Book Reviews

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A New Chemical Ecology Series

Cardé, Ring T., and Jocelyn G. Millar, editors. 2004. **Advances in insect chemical ecology.** Cambridge University Press, New York. x + 341 p. $90.00, ISBN: 0-521-79275-4.

Key Words: chemical communication; chemical ecology; insect ecology; pheromones; volatiles.

This is intended to be the first in a series of edited volumes ''. . . designed to provide in-depth overviews and syntheses of defined areas in the chemical ecology of insects and their closely related arthropods.'' The series is off to a strong start in those terms, with chapters on chemical defenses of plants against insect herbivores, floral odors in insect pollination, plant volatiles attracting parasitic wasps, pheromones of spiders, moths, and cockroaches, semiochemicals of mites, and moths that use plant alkaloids in mating and defense. Each chapter is quite comprehensive with extensive bibliographies (as many as 350 citations in some chapters), providing useful references on the topics well into 2004.

As is often true of edited volumes, topical breadth varies among chapters. Chapters on spider and cockroach pheromones, moths and alkaloids, and on mite semiochemicals are taxonomically focused but are exhaustive within those bounds. I was astonished at the richness of ecological chemistry among just the astigmatid mites. In a lucid, well-written review, Yasumasa Kuwahara takes us from mite life histories and rearing techniques through descriptive chemistry and analytical methods to current evolutionary questions and hypotheses. And I didn't even realize that spiders use pheromones; Schulz's comprehensive review is fascinating.

Chapters by Turlings and Wäckers on how plant volatiles attract natural enemies and by Raguso on floral odor chemistry and ecology deal with phenomena that involve more taxa, but each covers all the important facts and conceptual aspects of their topics. Turlings' chapter provides just about everything known about insect-elicited plant volatiles through early 2004. Raguso takes a more evolutionary approach, suggesting hypotheses about the adaptive significance of particular floral odor blends, the timing of odor release, and the evolution of odor deceit. While he raises more questions than he can answer, the questions alone ought to inspire some thought in students and researchers.

In a chapter titled ''Phytochemical diversity of insect defenses in tropical and temperate plant families,'' Arnason et al., bite off more than anyone could chew. Focusing heavily on a few types of plant chemicals and as a consequence on a few plant families, they attempt to address too many too-big questions with too little information. Questions like ''how did defenses arise?'' ''are diverse defense chemicals redundant?'' and ''how do various chemicals interact?'' are unlikely to have single, universal answers and demand a much more comprehensive understanding that spans many more taxa and chemistries. I got the impression that the authors' focus was on particular chemistries, and that conceptual justifications for discussing them were secondary. This chapter probably should have been titled ''What we know about limonoids, triterpenes, and. . . '' (and definitely not ''. . . insect defenses. . . in plant families''). The ecological implications of this chapter are based almost entirely on experiments done with artificial diets, the results of which frequently don't have anything to do with chemical functions in a natural context. For example, I found no convincing evidence in this chapter that any of the chemicals referred to as ''antifeedants'' actually function as such in plants.

Cardé and Haynes head off in quite a different direction in their chapter, ''Structure of the pheromone communication channel in moths.'' Their approach is extremely broad and conceptual, addressing issues of the adaptive significance of various types of signaling systems and constraints on the evolution of pheromones. Some interesting questions are raised, but not many are linked clearly to specific chemistries. It may be largely a style or organizational issue, but I thought that this chapter could have been more explicit about which data support which viewpoint and how. As written, it does a better job of rolling out the landscape of current issues in pheromone ecology and evolution than it does of telling us where we are on that landscape.

The production values of the book are very good, although I caught more editing errors than one might like, and I'd favor more extensive illustration. At $90 USD and 341 pages, the price is not out of line with today's costs. A couple of chapters probably will be dated soon, since their topics are evolving rapidly. Others (e.g., sex pheromones in spiders, roaches, and mites; alkaloids in moths; theory of pheromones) will probably remain useful for some time.

Most of the chapters in this volume demonstrate clearly that chemistry is as central to ecology and evolution as is any other trait, and should be regarded as an essential component of natural history. The editors have chosen to emphasize chemical signaling here; I hope they expand their view to more aspects of chemical ecology in future volumes. Several of the authors provide references going back to the 1970s and beyond, which is exceptional and very useful now that electrons don't reach back that far. This is the place to find the complete story of cockroach sex, from diet through behavior to pest control applications. The tale of moth and butterfly use of pyrrolizidine alkaloids in defense and mating is a classic in sexual selection, and it's all here. The fabulous bola spider story (a prime example of chemical natural history) and plants calling ''friends'' are phenomena that excite students. This book will be very useful to me in teaching both a graduate chemical ecology course and entomology for non-science majors. It would be a useful reference for teachers in other disciplines (ecology, evolution, behavior), as well as to researchers.

