American Journal of Botany 90(2): 330–332. 2003.

BOOK REVIEW

PLANT–ANIMAL INTERACTIONS: A SOMEWHAT EVOLUTIONARY APPROACH[1]

SUSANNE S. RENNER[2]

Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121 USA

The last texts aiming to introduce plant–animal interactions to students came out just over a decade ago (Abrahamson, 1989; Price et al., 1991). Has there been enough change in the field to justify a new compilation? A quick comparison of the earlier volumes with Carlos Herrera and Olle Pellmyr's book shows that the answer is yes. The single most striking change is the prominent role of phylogenies and the comparative approach to the study of adaptation, which did not exist ten years ago. The new book thus provides a fresh outlook on the topics one expects to be covered, viz. flower–pollinator interactions, seed dispersal, ant–plant interactions, and herbivory by insects and by mammals. (The same topics were covered by Abrahamson [1989]; Price et al. [1991] focused on insect herbivory.) The stated purpose of *Plant–Animal Interactions: An Evolutionary Approach* is ''to provide a manageable synthesis of recent developments in the field of terrestrial plant–animal interactions'' for ''upper-division undergraduate students and those starting graduate studies'' (p. viii). To achieve this goal, Herrera and Pellmyr have assembled a book of nine chapters written specifically for this project.

The stage is set by Peter Price, who provides an idiosyncratic introduction to ''species interactions and the evolution of biodiversity'' that captured my interest mostly for being so unpredictable. Price starts with the observation that the majority of terrestrial organisms fly and from there develops the view that ''flight of plants [as pollen or spores] and animals is perhaps the most fundamental element necessary for the understanding of such rich floras and faunas as exist today, and for understanding plant and animal interactions.'' One might instead have argued for plant chemistry as the key element for understanding plant–animal interactions or, on another day, for the constant tension between mutualism and antagonism. These are mentioned briefly later in the chapter, which also emphasizes the vast numbers of known or estimated interacting taxa (compare below), the kinds of interactions, trophic levels, the role of symbiotic interactions during the evolution of life, modes of speciation, modes of coevolution, and adaptive radiation.

Inexcusably for a book that promotes an evolutionary approach, phylogenetic analysis, where it is first introduced (p. 23), is described wrongly. ''We assume that they [the outgroup species] reflect to some extent the traits of the common ancestor of the group under study, thus the ancestral states. The species with these plesiomorphic characters then form an outgroup to help analyse how a derived group'' has radiated. Why in the world would plesiomorphic states tend to be conserved in one member of a diverging pair rather than another? And what happens if we change our focal group and a former outgroup now is part of the ingroup or, conversely, an ingroup species becomes the outgroup for a smaller-scale analysis? The key insight is, of course, that parsimony lets us prefer a single hypothesized origin of a trait in the ingroup and outgroup's recent most common ancestor over two independent origins. That ingroup and outgroup be sisters is crucial to phylogenetic reconstruction; who has the derived trait state(s) is irrelevant.

The following chapter by Conrad Labandeira on the history of the associations between plants and animals more than makes up for the uneven introduction and indeed is one of the highlights of the book. This very long chapter (which includes a 13-page appendix placed at the end of the volume with supplementary figure explanations and additional references) is a masterful review of a huge literature, enriched by high-quality plates with photographs and drawings of fossils showing traces of animal–plant interactions. One of Labandeira's salient points is that while plant hosts and their insect herbivores evolve and are constantly replaced in time and space, their associations nonetheless remain constant. This is illustrated with detailed case studies. In addition, there are sections on the temporary succession of kinds of interactions, and both fossil insect–plant interactions and tetrapod–plant interactions are covered.

Extant plant–insect interactions are treated by Sharon Strauss and Arthur Zangerl, and this chapter has the expected examples of plant chemical defenses and ways insects overcome them; defense and counter-defense are seen as underlying the diversity of plant and insect species. Kjell Danell and Roger Bergström next treat mammalian herbivory. As with the preceding chapter, the absence of phylogenetic approaches is striking. Danell and Bergström see the future of plant–mammalian herbivore studies in work at the landscape level (at various scales), with a focus on ''real species and their real characteristics and activities'' (p. 131). It would be glib to ask what the focus has been so far, but the book's subtitle does raise one's expectations.

