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Natural Selection, Coevolution, and the Web of Life

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

Just eight years after the publication of Darwin's *Origin of Species*, the first issues of *The American Naturalist* appeared in print. Although originally intended to "popularize the best results of scientific study," the journal gradually began accepting original contributions to science as well. Each decade resulted in an upping of the ante. The journal published papers on the natural history of species, geology, biogeography, anthropology, archaeology, and, importantly, the application of the theory of natural selection to the traits of species. By the early decades of the twentieth century, it had become one of the venues for competing views on the major processes that drive the evolution of populations.

As biologists tried to apply the theory of natural selection to what they observed in nature, studies of interactions among species provided some of the greatest insights. Pollination and mimicry were especially fertile topics, driven initially by Darwin's book on orchids. Soon thereafter, Henry Bates and Fritz Müller published their studies on the evolution of mimetic forms in the tropics, and Hermann Müller published his studies on reciprocal adaptation between alpine plants and their insect pollinators. Although the original results of these pioneers were published in other journals and in books, *The American Naturalist* summarized some of the conclusions and became a forum for further discussion and evidence by others. During those years, some biologists also began to explore the evolution of parasitic and mutualistic symbionts. The pages of *The American Naturalist* were, again, one of the outlets for discussion of these new ideas and results.

In the first decades of the twentieth century, however, published studies on interacting species diminished. Evolutionary biologists increasingly focused on the genetic bases of inheritance, and practitioners of the new discipline of ecology focused on nonevolutionary problems in physiological ecology and community ecology. To be sure, some biologists continued to probe how interactions evolved among species, and inklings of future lines of research can be found in some papers in *The American Naturalist* and other journals. Even so, the early decades of the twentieth century mostly lacked spirited inquiry, observations, and experiments on the ecological and evolutionary processes that mold the web of life.

Among the exceptions was a set of papers written by Charles T. Brues in the 1920s and published in *The American Naturalist*. These papers analyzed broad patterns in the evolution of dietary specialization in insects. The question that possessed Brues was, How and why do different degrees of specialization evolve? Or, stated another way that anticipates future major issues in ecology and evolution, Why is there a complicated web of life? In the early 1920s, Brues explored the problem by studying patterns of specialization in plant-feeding insects (Brues 1920, 1924) and parasitic Hymenoptera (Brues 1921). These are the most species-rich taxa on earth, and these lineages show great variation in diet breadth.

Brues's 1924 paper is particularly insightful because it shows us that many of the major questions on evolving interactions that we are trying to answer today had already been identified a century ago. Brues summarized the results from researchers studying variation within species in host preference, assessed the ecological and evolutionary causes and consequences of shifts of insects onto novel hosts, and evaluated the potential for the cross-generational preference of adults to lay eggs on the hosts on which they fed as larvae. He devoted a whole page to what later became a major model for studies of incipient speciation in insects through shifts onto novel hosts: apple maggot flies, *Rhagoletis pomonella*. He weighed carefully whether acquisition of new hosts by some populations of a species represents a reversion to hosts used earlier in the phylogenetic history of a lineage. He considered variation, host-mediated population differentiation, specialization, and phylogenetic constraints as parts of the answer to the

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question of why insect species vary so widely in diet breadth.

More broadly, Brues pondered how "parallel evolution" has occurred during diversification of some plant and insect lineages. He noted, for example, that many pierid butterflies feed only on crucifers, but some lineages have shifted to legumes, and some have become restricted even to the same genus of legumes in different parts of the world. He implied, but did not state directly, that these populations may represent independent evolutionary shifts onto the same legume genus. He imagined that, in such cases, a mutation allowing a host shift must have occurred, after which the new lineage evolved and diversified further to use other legume species. One waits for Brues to take all his knowledge of variation in insects and apply it to plants and then argue that reciprocal evolution may be part of the evolutionary mix. It doesn't happen. Instead, he argues that the diversification of plant and insect lineages may have simply proceeded "side by side" and that "diversification of the insects has proceeded not necessarily with any reference to that of the plants" (Brues 1924, p. 133).

It remains a puzzle why biologists during the early decades of the twentieth century did not consider the possibility that coevolution contributes to the evolution and diversification of species. After all, in *Origin*, Darwin had used reciprocal change as one of his first examples of how natural selection could shape the traits of species, while the Müller brothers had shown how coevolutionary approaches could provide insight into some observed patterns in nature. But time and again during those decades, biologists with a deep understanding of variation and evolution on one side of an interaction failed to consider the potential evolutionary responses on the other side. Plants were often simply resource templates for those studying animal diversification; herbivores were often viewed as problems to eradicate during experiments on plant niche diversification; and microbes, when considered at all, were diseases that lowered population numbers. It took a few more decades before plant pathologists started to show how coevolution could occur through gene-for-gene interactions. And it took a couple of decades more before evolutionary biologists and evolutionary ecologists began to suggest how the coevolutionary process could shape interactions and even fuel the diversification of lineages.

Although Brues did not make the leap to coevolution, he and some other biologists of his time showed in their observations, experiments, and discussions that they understood some of the reasons why the web of life is so complex. The pages of *The American Naturalist* were then, and have remained, one of the major venues for advancing our understanding of why the entangled bank is so entangled. Today many of us express concern about the erosion of knowledge of the natural history of species and their interactions in biological training and research. By 1951, however, Brues was already expressing that concern in the pages of *The American Naturalist* in a paper titled "Natural History and the Biological Sciences." He was concerned with "the insidious myopia that is creeping into teaching and research in the biological sciences" (Brues 1951, p. 208).

In the twenty-first century, we have come to realize that much of the evolution and diversification of life is about the evolution of interactions, whether parasitic or predatory, mutualistic or competitive. Our growing reappreciation of the natural history of natural selection is bound to deepen our understanding of the evolution of populations and the diversification of lineages. Brues's worry late in his life, though, remains our worry. An understanding of how natural selection shapes the web of life demands an understanding of how selection works in the untidy and complex environments of nature.

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