



Review: Why Plants Do Things the Way They Do

Reviewed Work(s):

Plant Reproductive Ecology by Mary F. Willson
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agreement, while expressed subtly in some of the contributions, emerges prominently in the highlights of the roundtable discussion. Powell advocates the employment of new techniques in molecular biology, while Don Levin stresses the continued application of common sense and imagination. But the proper tools for coping were not the only source of disagreement. Gill decisively decried the use of all the tools in what he considered to be artificial systems, from vinegar flies in bottles to chickens in production coops. While perhaps too strong a protest, Gill's comments reflect the dilemma that the ecology partners in this relationship recognize all too clearly: if genetics is to be applied to ecology, the introduction of some artificiality is nearly unavoidable. How much artificiality is tolerable? Conversely, the geneticist recognizes that the application of quantitative genetics to natural populations also introduces artificiality (one must assume no linkage, random mating, etc.). Where must one stop these introductions? This issue was not addressed clearly, lost in the reaction to Gill's comments. But this issue, along with the others raised in the discussion, probably echo in the corridors, labs, and field vehicles around the country, and every ecologist will be happy to read that she/he is not the only voice contributing to that echo.

In exploring any relationship in a critical way, one partner can always find fault. Geneticists may feel slighted by Gill et al.'s complaint about their lack of attention to environmental variability, when none of the plethora of papers on genetics in stochastic environments were cited. Ecologists may feel slighted by Hebert's attention to the problem of species diversity in cladoceran populations when they realize that much of that attention is focused on some naive ecological assumptions. But finding fault should not blind one partner to the virtues of the other. Geneticists should pay close attention to Gill et al.'s careful documentation of reproductive failures in natural populations. High variances among individuals, among populations, and among successive years in progeny

production can have profound consequences for the genetic structure of populations even if none of that variance has a genetic basis. Similarly, ecologists should pay close attention to Powell's discussion of genotype vs. phenotype and structural variation vs. regulatory variation. Such discoveries as are reviewed in this paper may have profound implications for our notions of which particular types of genes are actually acted on by selection through the phenotype.

The resilience of a relationship hinges on the partners' appreciation of their particular differences. Such mutual appreciation appears to be emerging. In Wyatt Anderson's overview, he points out that there are many levels of organization in population biology, and all are important if there is to be a population biology. Different questions for different levels require different technologies, and the profitable method of investigation at one level may be unyielding of answers at another level. While such perspective seems easy to maintain when reading about, it is all too easy to lose while promoting one's idiosyncratic view of science. To the credit of Anderson and all of his co-contributors, that perspective is never lost for very long.

Given the diversity of levels and approaches, it seems premature to proclaim a happy marriage between ecology and genetics. But the two fields are no longer the platonic roommates they were in 1968. In this sense, the prospects for a unified population biology are very good. The contributors are to be congratulated and, more importantly, read. The editors are to be congratulated and thanked for producing a book that is provocative, informative, outright enjoyable, and deserving of a place on the desk (not the shelf) of all population ecologists.

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WHY PLANTS DO THINGS THE WAY THEY DO

Willson, Mary F. 1983. **Plant reproductive ecology**. John Wiley & Sons, New York. ix + 282 p. \$35.00.

Plant reproductive ecology is intended to serve as a text for advanced undergraduates and beginning graduate students. The book is divided into four sections, each of which concentrates on a different aspect of the reproductive process: the evolution of life histories, breeding systems, pollination and fertilization, and seed biology. Within each section, the author explores a series of topics. By drawing on the literature, especially her own work and that of her students, she describes unexplored biological phenomena, identifies patterns, makes ecological generalizations, and speculates about a multitude of unanswered, neglected or brand-new questions: Why is dioecy so rare? What is the adaptive significance of double fertilization in angiosperms? Why do some seeds have dispersal polymorphisms? How do male-female conflicts affect selection on the process of pollen transfer? There are refer-

ences to a number of little-known and very intriguing occurrences, such as fern gametophytes that produce hormonal substances affecting the gender differentiation of their neighbors, and plants that produce smaller and shorter-lived clonal offspring as they age. A great deal of attention is devoted to "lower" plants such as ferns, algae, and mosses, taxa whose reproductive ecology has been especially neglected. As a source of ideas for research projects, the book is a gold mine. However, the students for whom it is intended might come away with a few misconceptions.

First of all, the coverage of topics is rather spotty. A few examples: predation on seeds is addressed, because seeds are reproductive units, but predation on vegetative parts is ignored, even though such herbivory is known to affect some plants' reproductive success. Ten pages are devoted to the likely adaptive significance of sexual reproduction, but there is no accompanying description of the nonsexual reproductive options available to plants (e.g. apomixis), options not nec-

essarily familiar to students. Despite a tremendous amount of attention both to the topic of reproductive effort and to the different selective pressures affecting male and female function, most of the evidence for differential costs of male and female reproduction is overlooked.

