Coevolution and Escalation: Are Ongoing Coevolutionary Meanderings Important?

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ABSTRACT: The nondirectional coevolutionary dynamics often produced by the geographic mosaic of species interactions may be precisely the important processes that allow interactions to persist in the midst of a constantly changing world. This view contrasts with that of Vermeij, who has argued that antagonistic coevolution has been largely replaced by a more diffuse macroevolutionary process that he has called escalation. It is likely that coevolution and escalation are both crucial as ongoing evolutionary processes. Although the geographic mosaic of coevolution may often not scale up to major macroevolutionary patterns, it is the true interface of evolution and ecology. These ongoing coevolutionary processes and patterns are what we need to understand how to develop more effective approaches to the conservation of species diversity, the manipulation of the geographic dynamics of diseases, and increased long-term effectiveness of biological control programs.

Keywords: coevolution, community dynamics, escalation, evolutionary trends, rapid evolution.

The ongoing geographic dynamics of coevolution found in the examples in this volume may often not scale up to become fixed traits of species and higher taxa. They are not necessarily the stuff of macroevolution and long-term evolutionary trends. Rather, most of the dynamics are part of the continual reshaping of interspecific interactions that keeps populations and species in the evolutionary game. This workaday coevolutionary tussle buffers populations in an ever-changing world. It is where evolution meets ecology.

Nevertheless, it is easy to dismiss these coevolutionary tugs and pulls as the inconsequential fine tuning of interactions. To biologists interested primarily in macroevolutionary trends, these coevolutionary meanderings would seem to mean little. Vermeij (1987, 1994), for example, has argued that selection imposed by enemies has increased over evolutionary time as adaptation and speciation have produced new and more dangerous predators, competitors, and other enemies. With so many enemies about, coevolution has been supplanted in many interactions by what he has called escalation. By this view, defenses and counterdefenses evolve not through any identifiable process of reciprocal evolutionary change in which individual species impose strong selection pressures on one another. Instead, species are evolving to increasingly high levels of defense and counterdefense through the sum total of ever more dangerous enemies.

Vermeij's hypothesis suggests that there is a long-term inherent direction to the evolution of antagonistic interactions. It is an important macroevolutionary hypothesis that takes a broader ecological approach than is common in much paleobiological research on evolutionary trends. But the hypothesis comes from a focus on trends over long periods of evolutionary time rather than on the ongoing ecological dynamics of organisms. Continual fluctuation of gene frequencies driven by reciprocal selection would be outside the bounds of important coevolutionary processes in Vermeij's comparisons of coevolution and escalation. Similarly, the routine incorporation, use, and abandonment of novel traits and countertraits, as they change over time in their utility, are not important in this view, unless they involve "key innovations" that change the future trajectory of the interaction. Vermeij (1994) refers to routine coevolutionary changes as "aimless yet continuous evolution" that is part of the "mutual adaptational stalemate" occurring between adaptive breakthroughs or key innovations. It is a strongly paleobiological view of what is important and unimportant in evolution.

Yet, at the interface of evolution and ecology, it is precisely this constant "aimless" interplay that is so important. Even if there is an evolutionary trend toward generalized escalation, it does not follow that escalation has replaced antagonistic coevolution as an important ecological process. For those of us interested in the genetic structure of populations, the dynamics of current biological communities, the organization of biodiversity

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at different landscape scales, the spread of diseases, and the effects of ongoing coevolution on conservation efforts, these coevolutionary changes are both real and important. Coevolution is not just a paleobiological mechanism for explaining long-term changes in the diversity of life on earth over multiple millennia. It is a central ecological process, partially responsible for organizing and reorganizing interactions and communities on the timescales of decades and hundreds and thousands of years.

Perhaps our most important current need in the study of coevolution is to make it a true evolutionary ecological science. We need to do much more than show that selection is acting on particular traits. We need to understand when, where, and how coevolution shapes the genetic structure of real populations, how it organizes and reorganizes the outcomes of interactions under different ecological conditions, how it molds and connects interactions across actual landscapes, and how it contributes to the ongoing organization of communities. The default position among most ecologists is either that rapid evolution and coevolution are uncommon in most interspecific interactions or that they are unimportant in the face of other ecological processes. Although examples of rapid evolution are proliferating (Thompson 1998), they are doing so slowly because we have rarely studied these effects in natural populations in detail. In the meantime, it has been easy to dismiss ongoing coevolution—and rapid evolution in general—as an esoteric side topic without great relevance to current ecological patterns and concerns.

It is becoming less easy to make these kinds of dismissals. As the articles in this volume suggest, ongoing coevolution occurs and can sometimes be quite rapid. Moreover, these studies emphasize that much of the process occurs across broad geographic scales that link populations, communities, and ecosystems.

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