0 226 79760 0).

No species lives in isolation. Other species, similar and different, constitute a dominant and dynamic component of any organism's environment. If evolution by natural selection is a major force responsible for the observed characteristics of living organisms, it goes without saying that members of interacting species are often agents of natural selection. It seems rather surprising therefore that it was only in 1964 that Ehrlich and Raven coined the term *coevolution* in their effort to describe the evolutionary interactions between plants and butterflies. Even after this belated recognition of what seems an obvious aspect of natural selection, coevolution has not had a smooth and swelling following among evolutionary biologists. In many ways coevolution is beset with the same problem as natural selection itself, namely, that it is an obvious explanation for many of the observed phenomena but can seldom be rigorously proved, and let's face it - it is less heretical to question coevolution than it is to question natural selection. One approach has been to take coevolution as granted and inevitable, and therefore treat it as a theory and only worry about testing specific hypothesis that stem from it and not to attempt to test the theory itself - much as we do with natural selection! A second approach has been to treat coevolution as an onerous concept, not to be invoked unless there is compelling evidence, an approach that is sometimes advocated also in the case of adaptation.

This dichotomy pervades all of evolutionary biology to a lesser or greater extent but has been a conspicuous feature of the history of the study of coevolution. In principle, coevolution can be invoked virtually everywhere - prey must have coevolved with their predators, hosts with their parasites, flowers with their pollinators, seeds with their dispersers, herbivores with their food plants and even parasitoids must have coevolved with the plants on which their hosts feed. What makes coevolution potentially even more omnipresent is that all organisms must coevolve with their neighbours whom they cannot eliminate and who in turn cannot eliminate them and so the two or more species inevitably coexist. Does not this infinitely liberal use of the concept of coevolution make it a useless concept? Many would say yes but I will argue that they will then have to admit the same misgivings about natural selection itself.

A lesson that comes home very effectively from reading John Thompson's *The Coevolutionary Process* is a solution to this apparent discomfiture of evolutionary biologists - a lesson that is well worth translating also to the context of natural selection and adaptation in general. Thompson deals not with coevolution but the coevolutionary process - the emphasis is not on the phenomenon - omnipresent and with infinite explanatory power - but on the mechanism of coevolution. What are the fitness consequences of interactions between species, what are the consequences when the interactions are intimate and one on one and what are the consequences when the interactions are loose and casual? An approach that focuses on the mechanism does not presuppose a degree of importance to the phenomenon that is implied when the phenomenon is merely used to explain observations as if use of the word coevolution itself is sufficient explanation. It is this shift in emphasis from phenomenology to mechanism that is so clearly, if implicitly, brought about by Thompson's book that will convert many skeptics like me into the coevolutionary fold. As one might expect, this requires a combination of theoretical and empirical approaches which is achieved in so subtle a manner by Thompson that biologists who are normally uncomfortable with theory will not even realize that they are being guided through many relatively abstruse theoretical ideas. Coming to think of it, much of what is in Thompson's book is not new, it is already in the published literature. But how many of us can keep up with the burgeoning literature outside our own narrow specialization's? It is impossible therefore to underestimate the value of books like the one under review in retaining the ability of biologists, even within evolutionary biology, to speak the same language and prevent them from developing a sarcastic skepticism of each other's themes of study. A notable feature of Thompson's book is his attempt at creating what he calls a *geographic mosaic view of coevolution.* What this means in essence is that ecology (with explicit consideration of spatial structuring of populations) and genetics are given

an equal place in the study of coevolution. Thompson's discussion of the relationship between coevolution and specialization is especially satisfying - coevolution does not necessarily mean extreme specialization - much will depend on the ecology of the interacting species and on how many partners are involved in effecting fitness consequences on their neighbours.

It is all too easy to overlook the importance of coevolution for applied ecology and again, this is not because coevolution is an esoteric concept but, on the contrary, it is far too obvious - of course species are coevolved - how can something so obvious help me in biological control or conservation efforts? Thompson's emphasis on the mechanism of coevolution tells a completely different story. Consider the following scenario: when we convert diverse natural habitats into monocultures or at any rate, into impoverished communities, what are the consequences for the parasites, predators and the coevolved partners? Consider another example: if I am using a Hymenopteran parasitoid for biological control of an agricultural pest, I am forcing the parasitoid to depend largely on one host. What are the resulting evolutionary changes in the parasitoid population? Are these changes good or bad for my purpose of effective biological control? If they are good, then I must periodically draw samples from the sites of release and use these field captured individuals for mass rearing. If they are bad then I must persist mass rearing with my original population or with individuals living on the more natural, diverse range of hosts. The practical implications of understanding the coevolutionary process are immense but, as it always happens, are not so obvious. I must end with a word of caution to potential readers of Thompson's book and I do hope there will be many. It is not easy reading, simply because it is not a collection of fascinating examples of coevolution - it is not a book on the phenomenology, it is *not* a book on coevolution - it is a book on the *mechanisms* of coevolution, a book on the *coevolutionary process*. I had to read and re-read many passages before a feeling of understanding began to set in. It is a tough one, but well worth the effort.

Reference

Ehrlich, P.R. & P.H. Raven. 1964. Butterflies and plants: A study in coevolution. *Evolution* **18**: 586-608.

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