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THE GEOGRAPHIC MOSAIC OF COEVOLUTION
John N. Thompson 2005. The University of Chicago Press. 425 pp.

In "The Geographic Mosaic of Coevolution," Thompson argues that coevolution is one of the most important ecological and genetic processes that organize earth biodiversity. One of the basic tenets of the book is that most of the evolution is coevolution, which is broadly defined as the process of reciprocal evolutionary change between interacting species driven by natural selection. The book emphasizes the idea that coevolution occurs in a discontinuous and heterogeneous environment. The evolutionary forces that act upon individuals are expected to vary in space and time, as a consequence of variation of abiotic characteristics and the interacting species present in local environments.

Thompson's book is composed of 16 chapters. The first part, encompassing the first eight chapters, discusses the ecological, evolutionary and, to a lesser extent, the population genetic processes on which the theory is conceptually framed. It explores the role of local adaptation in the maintenance of the geographic mosaic and presents evidence of the coevolution of interspecific interactions.

The theory is based on five major assumptions: 1) species are groups of genetically differentiated populations and most of the interacting species do not have identical geographic ranges; 2) species are phylogenetically conservative in their interactions, maintaining the same interactions for long periods of time; 3) local populations have specialized interactions with few other species; 4) the ecological outcome of interactions differs among communities; and 5) species are usually locally adapted to other populations and evolve rapidly.

Based on these assumptions, Thompson elaborates three evolutionary hypotheses. In the first one, geographic mosaic selection, the fitness of a species depends on the genotypic distribution of the other species. In the second one, coevolutionary hotspots, interactions are subject to reciprocal selection only in some local communities, termed coevolutionary hotspots, with the remaining local communities exhibiting nonreciprocal selection, termed coldspots. The third hypothesis, traits remixing, emphasizes how genetic processes such as mutation, drift, migration and local extinction contribute to geographic mosaic dynamics, altering the spatial distribution of the coevolutionary alleles and traits.

The second part of the book evaluates several hypotheses and predictions within the context of the geographic mosaic theory. It discusses concepts such as gene to gene coevolution, frequency dependent selection, Red Queen mosaics and Red Queen captured hypotheses. In addition, it examines the seven possible classes of coevolutionary dynamics, which involve different types of interspecific interactions. This part is illustrated with numerous case studies, some of them can be considered convincing demonstrations of the coevolutionary process, such as the interaction of crossbills (*Loxia curvirostra* L.) and pine cones (*Pinus contorta* Dougl. var. *latifolia* Engelm. ex S.Watson). However, other examples need further studies to demonstrate that reciprocal changes are indeed occurring in both interacting species. For example, the interactions between tritons, *Taricha granulosa*, and snakes, *Thamnophis sirtalis* (Brodie, Ridenhour and Brodie, 2002), and between moths, *Greya politella*, and woodland star *Lithophragma parviflorum* (Thompson and Pellmyr, 1992) present evidence of evolution for only one of the interacting species. Another limitation of this section is that none of the case studies discussed by Thomspon represent conflicting evidence for the theory. The section ends with a proposal to use coevolutionary models to solve social and environmental problems (including biodiversity loss and the emergence of new pathogens), with the main purpose of stressing the importance of preserving long-term coevolutionary interactions.

Throughout the whole book Thompson places particular emphasis on the ecological differences of interspecific interactions and how they can lead to multiple outcomes. In contrast, such emphasis is not made about the importance of abundance and density of individuals, nor regarding factors

like fitness or hybridizations as potential sources of variability in the geographic mosaic. Issues related to molecular biology are also superficially mentioned.

Thompson suggests most biological processes may be explained by coevolutionary processes. This excessive emphasis on coevolution is evident in some unfounded claims as regarding coevolutionary processes as the major cause of genetic biodiversity: "The more we learn about coevolutionary dynamics, the more evident it is that ongoing coevolution is a major cause of the origin and maintenance of genetic diversity," downplaying the role of gene mutations already mentioned by several authors (Futuyma, 2005). Furthermore, coevolutionary processes generating the geographic mosaic are not the only possible explanations for sexual reproduction, polyploidy associated to asexual reproduction and the reproductive incompatibilities mediated by symbionts. Surely, there are alternative mechanisms, including sexual evolution via repairing mechanisms of DNA (Cavalier-Smith, 2002) or evolutionary bottlenecks resulting from parthenogenesis (Moritz, 1993; Kearney et al., 2006). Finally, the evolution of a character influencing interspecific interactions in a community may not always generate a coevolutionary response.

The above criticisms notwithstanding, we believe that his theory is a solid background for the empirical study of coevolution processes. The Geographic Mosaic of coevolution summarizes a great number of ideas and concepts, bringing in new and broader perspectives. It is an excellent starting point for new research, given that numerous aspects of the theory still require experimentation and profound analysis. Thompson has managed to outline the initial framework for an integrative study of coevolution, emphasizing the combination of evolution and ecology.

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