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Herbivore-Plant Interaction: Temperate and Tropical Patterns: Review of Peter W. Price et al., eds., *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*

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Herbivore-Plant Interactions: Temperate and Tropical Patterns

Price, Peter W., Thomas M. Lewinsohn, G. Wilson Fernandes, and Woodruff W. Benson (eds.). 1991. **Plant-animal interactions: evolutionary ecology in tropical and temperate regions.** A Wiley-Interscience Publication. Based on papers from an international symposium, held at UNICAMP (Campinas State University), Campinas, Brazil, 1988. John Wiley & Sons, Inc., New York. xiv + 639 p. $125.00, ISBN: 0-471-50937-X.

This book is an interesting compendium of old and new thoughts on the interactions of herbivores, especially insect herbivores, with plants; the title, however, seems a bit more ambitious. Pollination, for example, surely an important "plant-animal interaction" in both temperate and tropical regions, is mentioned only in passing. This most likely reflects the book's origins in an international symposium on the evolutionary ecology of tropical herbivores. As usual in such a collection of papers, the papers vary in purpose, length, and new insights; even papers that are reviews of previously published information, however, seem to me to present the authors' perspectives and some of the main questions in a coherent and synthetic way. Moreover, the book strikes me as an heroic attempt to illustrate what we know about species interactions and diversity in the Neotropics, particularly outside of Costa Rica, and the work on current questions of interest from temperate systems presented should serve as a stimulus to tropical (and temperate!) ecologists for comparative study and for increased collaboration. I enjoyed the book, even while wanting more on non-herbivores and more from a plant's perspective, and recommend it to those who can justify the expense.

Section I focuses on tropical and temperate comparisons, a theme throughout the book. Coley and Aide compare herbivory and plant defenses in temperate and tropical broadleaved forests. Price presents a well-reasoned challenge to four truisms about tropical vs. temperate systems in the literature (higher diversity, specialization, competition, and vacant niches). In contrast to Coley and Aide, Price concludes that biotic interactions are no more intense in the tropics than in the temperate regions. Lawton, in a comparative review of insect species richness, population abundances, and body sizes, concludes that many of the earlier predictions about size structure, population size, and population stability in the tropics are not holding up. Fernandes and Price compare species richness of galling insects along altitudinal gradients of tropical southeastern Brazil and temperate southwestern North America in relation to environmental harshness and plant nutrient status. They suggest that gallers survive both parasitism and fungal attack better on plants in xeric rather than mesic sites.

Section II focuses on the mutualistic relationships between plants and animals that often characterize our understanding of the tropics. Fleming reviews ecological and evolutionary patterns in fruits and vertebrate frugivores and discusses the potential of coevolutionary interaction, concluding that the "loose" interaction is important to understanding patterns in the tropics. Davidson et al. focus on understanding ecological species sorting and the evolution of specialization in ants, and Oliveira and Oliveira-Filho discuss the distribution of extrafloral nectaries in the woody flora of tropical western Brazil, presenting original observations and ideas. This section would have been improved by a good comparative review of pollination systems.

Section III centers on antagonistic relationships between plants and animals. Marquis considers host specificity, diversity of herbivore faunas, and damage to host plant for species of *Piper* in wet tropical forest. Clark and Clark, in a refreshingly botanical paper, use growth and demographic data to examine the interaction of a cycad, *Zamia skinneri,* in wet tropical forest with its relatively restricted set of herbivores. They conclude that the phenology of leaf flush of *Z. skinneri* is consistent with the herbivory-minimizing predator satiation hypothesis. Whitham et al. review the idea of a continuum in compensatory responses to herbivory and then discuss underlying physiological mechanisms. While the bulk of experimental data on the negative impacts of insects on the performance and fitness of native plants is overlooked (in spite of statements recognizing its importance!), the treatment of compensatory responses is evenhanded, and a review of the hypotheses for over-compensation and discussion of the physiology of compensation are well done.

Also in Section III, Bentley and Johnson examine the role of nitrogen fixation and the potential effect of carbon dioxide enrichment on plants as food for herbivores. One of the main points that strikes me in this synopsis of a fascinating research program is the complexity of plant response; their analysis of the relation of herbivory to CO_2-enrichment and nitrogen source presents a challenge for further work. Dirzo and Miranda present their investigations on the effect of reduced populations of nocturnal vertebrate herbivores on the diversity of tropical wet forest in Mexico.

