Plant–pollinator Interactions: From Specialization To Generalization

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BOOK REVIEWS

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Plant–Pollinator Interactions: From Specialization to Generalization.—Nickolas M. Waser and Jeff Ollerton [editors]. 2006. University of Chicago Press, Chicago, Illinois. 445 pp. ISBN 0-226-87400-1. $45.00 (paper).

In 1985 I was present at a lecture in which Nat Wheelwright proposed that the mutualism between seed-dispersing birds and fruit-bearing plants was characterized by lack of specialization in both partners. He gave convincing evidence for the paucity of obligate one-to-one specialization, and explained the reason why extreme specializations in these systems ought to be rare (Wheelwright and Orians 1982). In the discussion after the lecture, Pete Feinsinger expressed a similar view of plant–pollinator systems. He suggested that pollination systems shared with dispersal systems a dearth of tight dependence, one-to-one coevolution, and reciprocal specialization. For over two decades, I assumed that Wheelwright's and Feinsinger's perspective was orthodoxy; my reading of the animal–plant interactions literature did not dispel this notion. John Thompson (1994), one of the influential voices in the field, wrote: "…extreme specialization occurs even less commonly in free-living mutualisms (*such as pollination and seed-dispersal* [emphasis added]) than in predators and grazers" (p. 178). Hence, I was interested when I read the title of this edited volume: *Plant–Pollinator Interactions: From Specialization to Generalization*. Maybe it was time to revise my old-fashioned notions and embrace a new paradigm—perhaps one in which specialization in plant–pollinator systems was more important than I had believed.

I was wrong. From the cover illustrations to the final page, the book is a thorough beating of what I thought was a very dead horse. A common theme that infuses most—albeit not all—chapters, is the perceived need to dispel the "…conventional wisdom shared by most evolutionary biologists… [that] …specialization is advantageous and…a crucial feature of many pollination systems" (p. 145, chapter 7). Declaring that the book is a proclamation of a new paradigm that emphasizes generalization over specialization in pollination ecology is both tardy and unfortunate. One does not need a straw man to make the question of specialization and generalization in plant–pollinator systems interesting.

Science often advances not as a result of new observations and experiments, but when someone clears up confusing and imprecise jargon. For example, Lavoisier's clarification of chemical nomenclature revolutionized chemistry (Sánchez-Ron 2002). Arguably, the rapid growth of phylogenetic systematics is a consequence of Willy Hennig's effort to purge this discipline's language of ambiguity (Richter and Meier 1994). Waser and Ollerton's (2006) book foregoes an opportunity to define the meaning, or rather the many possible meanings, of "specialized" and "generalized." Waser and Ollerton justify their decision not to have a chapter that defines and elucidates these terms: "…such a chapter may imply that its authors have a corner on the proper definitions or wish to impose their view on other authors or readers of the book, neither of which is true" (p. xi). Although the tolerance of diversity of thought implied in such a view may be commendable under other circumstances, in a scientific text it is not. In 1790, Lavoisier (quoting Abbé de Condillac) noted that "We think only through the medium of words… The art of reasoning is nothing more than a language well arranged" (Lavoisier 1965:xiii). Failing to define scientific terms unambiguously condemns us to use them inaccurately. The chapters' authors sometimes define the terms specialized and generalized, but more often leave it to the reader to divine the meaning of their words. The confusion that results can baffle readers, and can be damaging to readers who are only beginning to explore the ecological literature. It may give them the impression, perhaps sometimes justified, that ecologists are not conscientious about their vocabulary.

This failure to define terms led some of the chapters' authors to conflate unrelated concepts. For example, several chapters meld the idea of "pollination syndromes" with that of specialization, and imply that by rejecting one, the reader must reject the other (see Chapters 1, 4, 7, 10, and 14, and Waser et al. 1996, the original paper that initiated this mix-up). The hypothesis of "pollination syndromes" asserts that suites of certain floral traits, such as color, shape, timing of nectar production, and odors, associate the bearers of these traits with discrete groups of pollinators. Thus, plants pollinated by hummingbirds should be red, tubular, pendant, odorless, open during daylight, and secrete concentrated nectar. In contrast, plants pollinated by bats should be pale, open at night, smell like butyric acid, and secrete copious dilute nectar. Faegri and van der Pijl's (1979) much-criticized, but still relevant, text lists putative pollination syndromes and their characteristics. However, syndromes and specialized mutualisms are not logically linked. This is best illustrated with an example.

