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A TRIBUTE TO TOM WOOD

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Review of *Specialization, speciation, and radiation: the evolutionary biology of insects*. Tilmon, K. J. 2008. University of California Press, Berkley, CA. xv+ 341 pp. HC $65, ISBN 978-0-520-25132-8.

Understanding the evolutionary biology of any organismal group is a daunting task. The complexity of intertwining factors such as ecological processes, life-history, population genetics, geography, and macroevolutionary patterns is enough to keep any evolutionary ecologist happily occupied for at least one, if not several, careers. This is particularly true for diverse groups in which developing generalized "rules" may be more problematic due to an increased chance of exceptions arising. If we add biotic interactions to the mix—as we rightfully should if we are to understand the evolutionary biology of any taxon—the challenge requires a true jack-of-all-trades approach. An important role model in this regard was the fearless Thomas K. Wood (1942–2002). Tom spent his career studying the evolutionary biology of membracid treehoppers and his love for this group propelled his research in a myriad of directions. Although he is well known for his studies of sympatric speciation in *Enchenopa* treehoppers, Tom's interests were diverse and his research included among other things, morphological, phylogenetic, genetic, ecological, and physiological work (Tilmon 2002; Deitz and Bartlett 2004). In Tom's spirit of striving to understand the evolutionary history of a group of organisms, Kelley Tilmon organized a symposium for the Entomological Society of America which culminated in a multiauthored volume on *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*.

As the book is dedicated to the memory of Tom Wood, we would expect no less than a comprehensive and substantive accounting of the evolution of plant-feeding insects. Readers will not be disappointed; the book is text-like in appearance and contains 23 chapters that span the gamut of disciplines and techniques involved in the study of herbivorous insects. The overarching theme of the book centers on understanding why phytophagous insects are so species rich. What attributes of these insects have facilitated their divergence? Their feeding niche is an obvious trait that sets this group apart, and clearly adaptation to host plants has long been considered an important diversifying force (Hutchinson 1959). Ehrlich and Raven's (1964) seminal paper on butterflies and their host plants identified reciprocal speciation events between interacting plant and insect groups as a major mode of speciation. Given the voluminous literature on this subject, what do we have left to learn? Haven't we long since beaten this dead horse? One might think so; however, Tilmon's book may just change the minds of even the most skeptical readers.

Rather than simply asking why these insects are so diverse, the book succeeds in highlighting what we can learn about speciation by studying herbivorous insects. Some of the most dramatic examples of explosive species radiations occur within Insecta and these have been generated by a number of processes. For instance, Hawaiian crickets have been identified as one of the fastest evolving organismal groups and their rate of evolution is attributed to sexual selection (Mendelson and Shaw 2005). *Blepharida* leaf beetles have radiated in accordance to their host plant's chemistry rather than with patterns of host plant diversification (Becerra 1997). The pollinating fig wasps (e.g., Herre et al. 1996; Machado et al. 2001; Weiblen 2004) and yucca moths (Pellmyr et al. 2008) have diversified at least in part due to their intimate and mutualistic interactions with their host plants. Furthermore, insects can also be used to examine evolution in action. An excellent example of sympatric speciation has occurred within the last 150 years in

Rhagoletis fruit flies that have diverged due to a host shift from native hawthorns to introduced apples (Berlocher and Feder 2002). Tilmon's book abounds with interesting examples and case studies that clearly demonstrate why evolutionary biologists benefit from understanding more about insects.

The book is divided into three sections. Part I "Evolution of Populations and Species" (Chapters 1–10) focuses on the evolutionary ecology of herbivorous insects and reviews host plant specialization, the factors that drive preference and performance relationships, plasticity, and host shifts. The later chapters in this section center on speciation mechanisms and these serve as a transition to the second section of the book on "Co- and Macroevolutionary Radiation" (Chapters 11–18). These chapters rely heavily on phylogenetic analyses of herbivores and their host plants to infer the processes underlying speciation in coevolved lineages. The last section of the book, "Evolutionary Aspects of Pests, Invasive Species, and the Environment" (Chapters 19–23), examines anthropogenic sources of evolutionary change in herbivorous insects, and the final chapter addresses our prospects for conservation in the face of range shifts, species introductions, and extinction (Boggs and Ehrlich, Chapter 23). Although the intended audience is not explicitly mentioned in the book, the advanced topics are best suited as a reference for researchers or as fodder for a graduate seminar on insect–plant interactions. The chapters contain an effective blend of historical and ongoing research in a number of subdisciplines and most of the chapters also offer prospective areas for the next generation of investigations.