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Visiting the Old Boys of Biogeography

Lomolino, Mark V., Dov F. Sax, and James H. Brown, editors. 2004. **Foundations of biogeography: classic papers with commentaries.** The University of Chicago Press, Chicago, Illinois. xx + 1291 p. $135.00 (cloth), ISBN: 0-226-49236-2 (alk. paper); $45.00 (paper), ISBN: 0-226-49237-0 (alk. paper).

Key words: biogeography; history of ecology; geographic ecology.

''The history of a science is the science itself . . . ''—Goethe

Biogeography shares roots with ecology in the natural history of the 18th and 19th centuries. Ecology developed disciplinary identity, with societies and journals, by the early 20th century. In contrast, biogeography did not come into its own with dedicated journals until the 1970s, and had no international society devoted to it until the 21st century. It should therefore come as no surprise that biogeography remains a dispersed and undisciplined discipline. The thread holding its various elements together is an interest in understanding geographic patterns of life, past and present. This sounds like a partial definition of ecology, and indeed ecology and biogeography overlap substantially in theory, method, and data. But biogeography also encompasses much outside the traditional bounds of ecology, including evolution, systematics, and paleontology.

The International Biogeography Society, which held its first meeting in 2003, was developed to foster unity and integration in biogeography. The volume under review represents an important step toward that goal. The compendium, developed by a diverse group of prominent biogeographers, includes 72 items ranging in age from a 1781 Linnaeus translation (originally published in Latin in 1744) to a 1982 paper by Storrs Olson and Helen James (the sole female among the 67 featured authors). The book is intended as a companion to the widely used *Foundations of ecology* volume (Real, Leslie A., and James H. Brown, editors. 1991. University of Chicago Press, Chicago, Illinois). The editors' stated goal is ''to provide students with an introduction to the theoretical and empirical foundations of the field, and as a handy source of the classic papers for practicing scientists.''

Why should students, faced with mastering an ever-burgeoning contemporary literature, or practicing scientists, scrambling to keep their research programs moving, bother to read papers of a few decades ago, let alone those a century or more old? Why spend time with the old boys of biogeography when there are so many new boys and girls to meet?

There are plenty of good answers to these questions. Certainly, mastery of a field should include understanding how its key ideas developed. This holds especially for biogeography and ecology, where we still struggle to understand phenomena and explain patterns that were identified more than a century ago. Revisiting the classics is also necessary to clarify concepts and sweep away confusion. Meanings and definitions evolve and diverge over time, and understanding history can inoculate against unproductive controversy. Also, reading the classics can instill a healthy sense of humility in our contemporary practice. By bearing witness to the traps and blind alleys that lured the past masters, and to the deep historical roots of trendy new ideas, we can gain a realistic sense of the process of science. And, finally, we should read the classics to honor those who laid the foundations for our current efforts. This may be no more than enlightened self-interest: if we nourish a culture of scholarship among our students, our own work may not be forgotten. We all secretly hope that our most beloved contributions will be read in the decades after we're gone. There is no guarantee this will happen, of course; our reprints may be used someday, as Montaigne suggested, to ''keep some lump of butter from melting in the marketplace.''

The book is divided into eight topical sections, each with an introductory essay. Four sections, ''Species ranges,'' ''The importance of islands,'' ''Assembly rules,'' and ''Gradients in species diversity'' will be of broad interest to ecologists; indeed, these could easily have been incorporated into a ''Foundations of ecology: the sequel'' volume. The other sections (''Early classics,'' ''Earth history, vicariance, and dispersal,'' ''Revolutions in historical biogeography,'' and ''Diversification'') also include material of interest to many ecologists.

Compendia of this type can be judged by two criteria: how effectively the specific selections convey the complex history of the field, and how well the accompanying commentaries orient the reader to provide a realistic sense of the science's development. Selection entails tradeoffs between papers that were particularly influential and papers that are particularly instructive in terms of the process of science. Editors of historical volumes risk committing ''Whig history,'' presenting history as if it progressed inexorably towards the ''correct'' modern viewpoint. The history of science indicates that progress is lumpy, with plenty of false leads, reversals of fortune, and wasted energy.

The book measures up well to these standards. The selection includes warty works as well as bright jewels, and most of the commentaries provide a good accounting of the twists and turns as concepts and research avenues developed toward the present. Commentaries by Robert Whittaker (islands), Nicholas Gotelli (assembly rules), and James Brown and Dov Sax (gradients) are masterly, coming from individuals who have shaped contemporary thinking on these issues. The essay on species ranges by Hengeveld, Giller, and Riddle is also informed and provocative. Those authors underestimate the degree of early to mid-20th century interest in the biogeographic significance of physiological and population processes; certainly plant geographers and ecologists (e.g., Stanley Cain, H. A. Gleason, Herbert Mason, Hugh Raup, Wladislaw Szafer) were concerned with the mechanisms governing range dynamics. They are correct, however, that this perspective has proliferated in the late 20th century, a transition driven in no small part by Rob Hengeveld's efforts.