Imagine a group of plants characterized as bird-pollinated; the bean-tree genus *Erythrina* is a good case in point. (Bruneau 1997). The number of avian pollinator species that visits each *Erythrina* species can range from one to very many. Furthermore, *Erythrina* species can be visited and pollinated by hummingbirds, passerines, or both. Thus, the plant species in this taxon can range from specialized to relatively generalized. The metric "number of pollinator taxa" (most often, "number of visitors") is one that many authors use to quantify degree of plant specialization (see chapters 4, 7, 8, 9, 10, and 11). One may accept the notion that generalized pollination is prevalent in *Erythrina*, at the same time that one accepts that *Erythrina*'s floral characteristics associate it with a phylogenetically discrete set of pollinators. The debate over the usefulness of pollination syndromes as hypotheses, and of their reality as nodes in phenotypic space, is vigorous and unresolved. This debate, however, is independent of the prevalence of specialization in pollination systems, construed narrowly to imply tight reciprocal dependence between one plant and one pollinator. Readers may want to consult Fenster et al. (2004) for a perspective that differs from that advocated in many chapters of Waser and Ollerton's book.

The book has five sections, with 1–6 chapters per section, and each section is preceded by an overview. The overviews are written in friendly and lively prose and attempt to capture both each chapter's content and the section's conceptual unity. This proves to be a difficult task, because some sections have little thematic unity and the chapters are organized in many different formats. For example, the second section, called "The ecology and evolution of specialized and generalized pollination" includes the following disparate collection of chapters: an interesting theoretical analysis on the evolution of specialization in flowers; a thorough analysis of patterns, processes, and mechanisms in the shift between bird and bee pollination in penstemons; a study of a community of bees and flowers in the Chihuahuan desert; a revised nomenclature for the arcane jargon that bee biologists use to determine whether bees harvest the pollen of one, a few, or many species of plants; a review of the evolution of flowers that offer no rewards; and a detailed argument for why specialization and generalization in pollination systems must be investigated in the context of the complex life history of plants. While plodding through this miscellany of topics, I wished that the chapters had summaries so that I knew what to expect, and then was able to read more selectively. The section's overview in no way prepared me or guided me to the contents of the chapters. After much slogging, I realized that the section's title was chosen astutely to include anything that could fall within the generous shadow cast by the combinations and permutations of the terms "ecology," "evolution," "specialized," "generalized," and "pollination."

The book's third section, "Community and biogeographic perspectives," is its most cohesive and, in my view, potentially most influential. At its core is an overview by Pedro Jordano and coworkers of pollinator–plant systems viewed as networks. The authors introduce the tools of network analysis and conclude that plant–pollinator networks are "small-world" (no surprises there), nested, and lacking compartmentalization. I suspect that the last conclusion will be revised when data from more complex communities, such as tropical forests, are analyzed. Although the chapter is an important contribution, it is not light reading. I will tell my students to read Lewinsohn et al.'s (2006) beautifully lucid introduction to the network analysis of plant–animal assemblages before tackling the chapter. Three chapters that rely on network analyses follow Jordano et al.'s introduction. Vázques and Aizen use null models to begin unraveling the patterns revealed by network analyses, Petanidou and Potts analyze three Mediterranean communities in detail, and Medan et al. explore the effect of seasonality on plant–pollinator networks.

The use of network analysis may represent a breakthrough in community ecology, a field that has been relatively dormant for several decades. Network analyses seem to be splendid tools for detecting patterns, and thus may be ideal for the development of a comparative framework for community ecology. Unfortunately, network analyses are often opaque about the processes that generate the patterns they disclose. The scale-free power functions that describe the distribution of the number of interactions per species, for example, are an almost inevitable consequence of complex network architecture independent of underlying processes (Strogatz 2001). However, network analyses can reveal texture in the topology of ecological interactions, and thus suggest hypotheses that ecologists can test with further observations and even with experiments. Recently, Fontaine et al. (2006) used results from network analyses to inform field experiments that probed the effect of functional diversity on the persistence of plant communities. Although network analyses are an exciting development, they contain a peril. Their attractive results may tempt ecologists into indulging in the, in my view, sterile numerology that has characterized some of the theoretical literature on food webs. We can progress best by vigorous interactions between theory and empirical research (Polis and Winemiller 1996). Pollination ecologists must remain educated and vigilant to keep theoreticians on a short rein.