Chapter 5, on granivory by Philip Hulme and Craig Benkman, does not fulfill these expectations either. It has numerous trait comparisons across guilds, areas, and continents without any mention of possible phylogenetic effects. What contribution a comparative approach can make to the study of adaptation, co-adaptation, or coevolution remains unclear, and the chapter ends (p. 154): ''Finally, we suspect that coevolution occurs fairly commonly between plants and seed-predators. However, until we carry out careful studies testing specific models of coevolution this will remain only an opinion, which

[1] *Plant–animal interactions: an evolutionary approach.* C. M. Herrera and O. Pellmyr, eds. Blackwell Science, Oxford, UK. 2002. xi + 313 pp., ISBN 0-632-05267-8.

[2] E-mail: renner@umsl.edu.

is unfortunately the basis of many conclusions concerning coevolution between plants and seed-predators.'' Given that this is book is aimed at students, why not develop at least a theoretical case of how hypotheses about granivore–plant coevolution could be tested? This might have explained that phylogenies sometimes allow us to infer the sequence of trait evolution in interacting taxa and, when a molecular-clock approach is justified, also an absolute estimate of the ages of interactions or traits. For example, adaptations for collecting and storing floral perfumes are found in all (male) orchid bees and are the synapomorphy of this clade of bees, the Euglossinae. Sequence divergence and biogeography suggest that orchid bees arose 100 million years ago (Roubik et al., 2002). The bees' adaptations therefore evolved to collect exudates from bark or other floral sources before the relatively young groups of orchids that offer floral perfume as a reward for euglossines co-opted the bees' behavior. (The term ''molecular clock'' is mentioned once, in the glossary of Labandeira's chapter on fossil animal–plant interactions.)

The following two chapters, Pellmyr on pollination by animals and Herrera on seed dispersal by vertebrates, are the other highlights of the book. Pellmyr provides a wonderful summary of the mutual selective pressures between flowers and their pollinators, including a balanced discussion of pollination syndromes (''traits that are over-represented in flowers that attract specific types of pollinators. This is a criterion of inclusion rather than exclusion, in the sense that other visitors may very well visit the flower.'') The utility of the comparative method is illustrated with three phylogenies. One (Fig. 6.1, p. 159) shows ''the established phylogeny of seed plants,'' while the others illustrate Scott Hodges's findings on the likely diversity-enhancing role of nectar spurs in *Aquilegia* and Scott Armbruster and Bruce Baldwin's work on the evolution of floral rewards in *Dalechampia*. The seed plant topology Pellmyr uses shows Gnetales as sister to Pinaceae and thus embedded within conifers. Likely because of this, Gnetales are described as dioecious, never mind the morphological bisexuality of the cones of *Gnetum* and *Welwitschia*, and exceptionally *Ephedra*, which is the only way to understand the presence of sterile ovules producing pollination droplets mentioned in the next sentence. The phylogeny suggests that biotic pollination in seed plants evolved at least three times, in the cycads, Gnetales, and angiosperms (counting survivors only; animal-pollinated extinct groups, such as the Bennettitales, are left out here). Because of the unequal species diversity of these lineages, Pellmyr doubts that animal pollination per se was an important catalyst of lineage diversification. Arguments for and against this hypothesis and ways to resolve the question using a comparative approach are spelled-out clearly, and the book here more than lives up to its subtitle. It is said that ''there are no modern estimates of what proportion of the approximately 250 000 species of angiosperms are animal-pollinated.'' But since one need only subtract the number of taxa morphologically adapted for wind or water pollination (some 18 000 species) from the total, one can readily arrive at an estimate of animal-pollinated angiosperms. Such estimates formed the basis for studies that analyzed correlations between species diversity and biotic vs. abiotic pollination (Ricklefs and Renner, 1994; Dodd, Silvertown, and Chase, 1999, cited by Pellmyr). While these estimates are rough, greater error is likely introduced by our ignorance of the number of angiosperm species. The latter is thought to range between 250 000 and 400 000+ (Govaerts, 2001, the latter published after the book manuscript was submitted in late 2000).

The breadth and depth of Pellmyr's chapter is such that even pollination specialists are certain to learn something new. A section on ''auditory cues'' pleased me no end since collecting examples of the role of sound in plant–animal interactions is a personal hobby. The one provided by Pellmyr is that of *Mucuna holtonii*, a legume liana with bat-pollinated flowers. The erect petal reflects sound pulses produced by the echolocating bats and serves as a nectar guide (von Helversen and von Helversen, 1999). The chapter does not, however, get lost in cute examples, but manages to remain concise and focused. As elsewhere in the book, references are as recent as 2000, and there is also a general exposition of ''the utility of phylogenetic methods'' missing from other chapters.