Section IV focuses specifically on plant-butterfly interactions, an area of long-standing special interest to people concerned with tropical vs. temperate comparisons and insect vs. plant interactions. Vasconcellos Neto reports original observations on interactions between Ithomiine butterflies and Solanaceae. Feeny examines chemical constraints on the evolution of swallowtail butterflies. Scriber et al. follow up with a detailed review of the patterns of speciation and host plant use within two contrasting species groups from temperate North America: the wide-ranging polyphagous *Papilio glaucus* group and the more narrowly ranging and feeding *P. troilus* species group. To me, one of the striking differences illustrated is the behavioral antixenosis (larvae starve rather than sample unrecognized plants) of the more narrowly ranging group. Brown et al. discuss aposematic insects on toxic plants, suggesting some of the prerequisites, processes, and results of coadaptation between populations in strong ecological interactions. I do not keep up with literature on this topic and find the evidence for progressive chemical emancipation from the host fascinating and yet another example of the unexpected complexity at the interface between plants and their insect herbivores. Gilbert, discussing biodiversity of *Heliconius* within his study community, emphasizes both the ecological and evolutionary implications of pollen feeding and of pupal mating observed within the group and makes a strong argument for the ecological (as opposed to the physiological specialization) hypothesis for monophagy.

Section V examines a currently "hot" topic, the evolution of host plant specificity by insect herbivores. Futuyma reviews genetic, ecological, and phylogenetic factors in the evolution of host specificity. Heyneman et al. report new preference experiments for flower mites transported by hummingbirds, concluding that discrimination of hosts is strong in both tropical and temperate systems. Zwölfer and Romstöck-Völkl continue their interesting work analyzing interactions in the evolution of the flower- and seed-feeding insects of Cardueae hosts. Although entirely temperate in scope, this review suggests important patterns and sets the stage for the tropical comparison made later in the book by Lewinsohn. McNaughton reviews the evolutionary ecology of large tropical herbivores, emphasizing the importance of mineral heterogeneity in grasslands and the response of the large mammals of Africa.

Section VI covers some of the community patterns in natural and agricultural systems. Lewinsohn presents data on insects in flower heads of Asteraceae in southeast Brazil. After reviewing theoretical explanations for the size of phytophage assemblages, he examines local vs. total species richness using both rarefaction and path analysis in evaluating the importance of contributing factors to the patterns of species richness observed. His discussion of the constraints on typical analyses at the end is one of the most lucid I have read. Cytrynowicz discusses local herbivore richness in a subtropical cerrado area of Brazil and documents the importance of size, but finds little correlation with local abundance and taxonomic isolation of host plant. Kogan discusses contemporary adaptations of herbivores to introduced legume crops, using soybean as the model. He argues for the existence of ecological homologues, vacant feeding niches, and restriction of host range by induced defenses (phytoalexins). Altieri presents a clear review of the main hypotheses, their constraints, and newer work on the mechanisms underlying the observed decrease of herbivore assemblage richness in tropical polycultural agroecosystems. And, Garcia examines the effects of weeds and insecticides on the composition of arthropods in a tropical corn system. She finds that weeds facilitate establishment of more arthropod species; vegetational complexity decreases herbivore levels and increases those of predators.

The "flavor" of the book is entomological, with most of the authors having entomological training, interests, or perspective. This is perhaps why one of the strongest impressions I come away with is that, in spite of lip service to the importance of understanding the variation in plants and plant populations (and thus the potential for quantitative effects both ways), our thinking is still oriented toward a static view of plant numbers, distributions, vulnerabilities, and defenses. We seldom, if ever, talk about frequency distributions of concentrations of defensive compounds, or of either environmentally or genetically based variation in resistance among plants to significant loss. Nowhere in the book is any of the evidence from temperate experimental exclusion studies which shows that insects can affect growth, reproduction, and local density of native plants or alter their distributions in nature. Such data mean that suites of insects sometimes alter the performance, abundance, and distribution of their food resource plants. If insects can alter resource availability, then the view of plants as a slowly-evolving, well-protected, sedentary, self-renewing resource for insects (and other herbivores) is short-sighted and incomplete. And, in particular, we need to know if the evidence that suggests higher herbivore pressure in some habitats in the tropics, such as broad-leaf wet forest (Coley and Aide), represents reality. If so, does that imply that the demographic effects observed experimentally for short-lived perennials in temperate systems are as (or more) common for ecologically similar species in the tropics?

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