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BOOK REVIEW

POPULATION BIOLOGY 20 YEARS LATER[1]

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When Jonathan Silvertown's *Introduction to Plant Population Ecology* was first published in 1982 (Silvertown, 1982) it was a very good little book that covered an important niche. John Harper's magnum opus, *Population Biology of Plants* (Harper, 1977), had come out five years previously and become an instant classic reference, serving as a manifesto for the new field of plant population ecology. While not covering much new ground conceptually, the Silvertown volume was, well, short. And engaging! It started off with a story about two female plant ecologists on a field trip to a forest, one of whom merely made lists of species, while the good one (the population ecologist) was armed with a tree borer, tape measure, and a quadrat. The first one found out what the forest was like, but the second found out why and how it seemed to be changing. As a nerdy young professor, I didn't understand why my undergraduate plant ecology students preferred reading this to reading the chapters I assigned from Harper's book. Yet here was the cream of the story in a quick and interesting 200-page read. And, just as it was becoming a bit dated, Silvertown came out with a new edition in 1987, which covered many of the new developments of the preceding five years.

While these volumes provided nice short introductions to the ecological side of the plant population biology revolution, it was much harder to find good textbook readings for the burgeoning evolutionary and genetic side of the field. To teach plant life history evolution and the evolutionary ecology of plant reproduction and breeding systems in undergraduate plant ecology or plant population biology courses we all made many detailed handouts and assigned research papers and reviews from the original literature. This was addressed with the third edition, now titled *Introduction to Plant Population Biology* and coauthored with Jonathan Lovett Doust (Silvertown and Lovett Doust, 1993). The new volume contained totally new chapters on variation and its inheritance, ecological genetics, and the evolutionary ecology of plant sexuality and mating systems. Now eight years later, minus Lovett Doust, plus Deborah Charlesworth, we have the fourth edition. And it still is doing a good job of filling its expanded niche as a concise and engaging up-to-date introduction to plant population ecology and evolution written by two knowledgeable leaders in these fields.

What makes a book like this appealing is that it takes general concepts of ecological and evolutionary population biology and explores them in relationship to a specific group of organisms, one that the readers of the *American Journal of Botany* are particularly fond of. Is it a book about general ecological and evolutionary principles or a book about plants? It's both. How are demographic projections and competitive dynamics affected by modular growth and size indeterminism? How does being sessile affect spatial patterns and hence genetic structure and species coexistence? What happens to gene flow and breeding systems when you are sessile, hermaphroditic, and have multiple sets of sex organs? After a review of the classic metapopulation model the authors explain how recolonization of vacant sites from seed banks rather than immigration alters the way metapopulation dynamics work for many plant species. The general principles gain meaning and become tangibly concrete as they are fleshed out with the specific quirks of our green sessile friends.

So, what's new? First of all, eight years have passed since the last edition and they haven't been dull ones in most of the various areas under the heading of plant population biology. The new edition catches up on many of these new developments and has also jumped from 200 to over 300 pages. Not surprisingly, given the switch in coauthors, the greatest expansion and change in coverage occurs in the more evolutionary chapters. The book still consists of the same ten similarly titled chapters, including an introductory chapter that covers, among other things, some of the more salient consequences of being a plant. The almost doubled chapter on variation and inheritance now includes a brief discussion of QTLs and their estimation, RFLPs, RAPDs, and microsatellites. Gone are pollination syndromes, but the coverage of selfing, mechanisms that prevent it, and its consequences are greatly expanded. The more-than-doubled chapter on evolutionary and ecological genetics has expanded coverage of gene flow, drift, and selection with many new empirical results. The chapters on intraspecific (competitive) interactions and single species population dynamics have a similar, if updated feel. An incremental advance in this area over the last eight years is that the slopes on the thinning curve has moved up from $-3/2$ to $-4/3$! The chapter on age- and stage-structured plant populations has a little more coverage, e.g., a short section on demographic stochasticity and an overview of empirical elasticity results using the demographic triangle approach. The largely new chapter on metapopulations and regional dynamics (up from 9 to 20 pages) has new sections on regional dynamics, extinctions, range limits, and the reconstruction of migratory histories using DNA haplotypes. The chapter on interspecific competition and coexistence has a new section on neighborhood models, and the coverage of species coexistence goes into considerably more depth. The ninth chapter has perhaps changed the most, as reflected in the title change from ''Sex and Mating'' to ''Breeding Systems.'' Coverage of the evolution of sex and sexual selection has been reduced or eliminated in favor of expanded coverage of the evolution of selfing rates, inbreeding depression, self-incompatibility, and the evolution of separate

[1] *Introduction to plant population biology*, 4th ed. Jonathan Silvertown and Deborah Charlesworth. Blackwell Scientific Publications. 2001. viii + 347 pp. ISBN 0-632-04991-X (paper; $59.95).

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sexes. The last chapter on survival growth and fecundity aspects of life histories is broadly similar to that in the previous version, but with more coverage of seed size and dispersal in space and time and a new section on the evolution of senescence. Another helpful change from the previous edition is the listing of further readings and questions at the end of each chapter.

So here you have a whirlwind tour of much of what's going on in the field of plant population biology. As in any concise text, there is no space to go into all the nuances of uncertainty and controversy on most topics. Hence, experts in a particular field may occasionally be shocked at the way some issue close to their hearts is resolved in a seemingly cavalier sentence or two. Certainly there is much to take issue with, depending on your particular view of individual topics or even of what topics might be under- or overemphasized. For example, the organization and discussion of species coexistence mechanisms here is quite different from that in a recent review (Chesson, 2000). But as I see it, they wrote the book and did quite a nice job of presenting a short illuminating summary of a complex and diverse field. So they get to decide what they want to emphasize, and if I take issue with something, I can develop it in class.

Plant population ecology contains many theoretical developments and the authors have by and large done an excellent job of effectively presenting the intuition behind these theories (I was very satisfied with how they presented some of my ideas). However, as might be expected in a book not exclusively dedicated to theory, there is little development of the mathematical formulae, so the actual functional forms of most equations provided in the book will remain mysterious to the novice reader (e.g., those for estimating the number of QTLs, the ESS dispersal rate from Hamilton and May's model, or the conditions for invasion of cosexual populations by female mutants). Someone unfamiliar with these theories might stare at these equations for a long time, wondering how they relate to first principles and if they're supposed to make intuitive sense. The answer in many cases is yes they do make intuitive sense, but probably not from the development given here. The authors are surely competent to have done this, but to do so would have changed the scope and length of the book, so perhaps it is just as well that they didn't. But it is something to keep in mind when teaching from this book to potentially math-shy students.

Reading this book would provide a quick entry into the literature of plant population biology for graduate students or professionals. It would also make an excellent choice for a relatively short undergraduate or even graduate text covering ecological and evolutionary aspects of plant population biology. Though now 50% longer, it is still the kind of text you can read or assign cover-to-cover rather than being a large reference text from which to pick and choose topics. Coursework could easily be developed around this book possibly by assigning some papers from the primary literature to follow up on selected topics in greater depth. Likewise, one might be tempted to provide additional handouts and homework assignments to more fully develop and practice techniques you want students to master or to explain how some of the simpler theoretical results are derived from first principles. I have found this book in its various editions so useful for quickly imparting the flavor of plant population biology that I always buy at least two copies of the newest edition to keep a loaner on hand.

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