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Evolving Theory of Coevolution

Thompson, John N. 2005. **The geographic mosaic of coevolution.** The University of Chicago Press, Chicago, Illinois. xii + 443 p. $75.00 (cloth), ISBN: 0-226-79761-9 (alk. paper); $28.00 (paper), ISBN: 0-226-79762-7 (alk. paper).

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Interactions between populations of different species play important roles in shaping both the dynamics of ecological systems and the evolution of constituent species. Study on the evolution of species interactions has focused on the coadaptation between interacting species that has resulted from natural selection over long periods of evolutionary time. Such matching (and mismatching) of evolved traits between species has yielded valuable insights into coevolution. However, this approach to the coevolutionary process overlooks much of the ecological context under which coevolved traits emerge, including variation in interspecific interactions and ensuing selection pressures. Ever since Hutchinson's *The ecological theatre and the evolutionary play* (1965. Yale University Press, New Haven), there has been an ever-growing appreciation of the interplay between short-term ecological dynamics and long-term evolutionary processes. Indeed, the community context and ecological dynamics of interspecific interactions can have profound influences on the (co-) evolution of species interactions. Nevertheless, a general conceptual framework has largely been lacking for the ecological theatre of species interactions that choreographs the coevolutionary play. John Thompson's book, *The geographic mosaic of coevolution,* develops such a conceptual framework for understanding the ecological conditions and population processes that give rise to coevolution. This framework represents an important contribution to our understanding of species interactions, as it can be extended beyond the evolutionary and coevolutionary dynamics of interspecific interactions to include how geographic variation in species interactions can influence the structure and dynamics of communities, even in the absence of emerging coevolution.

The geographic mosaic of coevolution is a logical progression in Thompson's evolving ideas on coevolution and the evolution of species interactions. While this book expands upon his prior works, the ideas contained within this book are well organized and clearly presented, such that interested persons need not necessarily have read his prior books to fully grasp his current thinking on coevolution. As with Thompson's past books, a strength of this book is its extensive use of case studies to exemplify the conceptual framework developed throughout the text. Unique to this book, however, is a very useful appendix that presents a concise summary of the major concepts, mechanisms, and predictions contained within the book. Prior to reading the book, one may wish to first turn to this appendix for an overview.

The book is divided into two major parts. Part 1 (Chapters 1–8) develops the geographic mosaic theory of coevolution. The majority of this section expounds on Chapter 13 of his

prior book (Thompson, J.N. 1994. *The coevolutionary process.* University of Chicago Press, Chicago) in an endeavor to more thoroughly and logically develop the conceptual framework. Chapters 2–5 put forth the underlying ecological and evolutionary premises from which the conceptual framework is then developed in Chapter 6. These assumptions include that populations exhibit genetic differentiation; interacting species have geographically incongruent range distributions; species tend to be phylogenetically conservative in the species with which they interact; local populations of species tend to interact with only a few of the constituent species of communities; and the outcomes of interspecific interactions vary within and among communities. Based on these premises, Thompson predicts that the geographic mosaic of (reciprocal) selection pressures on species traits leads to coevolutionary hotspots and coldspots, which in combination with trait remixing (gene flow, genetic drift, mutation, population extinction), lead to a shifting geographic dynamic in the coevolutionary process, and ultimately to speciation and diversification.

Seven general classes of local coevolutionary dynamics are identified within Part 1 of the book, along with the forms of selection (e.g., frequency dependent, directional) that drive their coevolutionary outcomes. Part 2 (Chapters 9–16) then examines these seven outcomes of coevolutionary dynamics, which represent the author's categorization of how different types of interspecific interactions lead to various coevolutionary dynamics. For example, Chapters 9–11 explore antagonistic interactions (predation, parasitism, and grazing), which are suggested to result in outcomes of coevolutionary polymorphisms, alternation, escalation, and attenuated antagonism. Chapters 12–14 then examine mutualistic interactions and the outcomes of coevolutionary complementarity and convergence. Chapter 15 considers competition and coevolutionary displacement. Part 2 of the book develops some new ideas (and terminology) for which the reader will benefit from first reading the appendix. While I found that the first part of the book drew fairly clear conclusions from well-reasoned premises and supporting case studies, the second part of the book required some leaps of faith in inductive reasoning. Conclusions in Part 2 may seem tenuous, but the reader should keep in mind that this is one of the first attempts to develop a cohesive framework for classifying coevolutionary dynamics. Part 2 represents a valuable component of the book, as it will stimulate discussions among researchers and guide research on the evolutionary dynamics of species interactions. Part 2 will make this book a thought-provoking read for discussion groups and graduate seminars. Thompson concludes with a final chapter on applied coevolutionary biology, including conservation and management.

As with his prior book, throughout this book Thompson draws upon his command of the literature to present examples supporting his ideas. Yet, given how thorough the bibliography is, it was surprising that there was not more discussion of examples opposing the geographic mosaic of interspecific interactions. Such contrasting case studies and inconsistencies could provide insights into the actual processes of interest. Moreover, little discussion occurs of alternative hypotheses, though this is likely because they are largely lacking. Not every reader will share Thompson's view on the role of coevolution in the ecological and evolutionary dynamics of species interactions. Yet, it is clear that Thompson has again heightened our attention to coevolutionary processes, and certainly to the role of geographic variation in the spatio-temporal dynamics of species interactions. In fact, some readers will be pleased that in many cases, the conceptual framework developed can extend beyond authentic coevolution as defined by reciprocal selection, to provide insights into the evolution of single species resulting from interspecific interactions.

Throughout the book, great emphasis is placed on how differences in the ecological context of interspecific interactions can lead to variation in interaction outcomes, and hence drive the geographic mosaic of coevolution. Many ecological factors are identified to contribute to such variation in interspecific interactions. Yet, there is little to no discussion of the density or abundance of individuals of a population, even though population density is one of the most fundamental attributes of populations contributing to the strength and outcome of interspecific interactions. Variation in outcomes of interspecific interactions due to density dependence could also play an important role in geographic variation in selection mosaics.

The geographic mosaic of coevolution not only builds on, but also improves upon, Thompson's prior books. Thompson's evolving view of coevolution presented in this book will be influential, as it raises many questions that will stimulate much research at the interface of ecology and evolution. The author's conceptual framework on the coevolutionary dynamics of species interactions has evolved into a more mechanistically based theory, with explicit predictions and assumptions that can be quantitatively examined through both theoretical and empirical studies. The book includes a discussion of quantitative models of coevolution, while also providing practical ''how to'' suggestions for the empirical study of coevolution. This book should be read by all with interests in coevolution, and warrants reading more generally by biologists with broad interests in evolutionary ecology, species interactions, natural selection, adaptation, and among other topics, spatio-temporal dynamics of natural systems.

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