

## BOOK REVIEWS

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### EXPLORING THE IMPLICATIONS OF MOSAIC COEVOLUTIONARY OUTCOMES<sup>1</sup>

EDWARD ALLEN HERRE

*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948*

*E-mail: herrea@si.edu*

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The coevolution that can be spoken of is not the constant coevolution; the name that can be named is not the constant name. . . . Mystery upon mystery—the opening gateway reveals the manifold secrets.—Paraphrase of Lao Tzu from Tao Te Ching.

What is interesting about species interactions? Their often strikingly matched patterns of phylogenetic coevolution? Their often superbly fine-tuned coadaptations? The fact that their associations often show neither striking phylogenetic matching nor fine-tuned coadaptation? Should we be interested in what mechanisms prevent predators, herbivores, and parasites from annihilating their prey? Should we be interested in the mechanisms that maintain the reciprocal benefits that define mutualisms? Or in the variation in outcomes and character states that we can observe across the ranges of interacting species? Or should we be more interested in the constants that may seem to run through those same ranges? Can principles with applied utility be gained from any of this?

Out of many possible coevolutionary themes, John Thompson's ambitious book touches on several, but primarily as a means to focus on the factors that may influence the actual *process* of coevolution. Specifically, his fundamental assertion is that focusing on strictly local processes is often insufficient and that taking larger spatial structure of interacting populations into account (i.e., "the geographic mosaic") is critical for explaining many, if not most, coevolutionary patterns.

In developing the proposition that the geographic mosaic is the organizing framework for the process of coevolution and should provide the appropriate context for its study, Thompson first does a fair bit of naming and categorizing. He names seven types of local coevolutionary dynamics (pp. 89, 367–370) that themselves can depend on geographic mosaic forces. He identifies 11 classes of data collection and analysis that can help identify coevolutionary processes that occur at different spatial/phylogenetic levels (pp. 164–165). The theoretical structure itself (the geographic mosaic theory) consists of five major assumptions, three evolutionary hypotheses, and three general predictions (pp. 7–8, 11–12, 97–135, 365–370, summarized as a table on p. 98). The elements of the theory follow.

*Assumptions.*—Thompson's five assumptions are that (1) "species are groups of genetically differentiated populations, and most interacting populations do not have identical geo-

graphic ranges" (p. 365); (2) "species are phylogenetically conservative in their interactions, and that conservatism often holds interspecific relationships together for long periods of time" (p. 365); (3) "most local populations specialize their interactions on a few other species" (p. 365); (4) "the ecological outcomes of these interspecific interactions differ among communities" (p. 365); and (5) "species often become locally adapted to local populations of other species and continue to evolve rapidly" (p. 365).

*Evolutionary hypotheses.*—Thompson presents the following three evolutionary hypotheses: (1) "*geographic selection mosaics*: there are geographic differences in how fitness in one species depends on the distribution of genotypes in another species" (p. 365); (2) "*coevolutionary hotspots*: interactions are subject to reciprocal selection only in some local communities. These coevolutionary 'hotspots' are embedded in a broader matrix of coevolutionary 'coldspots' where local selection is nonreciprocal" (p. 365); and (3) "*trait remixing*: the genetic structure of coevolving species also changes through new mutations, gene flow across landscapes, random genetic drift, and the extinction of local populations. These processes contribute to the shifting geographic mosaic by continually altering the spatial distribution of potentially co-evolving alleles and traits" (p. 366).

*General ecological predictions.*—Thompson's general ecological predictions are that (1) populations differ in traits shaped by an interaction; (2) traits of interacting species are well matched only in communities; and (3) few coevolved traits spread across all populations to become fixed within species because few coevolved traits will be favored across all populations.