Herrera's overview of seed dispersal is outstanding. Pity that the single phylogeny included in his chapter, a morphology-based phylogeny of seed plants (Fig. 7.1, p. 186), was not cross-referenced to the DNA-based phylogeny for the same group in Fig. 6.1. This one shows the Gnetales as sister to the angiosperms. Since the phylogeny of seed plants is unresolved, the contrasting topologies are not a problem, but why not use the opportunity to explore their implications and practice tree thinking (O'Hara, 1992)? Herrera was among the first to move evolutionary ecology from undiluted adaptationism to a view that includes phylogenetic inertia and trade-offs, as well as rapid evolution. He predictably stresses that we need to get away from null expectations of mutual adaptation and coevolution between fleshy-fruited plants and their vertebrate dispersers, which were in part motivated by the superficial resemblance of pollen dispersal and seed dispersal by animals. Among the evolutionary ramifications of the fundamental dissimilarities between the flying life stages of plants (to take up Price's ideas from chapter 1) are that there are fewer opportunities for evolutionary diversification and coadaptation associated with animal seed dispersal than with animal pollination.

The remaining two chapters, grouped under the header ''Synthesis,'' review ant–plant interactions (Andrew Beatty and Lesley Hughes) and future directions (John Thompson). The ''plants'' interacting with ants include fungi, and the chapter provides an encyclopaedic summary of research published during the last decade. Missing is a recently discovered chemically mediated tripartite ant–plant interaction. Ants that inhabit the domatia of a western Amazonian *Tococa* inject exocrine secretions into the bases of major leaf veins of surrounding plants. The secretions lead to rapid tissue necrosis and eventually defoliation and death (Morawetz, Henzl, and Wallnoefer, 1992; Renner and Ricklefs, 1998). The results are monospecific stands of up to a kilometer across of ant-inhabited species.

John Thompson's ''future directions'' is stimulating reading and makes clear what an evolutionary approach can add to the field of plant–animal interactions. In his view, ''Community ecology and physiological ecology, two of the mainstays of ecology during the first half of the last century, were two of the last strongholds of [should this be ''holdouts from''?] the Evolutionary Synthesis that took place during the middle third of the twentieth century'' (p. 241). During the 1960s and 1970s evolutionary ecology blossomed and these fields, too, came into the fold, but currently there is ''a retrenchment of community ecology into mechanisms of ecological dynamics that exclude rapid evolution of species and interactions as one of the working hypotheses.'' In Thompson's view we need to focus on such rapidly changing interactions across landscapes, especially in the face of increasing numbers of invasive species. (This focus fits with Thompson being the originator of the geographical mosaic theory of coevolution, which is laid out in this chapter.)

This is a broad volume that achieves what it set out to do, to provide a manageable synthesis of recent developments in the field of terrestrial plant–animal interaction. There are over 1100 references, and the illustrations and index entries are carefully chosen. The book will make an excellent backbone for courses on plant–animal interactions, although personally I would give such a course more of a comparative biological flavor. What exactly constitutes an evolutionary approach, however, has many meanings; witness the Evolutionary Programming Society or the subtitle of the *Journal of Memetics, Evolutionary Models of Information Transmission.*

LITERATURE CITED

ABRAHAMSON, W. G. [ED.]. 1989. Plant–animal interactions. McGraw-Hill, New York, New York, USA.

DODD, M. E., J. SILVERTOWN, AND M. W. CHASE. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. *Evolution* 53: 732–744.

GOVAERTS, R. 2001. How many species of seed plants are there? *Taxon* 50: 1085–1090.

MORAWETZ, W., M. HENZL, AND B. WALLNOEFER. 1992. Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon. *Biodiversity and Conservation* 1: 19–33.

O'HARA, R. J. 1992. Telling the tree: narrative representation and the study of evolutionary history. *Biology and Philosophy* 7: 135–160.

PRICE, P. W., T. M. LEWINSOHN, G. W. FERNANDES, AND W. W. BENSON. 1991. Plant–animal interactions. John Wiley and Sons, New York, New York, USA.

RENNER, S. S., AND R. E. RICKLEFS. 1998. Herbicidal activity of domatia-inhabiting ants in patches of *Tococa guianensis* and *Clidemia heterophylla*. *Biotropica* 30: 324–327.

RICKLEFS, R. E., AND S. S. RENNER. 1994. Species richness within families of flowering plants. *Evolution* 48: 1619–1636.

ROUBIK, D., C. DICK, K. GRUBER, AND E. BIRMINGHAM. 2002. Tropical phylogeography and orchid bees (Euglossini). Abstract. Association of Tropical Biology Meeting 2002. Panama City, Panama.

VON HELVERSEN, O., AND D. VON HELVERSEN. 1999. Acoustic guide in bat-pollinated flower. *Nature* 398: 759–760.