



Coevolutionary diversification unfettered

David M. Althoff^{1,2}

¹Department of Biology, Syracuse University, Syracuse, NY 13244

²E-mail: dmalthof@syr.edu

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Coevolution, the reciprocal selection among interacting species, is still in the midst of a long and tumultuous, perhaps torturous, scientific debate that has not abated even since Janzen's (1980) succinct paper, "When is it coevolution?" In 2011, at a Mathematical BioSciences Institute workshop on "Coevolution and the ecological structure of plant-insect communities," there was no general consensus on the importance of coevolution—it is either everywhere or it rarely happens—and these same perspectives abound in the literature. How can such disparate views remain about a process that has been central to ecology and evolution? The major issues with studying coevolution are that it is extremely difficult to demonstrate, and connecting coevolution with speciation is generally done as a pattern-based endeavor. It is perhaps not unexpected, then, that two recent reviews on coevolution and diversification found very limited evidence for the process and its consequences for interacting lineages (Althoff et al. 2014; Hembry et al. 2014) even after decades of studies on the topic.

Coevolution of life on hosts by Clayton, Bush, and Johnson could not be more timely. This focused and detailed book uses the interactions of lice and their hosts as a means to guide the reader through a series of nicely crafted chapters outlining how one would pursue testing the importance of coevolution in diversification of interacting lineages. At the same time, the reader is also made keenly aware of the state of the field by the use of studies published on a wide range of taxonomic groups. This is not only a book about lice and host adaptations and counter-adaptations, this is a book about how one tests for the role of coevolution by studying a fascinating system. It is the way the authors lay out the logic and rationale for the tests and comparisons they present that will make this book timeless.

The framework that the book presents is one that could be adopted by anyone empirically testing the role of coevolution in macroevolution. Step one—combine natural history observations with key experimental tests to identify the coevolutionary selective regimes that promote specialization. Step two—examine how changes in coevolved traits at the microevolutionary scale will translate into the conditions that lead to speciation. Step three—examine phylogenetic patterns in light of the results from the first two steps. It is the culmination of research at all three steps that Clayton, Bush, and Johnson give to the reader. With nice illustrative pictures and data presentation, the authors build an argument about the pervasiveness of adaptations in lice and birds and then use these adaptations to explore the role of coevolution in the evolutionary trajectory of the two groups.

Their work also speaks quite clearly to the "coevolution is everywhere" versus "it rarely happens" perspectives. For example, documented loads of lice on birds are usually quite low in many individuals, suggesting that there is relatively weak selection on birds for defense traits. As the authors document through a series of studies on bill manipulations, however, one sees quite forcefully the continual onslaught of parasitism that would occur without the appropriate bill morphology for preening. Thus, dramatic changes in traits due to coevolutionary selection may occur quite rapidly and what we are left observing is stabilizing selection. For birds and lice that means certain bill modifications for preening and dorsal-ventrally flattened bodies and gripping appendages will likely change relatively modestly if at all over the course of generations, but variance will be continually reduced. This is an important take-home message because it suggests that we might need to redirect our efforts in how we look for the signature of coevolution.

Although not evident from the book's description or through just quickly paging through the volume, there is also much to

learn about the community ecology of parasites. The idea of host species as providing ecological replicates akin to islands is used to make comparisons about the processes that govern parasite communities and also demonstrates the power of natural selection in fine-tuning parasite lineages to the “topography” of the host body. Examples of lice that have divided up the host’s body because of slight changes in microhabitats provide fertile ground for exploring the role of competition and resource partitioning in the ecology and evolution of parasites. It is this perspective that adds to the richness of our understanding about the role of multiple species interactions in shaping parasite communities.

Whether you will become fascinated with birds and lice or other parasites is perhaps not as important as the insight into the complexities of disentangling the role of coevolution in diversification. The authors conclude the book by presenting a more nuanced picture of what is likely happening as lineages bump along through evolution, sometimes responding to one another, sometimes responding to other factors, all of which together influence speciation. To more finely dissect the role of coevolution in this process, additional terminology is invoked. Although I usually do not encourage increasing jargon, these five terms could go a long way toward clarifying the potential misconceptions about what constitutes evidence for coevolution when looking across hierarchical scales. Proposed are five different categories that encapsulate the possible evolutionary scenarios among interacting lineages—coadaptation, coadaptive diversification, coadaptive

codiversification, adaptive codiversification, and codiversification. The first three are coevolution, diversification by one lineage in response to coevolution, and diversification of both lineages as a result of reciprocal selection. The remaining two emphasize that lineages may diversify either because of unidirectional selection or for other reasons such as shared vicariance. If adopted by the field, these terms would help categorize many studies into a logical framework that would allow a better evaluation of the role of coevolution in diversification.

There is no question that the culmination of decades of work by Clayton, Bush, and Johnson has provided a rich tapestry woven together in *Coevolution of life on hosts*. Champions and skeptics of coevolution alike will find a wealth of studies and ideas that are sure to generate deep thought. In my opinion, Clayton, Bush, and Johnson have shown us that coevolution is a continual and important source of selection between interacting lineages.

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