But this book was not intended as a compendium of plant reproductive biology. Rather the aim was to focus on those areas that, in the author's view, are most productive of untested speculation, and to generate in the reader excitement and enthusiasm for the pursuit of those questions.

A more serious criticism is that the use of the literature is disappointingly uncritical. Papers are cited despite their failure to demonstrate what their authors claim to demonstrate. Other references are used somewhat inappropriately. For example, to substantiate the claim that "Fecundity is often inversely correlated with amount of parental care . . .," a theoretical paper is cited that, rather than providing data on this score, is actually a model that predicts this result.

Perhaps in an attempt to make plants more interesting, they have been portrayed as warm, cuddly creatures, using terms borrowed from animal behavior, like "mate choice," "litter size," and "parental care." These zoomorphisms will rile more than a few botanists, and for good reason: the use of these terms, which are undefined for plants, tends to cloud the explanations.

The amount of genetic and mathematical detail presented is minimal; a reader who has never had a college-level mathematics or genetics course would only rarely encounter unfamiliar material. Consequently, certain areas of the book have had to be vastly oversimplified. Questions about the

evolution of sex and outcrossing are presented with only superficial reference to the genetic consequences of such behaviors. The chapter on life history evolution contains a few simple mathematical arguments, but does not provide sufficient detail to motivate clearly and effectively the theoretical predictions presented. Perhaps the object was to avoid intimidating unsophisticated readers, but these simple summaries of complex issues are often misleading, and rarely as clear as one might wish.

Finally, the whole subject is dealt with by strict adherence to what has come to be known as the "adaptationist programme." Traits are treated as disembodied entities, and adaptive explanations are constructed without consideration of genetic or other constraints. Though the book's first few pages are devoted to an acknowledgement of the pitfalls of this approach, those pitfalls are quickly ignored. Willson argues that the merits of this approach outweigh its disadvantages, at least at this stage of ecology's development. Not all her readers will be convinced.

The value of this book lies in its infectious enthusiasm for the subject, and in its profusion of provocative ideas. Too many texts give the (albeit unintentional) impression that we know all the answers. Willson's book raises as many questions as it answers, and has the potential to generate exciting new work. The investigation of these questions, however, will require a somewhat less cavalier approach.

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COEVOLUTION: ATTEMPTS AT A SYNTHESIS

Futuyma, Douglas J., and Montgomery Slatkin (eds.). 1983. **Coevolution**. Sinauer Associates, Inc., Sunderland, Massachusetts. x + 555 p. \$46.50 (cloth), \$24.95 (paper).

The concept of coevolution has had a great appeal in ecology and evolution. It is invoked for events as singular as the origin of eucaryotic cells and for topics as mundane as the difference in body size between two competing animals. Yet the rapid proliferation of coevolutionary ideas has created confusion about its conceptual domain (e.g., does it encompass all evolution due to biotic interactions?), and its popularity has drawn attention away from basic empirical uncertainties about the process itself. The volume edited by Futuyma and Slatkin is not only timely, but comprehensive in its reevaluation of this field. With 19 chapters that treat subjects ranging from bacteria-virus interactions to the role of coevolution in ecological community structure, the book achieves one of its key aims: encouraging a synthetic assessment of coevolution by drawing together critical viewpoints from diverse biological disciplines.

By stressing the utility of a narrow definition of coevolution, the editors provide a common ground for comparison of ideas. Most authors agree that reciprocal, pairwise coevolution be-

tween two species is a rather rare, or empirically elusive phenomenon, and discuss ecological factors that limit the potential for extensive mutual adaptation: asymmetries in the strength of selection exerted by partners on each other; the diversity of species that most organisms must interact with, which limits the opportunity for coevolution with any one partner; the unreliability of other species as agents of selection, due to spatial and temporal variation in their abundance. These points are perceptively developed in chapters by Futuyma (on herbivorous insects and plants), Janzen (on seed dispersal by vertebrates), Gilbert (on mimicry), and Feinsinger (on pollination biology).

In an excellent introductory chapter, Slatkin provides a lucid discussion of constraints on genetic evolution. While most of this volume attests to the continuing lack of synthesis between ecological and genetic approaches in the study of coevolution, some authors do give serious attention to the genetic architecture of species interactions. Barrett's review of crop plants and fungal pathogens is most noteworthy, critically treating the concept of complementary genetic systems, evidence for microevolution, and differences between natural communities and crop systems.

Theoretical research on coevolution is discussed in chapters