The greatest strength of the book is the use of a multifaceted approach to examine the evolutionary biology of herbivorous insects. Simply using a phylogenetic or ecological approach, for example, would only begin to scratch the surface of the complex processes involved in the generation of diversity. Tilmon sets the ambitious goal of fostering a synergy among researchers working in somewhat disparate fields. In this regard, the book is a wonderful addition to the field by uniting ideas from multiple disciplines in an effort to build a more synthetic perspective. Even if synthesis becomes too mind-boggling, the assortment of topics and techniques means that most everyone will find something of interest. The book also covers a broad taxonomic range including swallowtail butterflies, walking sticks, flies, treehoppers, and sawflies among a number of other insects. The strength of this approach is that it emphasizes general trends among many lineages of insects. There are also a number of classic examples that are reexamined in light of new data that show how recent work has provided additional insight. For example, Feder and Forbes provide a chapter on speciation in *Rhagoletis* fruit flies that is integrative, presenting data on behavior, chemistry, and genetics (Chapter 8). Recent studies using synthetic host odors and crossing experiments have revealed the complex genetics underlying a key trait involved in speciation: host recognition. They find that host choice is a combination of both preference and avoidance and that these traits can evolve quickly. This type of synthetic approach in model systems holds great promise for chipping away at these complex problems.

There are also a few minor weaknesses of the book that I am compelled to mention even though they will not diminish the importance that this book will have in shaping research on herbivorous insects. Although the content of the book covers nearly everything from chemistry to coevolution, there were several gaps that would have strengthened the breadth of the book. The role of bacterial endosymbionts in shaping evolution of phytophagous insects is an area ripe for exploration. Roderick and Percy's chapter on diversification and coevolution in island insects (Chapter 11) and Abrahamson and Blair's chapter on speciation by host race formation (Chapter 14) briefly mention endosymbionts, but this could easily have been an entire chapter. Endosymbionts are ubiquitous and many can have drastic impacts on the ecology and evolution of their host insects (e.g., Charlat et al. 2005; Koukou et al. 2006). From my own personal bias, another area that could have been more clearly fleshed out was how phylogeographic and biogeographic studies could enhance our understanding of the evolution of herbivorous insects. A few chapters hinted at the usefulness of these types of studies (e.g., Thompson, Chapter 16); however, if we are to truly bridge the gap between micro- and macroevolutionary processes, we must also work at the phylogeography-phylogeny interface. The book also lacked a grand synthesis to help readers draw more general conclusions on the common themes—I realize this may be a tall feat for such a diverse and information-rich volume. Some readers may find the chapters somewhat redundant and few authors reference other chapters within the book. This redundancy, however, may be a strength in the sense that each chapter can be read independently and stands alone as a nice contribution to the field.

To help provide an overview of the book, I will highlight a few of my favorite chapters here. Funk and Nosil present a "comparative" approach to determine the role of ecological divergence in speciation (Chapter 9). Comparative refers not to the traditional phylogenetic analysis, but rather to comparisons of reproductive isolation of multiple populations on the same or different hosts. Funk (1998) and Funk et al. (2006) use this approach to test for ecological speciation at a microevolutionary level. In this chapter, Funk and Nosil expand on these studies by presenting a novel analysis comparing reproductive isolation, genetic distance, and ecological divergence in four exemplar insect groups. They demonstrate that a significant portion of reproductive isolation could be explained by ecological divergence. This chapter was followed by Futuyma's discussion of sympatric speciation that was thought provoking and is certain to raise the hackles of strong proponents of this somewhat controversial mechanism (Chapter 10). He argues that there are few instances (perhaps only

one!) where there are enough data to convincingly demonstrate sympatric speciation. In another chapter, Adler discusses the tug of war between contrasting selection pressures generated by herbivores on floral traits and by pollinators on plant resistance traits (Chapter 12). Her chapter demonstrates there are trade-offs between plant resistance and attraction traits and, thus, plant traits will necessarily be shaped by both herbivorous insects and pollinators. In the final section of the book, Maron and Vilá consider the question of whether exotic plants have evolved in response to the loss of their native pests and whether there is rapid evolution when biological control agents are introduced into the invasive plant's range (Chapter 20). They question whether differences observed between plants in the native and exotic range is due to rapid evolution, and they call for additional data on the natural histories of herbivores. Most importantly, their approach highlights the need for studies of multiple populations as there can be substantial among population variation in resistance to herbivores.

As Tilmon's book demonstrates, making the link between pattern and process is arguably one of the most difficult tasks facing evolutionary biologists. For instance, phylogenetic information abounds for both plant and insect taxa. What can we glean about coevolution or speciation from observing matching phylogenies between insects and plants? Perhaps vicariance events and host tracking produced the matching pattern. Conversely, what can we conclude when the phylogenies fail to match? Host shifts or other factors have instead shaped the (separate) evolutionary histories of the groups? Clearly, the evolutionary histories of phytophagous insects and the plants they feed on are intimately connected and have probably shaped each other's phylogenetic patterns, but inferring process from this pattern is challenging. What are the causes of evolutionary divergence? Can we determine the proportion of the "phylogenetic variance" (Althoff 2006) that can be attributed to the host plant, predation, interactions with mutualists, key innovations, or climate change? Furthermore, can this be extended to other taxonomic groups with somewhat similar lifestyles (e.g., parasites) or disparate ones? Blurring the lines among fields will certainly foster new ideas and tests by providing an integrative and interdisciplinary approach. Tilmon's book makes a great push toward this goal and provides a wealth of information and approaches to digest.

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