A great strength of the book is that Thompson draws on a series of classic studies and from them extrapolates how geographic structuring of populations might play a crucial role in the general process of coevolution. He cites numerous studies in which different populations of interacting species show geographical structure and differentiation in their interactions. These studies involve a diverse suite of taxa, including *Daphnia* and their bacterial endoparasites (Ebert et al. 1998), *Drosophila* and their parasitoid wasp, *Leptopilina boulardi* (Kraaijeveld and Godfray 1999), toxic *Taricha* newts and their garter snake (*Thamnophis*) predators (Brodie et al. 2002), *Potamopyrgus* snails and their castrating *Microphallus* trematodes (Lively and Jokela 2002), wild flax and a pathogenic rust (Thrall and Burdon 2003), the woodland star (*Lithophragma parviflorum*) and its sometimes mutualist, sometimes parasitic prodoxid moth pollinator (*Greya politella*) (Thompson and Cunningham 2002), and the constellation of moths associated with yucca plants (Pellmyr 2003).

<sup>1</sup> *The Geographic Mosaic of Coevolution*. John N. Thompson. 2005. University of Chicago Press, Chicago. xii + 443 pp. PB \$28.00, ISBN 0-226-79762-7.

From these and other studies, several messages come through very clearly. There is a great deal of inherent genetic variation for many traits involved in interactions (e.g., Henter 1995; Frank 2002; Grant and Grant 2002). Further, Thompson cites many cases in which different local populations of particular pairs of interacting organisms show different outcomes to their interactions, often with clearly corresponding or “matching” variation (see pp. 104–110). It follows that coevolution and coadaptation are active, ongoing processes that can proceed very rapidly, usually much more rapidly than phylogenetic change or speciation events (also see Machado et al. 2001, 2005; Segraves et al. 2005). Thompson posits that most rapid coevolution within populations is not fixed at higher phylogenetic levels (e.g., Herre 1989; Machado et al. 2001; Kato et al. 2003; Currie et al. 2003, 2005) because of lack of consistent across-population selection that would allow sweeps. Finally, the fact that many “keystone” species are involved in essential mutualistic interactions (Herre 1996; Rowan et al. 1997) and that essentially all organisms are involved with some biotic interaction emphasizes the crucial role that coevolution plays in organizing communities. It is difficult to come away from reading this book without being convinced that coevolution plays a fundamental role in shaping essentially all biotic diversity.

However, part of this effort is intended to produce a theoretical structure, the mosaic theory, that will lay the groundwork for a predictive science of coevolution (p. 6), and many readers may find that they are less than satisfied by a theory with predictions that essentially say that there are no concrete predictions. That populations are predicted to differ in the traits selected by the interaction, that coadapted traits are predicted to be well matched in some populations but not others, and that few coevolved traits are predicted to be favored across all populations may not seem to constitute much predictive progress. Also unsatisfying is the assumption that species are phylogenetically conservative in their interactions and that this conservatism holds interspecific relationships together for long periods of time. What underlies this assumed conservatism? How is it supposed to operate to hold interactions together? Further, the concepts of “hotspots” and “coldspots” form an integral part of the conceptual machinery of the mosaic theory and refer to sites where active coevolutionary change is or is not taking place locally. However, it is not clear whether the hotness or coldness of spots can be identified a priori and thus provide an independent basis for predictions (see Hochberg and Van Baalen 1998), or whether these concepts are simply convenient post hoc explanations to account for why a particular prediction may not be met in a particular population.

Finally, it is not always clear whether Thompson means that the geographic mosaics are actively driving coevolution or whether they are more passively reflecting it (e.g., “The evolution of sexual reproduction, parthenogenesis mediated by symbionts, and symbiont-mediated reproductive incompatibility are all mediated by the geographical mosaic of coevolution” [p. 226]). We can recognize that local populations of interacting species do show different outcomes in different aspects of their interactions. But does this mean that it is necessary to invoke geographical mosaic-dependent processes to account for this? The crux of the issue seems to be