The last two chapters in this section tackle the question of whether latitudinal differences exist in the degree of specialization and generalization in pollination systems. Armbruster compares four systems using a battery of approaches. His chapter contains effective, and nuanced, operational definitions of specialization and generalization, which I welcomed. His analyses are also firmly grounded in phylogenetic data. I suspect that informing network analyses with phylogenetic information can be a powerful tool, as Armbruster hints. He concludes, appropriately, with two hypotheses: 1) extreme specialization is probably rare everywhere, but 2) it is more common at lower latitudes. Ollerton et al. compared a large number of communities across latitudinal, altitudinal, and "complexity" gradients. They found "considerable variation in both the diversity and the level of specificity in plant-pollinator systems on a global scale" (p. 303).

Although I learned much from both Armbruster's and Ollerton et al.'s chapters, I found these chapters lacking a unifying comparative structure. Because I suspect that network theory provides the framework to compare communities, these two chapters can be characterized as "prenetwork." Ollerton et al., for example, relied on "pollination systems," defined *a priori*, presumably from much-disparaged pollination syndromes, to compare the prevalence of bee, bird, bat, and moth pollination across communities. Presumably, in a postnetwork world these pollination systems will be detected as compartments in a network. I suspect that the analyses of Armbruster and Ollerton et al. give only glimpses of what the conceptual development of network theory, together with the documentation of plant–pollinator interaction networks throughout the world's biomes, can reveal.

The book concludes with two sections entitled "Applications in agriculture and conservation" and "Final considerations: pollination compared with other interactions." With the exception of brief mention in Sarah Corbet's chapter, the emphasis is on conservation rather than on agriculture. Researchers interested in finding out whether or not we are facing a pollination crisis in agricultural systems (Ghazoul 2005), and on how to face it if we are, will be disappointed. Suzanne Koptur gives a sometimes entertaining, graceful chronicle of her research on the conservation of pollination systems in south Florida. Her chapter emphasizes that conservation strategies are often more dependent on the idiosyncratic details of local situations than on the availability of unifying frameworks or theoretical constructs. This "applied section" is closed by a wonderful account of several research projects on the effects of habitat fragmentation and changes in landscape structure on plant–pollinator interactions in limestone quarries and calcareous grasslands in Germany and coffee plantations in Indonesia by Steffan-Dewenter et al. These authors make a convincing case for the study of plant–pollinator systems in the context of landscapes, and give a tantalizing glimpse of the panoramas that open up when we study these interactions at these broader, and perhaps more appropriate, scales. The book concludes with a one-chapter section, "Final considerations: pollination compared to other interactions," in which Jeff Ollerton compares the specialization of plant–pollinator systems with other mutualisms. He concludes, perhaps not very surprisingly, that "biologically intimate interactions between species tend to be more ecologically specialized and taxonomically exclusive" (p. 428).

After the diversity of themes touched on by this book, I finished it with the uneasy feeling that something was amiss. Plant–pollinator interactions involve partners that obtain a reward (nectar or pollen in most cases) and partners that obtain dispersal of their gametes. Ultimately, the interaction results in reproduction for plants and in the transfer of energy and nutrients to pollinators. Curiously, plant reproductive systems, the population genetic consequences of pollination, and the trophic biology and energetics of pollinators are, with a few minor exceptions, de-emphasized in the book. It is possible that we can probe the specialization and generalization of these systems by abstracting the interaction into entities that visit and are visited, but I doubt it.

We can enrich our understanding of the patterns of specialization by considering the genetic and energetic mechanisms that shape them. Sargent and Otto (2006) showed one way this can be done. They devised an ingenious population genetic model to explore the role of species abundance on the evolution of specialization. Their model predicts that plant species evolve specialization to either a few species or functional groups of the most effective and common pollinators when their abundance is low relative to that of other plant species in their community, and evolve to be generalists when they are numerically dominant. This result has implications for how we interpret patterns of specialization in plant–pollinator networks, and is best tested in the context of plant–pollinator networks in which floral abundances have been measured.

In sum, although I believe that pollination ecologists can profit by reading this book, readers will have to pan hard for the many gold nuggets that the book contains. With few exceptions, the book's chapters are not synthetic. They are a heterogeneous mingle of data-rich accounts, reviews, and essays, and sometimes single chapters contain all three elements. Because at least one of the editors coauthored the opinion pieces that precede each section, the editors' views bring a significant tilt to the book's themes. Hence, I would also recommend some circumspection while reading it, especially to readers aiming to become familiar with specialization in pollination systems. Although the book is long it covers only a small fraction of the biological richness of plant-pollinator systems. It is not an overview of the state of the art in pollination ecology.—CARLOS MARTINEZ DEL RIO, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166. E-mail: cmdelrio@uwyo.edu

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