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# MACROECOLOGY FROM A SAWFLY'S PERSPECTIVE[1]

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By now, the use of phylogenetic methods in ecology has become mainstream; it is 13 years since the two first major books on the subject were published (Brooks and McLennan 1991; Harvey and Pagel 1991) and one of them just had a major sequel (Brooks and McLennan 2002). So at first I was a little surprised by the bold claims of Peter Price's new book of being ''a completely novel approach.'' But although ecological studies on behavior, life history, and distribution (biogeography) have a strong evolutionary tradition and have incorporated phylogenetic methods as a natural part of the toolbox, studies on abundance and population dynamics have long remained nonhistorical, and in Price's own words have ''remained largely aloof from evolutionary thinking.'' This is indeed surprising, and Price's book is an attempt to correct the situation.

The central thesis is to show how certain plesiomorphic ''constraints,'' such as to oviposit into the soft plant tissue of developing shoots with a piercing ovipositor, can give rise to similar adaptive syndromes, with far-reaching impact on the ecology and evolution of the descendant species. Price argues for this central thesis through a suggestive voyage from his own well-studied focal species, through its relatives among the gall-inducing sawflies, to other distantly related species that share similar constraints or that carry entirely different constraints. He argues that differences in these basal constraints are a good predictor of the type of population dynamics a species will show. This is, in short, Price's phylogenetic constraints hypothesis.

Above all I'd like to view the book as a grand summary of four decades of dedicated research into the life and habits of sawflies. As such it is an interesting text on an impressive life's work. It starts with a historical overview of the development of theory on population dynamics and abundance, where Price explains how this field could fail to incorporate historical and evolutionary explanations into its toolbox for such a long time. This is followed by a fascinating summary of several decades worth of intensive work on the focal species, its life history, patterns of geographic distribution, and population dynamics. The manner of oviposition forces females to search out and oviposit into young and vigorous shoots which are patchily distributed in space and time. Hence, these species are destined for noneruptive population dynamics with low abundance. The insights gained from these studies are then applied to other related sawflies before they are extended to other groups of insects that share the same basic constraint—the piercing ovipositor. Price shows how many aspects of these insects' behavior, life history, and population dynamics are remarkably similar across these taxa. Finally, he extends the discussion by looking at groups of insects with different ''basal constraints,'' such as the Lepidoptera with their nonpiercing ovipositor, and argues that these are predisposed for a decoupling of oviposition preference from larval performance and consequently, for more eruptive population dynamics. In the last chapters he even extends his scope to discuss his hypothesis with regard to wholly different taxa, such as plants and vertebrates.

Despite the title, macroevolutionary studies using phylogenetic methods are actually rare in the book. Because of this, most of the arguments in the book are simply not testable, and therefore at best remain suggestive hypotheses. It can be argued that many comparative studies are performed with limited knowledge of the natural history of the species under study; species are merely numbers in a spreadsheet. Here we have what seems to be the opposite; vast knowledge of natural history but limited actual phylogenetic testing. Hence, the reference to ''macroevolution'' in the title should be taken more as a description of a perspective than of methodology.

Still, the chapters on sawflies show how fruitful a macroevolutionary perspective can be when combined with deep knowledge of the system under study, and this is a case in which there is some actual phylogenetic testing. These chapters also demonstrate how laborious it is to collect first-hand field and experimental data for use in a phylogenetic framework, and hence gain a good macroevolutionary understanding of a group. Moving away from the focal group, first-hand knowledge naturally decreases and, unfortunately, there is no phylogenetic testing at all. Hence, the arguments become less convincing when extended to groups outside the focal group.

Price and colleagues have been able to single out plesiomorphic traits (such as the shape of the ovipositor) that have cascading effects on the subsequent evolution within the focal group, right down to population dynamics. They can do this, with reasonable confidence, because they know the system so well. In other cases it is not so easy to make a priori assumptions about what is the constraint and what is the subsequent ''adaptive syndrome.'' Is, for example, the capacity of budworm larvae to spread by silken threads and find suitable hosts an adaptation to the female's habit of ovipositing in the fall on mature foliage, not suitable for larval growth? Or is it the other way around? One cannot

[1] *Macroevolutionary Theory on Macroecological Patterns*. P. W. Price. 2003. Cambridge University Press, Cambridge, U.K. x + 291 pp. HB $90.00, ISBN 9-521-81712-9; PB $33.00, 0-521-52037-1.

simply assume that one trait acts as a constraint for the other, without investigating what actually came first.

Much of this problem falls back on the dichotomy made in this book between constraints and adaptive syndromes. What is a constraint, really? In a general sense, we use the word to describe something that limits evolution in certain directions, but allows evolution in other directions. Such constraints arise because all evolutionary changes alter the range of possible evolutionary pathways available to a species. With a more optimistic worldview we could just as well call them opportunities, as they not only define what is impossible, but also what new possibilities arise. Each adaptation is also a constraint, in that it sets limits to future evolutionary change, but this is true for all adaptations, plesiomorphic as well as apomorphic. Typically, constraints are just plesiomorphic adaptations. Thus, Price's ''phylogenetic constraints'' and ''adaptive syndromes'' are really two sides of the same coin. The clear distinction between the constraint and the ''adaptive syndrome,'' as made in this book, is misleading in that it creates an illusory dichotomy between the concepts. I think it would be more productive in future research to investigate the character syndromes without a priori assumptions of what constitutes the important constraint in the group and what constitutes adaptations in response to it, and instead let the phylogeny advise on the causal relationships. I do think that these syndromes are real, in the sense that there are often clusters of interrelated characters that tend to occur together, and Price is certainly correct that these ''evolved characters of behavior and life history are critical for a predictive view of population ecology.'' But leaving the constraint/adaptation dichotomy aside will prevent preconceived notions about what is the constraint and what is the adaptation, and allow for the possibility that different pathways can reach the same end result; that is, produce the same character syndrome.

I actually question the usefulness of the phylogenetic constraints hypothesis. In a general sense, it is almost a truism today that a species' ecology is influenced by its evolutionary history or that present evolution is constrained by past evolution; there is no need to invoke new hypotheses for this purpose. Likewise, on a finer scale, more specific hypotheses are needed about how the character syndromes build up over time and how they affect various ecological traits, and here the constraint/adaptation dichotomy will often lead to wrong preconceptions of what is the constraint and what is the ''adaptive syndrome.'' The true pattern will almost certainly be more hierarchic than dichotomous, probably with quite complex relationships between characters in the ''syndrome''.

With the possible exception of the sawflies, Price's scenarios should really be seen as suggestive possibilities; it is certainly possible to think up alternative pathways behind many of the adaptive syndromes he describes. Without rigorous phylogenetic testing it is simply impossible to tell these alternatives apart.

Having said this, the ambitious attempt to grasp and explain whole suites of interrelated characters, the ''adaptive syndromes,'' and their ecological consequences within a macroevolutionary framework is admirable. Understanding how characters evolve and reinforce each other through time, why certain traits often occur together in a predictable way, and why a particular set of characters give rise to particular ecological features and population dynamics are major questions in biology where Price has a lot of insight. Anyone interested in these issues will find much food for thought in this book.

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