the degree to which different phenomena can be explained by local processes and where we need to invoke mosaic differences among populations. Is there a distinct geographical mosaic of coevolution? Is it the driving force of coevolution in the sense that it drives or mediates some, many, or most of the coevolutionary phenomena that we observe? Or are the mosaics observed in many systems simply a reflection of differences in local outcomes? Is there a tangible, discrete theory of the geographical mosaic that generates tangible, discrete predictions? Fundamentally, if the geographic mosaic is an important component of coevolution, we should expect different patterns in more panmictic systems in which one or both members show extreme dispersal and gene flow (e.g., the dinoflagellates in corals or figs and their wasps; Herre 1996; Rowan et al. 1997) compared with those systems that show more structured populations, but do we? These are among the questions that critical readers should ask of the book and answer for themselves.

This book summarizes and synthesizes a great deal of information on many aspects of very diverse types of interactions. In doing so, it is particularly helpful in drawing attention to one of the ecologically most important, but still most poorly understood, types of interactions: mutualism (chaps. 12–14). As Thompson (among others) points out, stability in many mutualistic systems appears puzzling (e.g., the cases in which symbionts are horizontally transmitted and those in which multiple genotypes of symbionts are found associated with a single host). Particularly challenging in these respects are the arbuscular mycorrhizal fungi (AMF). Here, the fungi appear to break with convention on at least two levels. Some work (e.g., Sanders et al. 2002, but see Pawlowska and Taylor 2004) suggests that multiple genetically distinct nuclei routinely share common AMF cytoplasm. Other work suggests that individual host plants may host multiple species of AMF, and more intriguing, “individual” AMF may connect to multiple different host plants. These observations present a series of fascinating conundrums at genomic, population, and community scales of biological organization. As Thompson recognizes, progress in understanding these systems requires more than the metaphor of “genetic handshake” (pp. 261, 269, 286), and indeed, apparent progress is being made in understanding stability in many of the apparently simpler systems. The idea of host-imposed sanctions on noncooperating mutualists has gained empirical support in systems as divergent as the nitrogen-fixing rhizobia plant systems and the yuccamoth systems (West et al. 2002; Kiers et al. 2003; Pellmyr 2003). Time and research will tell how well these ideas stand up and transfer to other systems.

Moreover, new systems are being recognized, and novel aspects of previously recognized systems are being newly appreciated. Recent research on the seemingly familiar leaf-cutter ant systems demonstrates fine morphological coadaptation with bacterial mutualists (Currie et al. 2005) and clear evidence for an active role for the fungal mutualists (Poulsen and Boomsma 2005). Horizontally transmitted endophytic fungi show extreme within-host diversity in many tropical plants, yet they defend their hosts against pathogens that are also horizontally transmitted (e.g., Arnold et al. 2003; Van Bael et al. 2005). The list of obligate pollination mu-

tualisms has been dramatically expanded by the example of species rich *Glochidion* trees and their moth pollinators (Kato et al. 2003). Multiple reversals between active and passive pollination syndromes involving a complex suite of traits in both fig and wasp have been documented in a closely related group of figs and their wasps (Cook et al. 2004; also see Machado et al. 2001). Hybridization is being found in some unexpected places, and its potential roles vis-a-vis mutualisms are being re-evaluated (Machado et al. 2005, Segraves et al. 2005). Tropical mycorrhizae exhibit high diversity, and individual species show differential associations with host and site, and different effects on host growth and survival (i.e., all the prerequisites for playing a major role in shaping above-ground community structure; Lovelock et al. 2003; Herre et al. 2005). As Thompson correctly points out, this is a very exciting time for the study of interactions.

Ultimately, the phenomena that Thompson is trying to describe and then use to produce useful general theory are inherently complex and in many cases still only vaguely understood ecologically. Explaining the processes that almost certainly account for the bulk of the biological diversity on Earth is not an easy task. In compiling so many recent and exciting studies and then attempting to use them to forge a coherent general theory, Thompson has provided a very useful work that deserves to be read and carefully considered by anyone seriously interested in the myriad fascinating aspects of species interactions.

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