The sections on earth history, vicariance, and diversification are also well done. In her commentary, Vicki Funk does an admirable job negotiating the contentious terrain of historical biogeography, which seems to have attracted a particularly bombastic set of personalities. Giller, Myers, and Riddle provide a nuanced treatment of dispersal and vicariance, another area that has seen bitter disputes. The evolutionary perspective on diversification provided by Heaney and Vermeij will be of interest to many ecologists. I wish they had complemented their supply-side view by discussing extinction. Species diversity can accumulate via high speciation or low extinction rates, but the latter receives relatively little attention.

The inclusion of the ''Early classics'' is welcome, especially since *Foundations of ecology* included no papers before 1887. Ecological readers will find excerpts from Buffon, de Candolle the elder, Humboldt, Edward Forbes, Darwin, Wallace, Merriam, and others interesting and rewarding. Unfortunately the accompanying commentary is largely enumerative, and the section is poorly articulated with others. Janet Browne's outstanding book, *The secular ark* (1983. Yale University Press, New Haven) or Peter Bowler's *The earth encompassed* (2000. W. W. Norton, New York) can supply the glue missing from this volume.

Another standard for judging a compilation is how many surprises we encounter. Again, the volume stands up well. How many ecologists know that island biogeography didn't start with MacArthur and Wilson, that assembly rules were proposed by Charles Elton three decades before Diamond's classic papers, and that C. B. Williams pioneered the use of null hypotheses while critiquing Elton's work? Or that the ecological maxim that abiotic factors control high-latitude species, while biotic influences dominate low-latitude species, traces back to the evolutionary geneticist Theodosius Dobzhansky? Similar nuggets are scattered throughout the book.

It's impossible not to be disappointed by omissions—such is the nature of compilations. I can't fault the editors for the inclusions, with a few exceptions (e.g., the Asa Gray essay is irrelevant; a better choice would have been his 1859 work on the flora of Japan or the 1878 essay on ''Forest geography and archaeology''). And it's hard to fault them for omissions in view of the book's length. It's too bad, though, that room couldn't have been found for Margaret Davis' influential 1976 paper on ''Pleistocene biogeography of temperate deciduous forests'' (*Geoscience and Man* **13**:13–26) which I benefit from re-reading every few years. That paper receives honorable mention in the species-range essay, but since it was published in a hard-to-find journal, inclusion in a compendium would be a service to the community. Other readers will doubtless find their own favorite omissions.

I'd like to have seen a section devoted to the tension between modern distributional and paleontological data in inferring biotic history. The development of phylogeography and proliferation of papers using genetic data to infer population and species history renders this highly topical. Biogeography underwent a mid-century shift from reliance on distribution patterns (with such diverse figures as Darwin, Wallace, C. C. Adams, Frederic Clements, H. A. Gleason, E. Lucy Braun, Gote Wilhelm Turesson, and Jens Clausen adopting this approach) to a near-exclusive emphasis on the fossil record. Edward Deevey, Jr.'s monumental 1949 review (Biogeography of the Pleistocene. I. Europe and North America. *Geological Society of America Bulletin* **60**:1315–1416) was pivotal in this transition. A half-century later, the distribution-pattern approach is resurgent based on genetic markers, but is poorly articulated with the (now-traditional) paleontological approach. A set of key papers and accompanying commentary might foster much-needed synthesis.

How might this book be used in graduate education? As the editors suggest, it could support a seminar covering the history of biogeography. A reading of the entire book, weighing in at 2 kilograms, is not for the fainthearted; only the most dedicated will slog through it all. (On the positive side, Carlos Martínez del Rio and I, with some intrepid students, survived a semester of another shelf-gorilla, Gould's *The structure of evolutionary theory* [2002. Harvard University Press, Cambridge, Massachusetts] with no apparent psychological damage.) Most ecologists would probably use the book selectively, focusing on particular sections, topics, and readings. Any of the sections and accompanying commentaries could be used together with more recent literature and contemporary reviews as a basis for a stimulating topical seminar.

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Simple Models in a Complex World

Rousset, François. 2004. **Genetic structure and selection in subdivided populations.** Monographs in Population Biology. Number 40. Princeton University Press, Princeton, New Jersey. xvi + 264 p. $79.00, £52.95 (cloth), ISBN: 0-691-08816-0 (alk. paper); $39.50, £26.95 (paper), ISBN: 0-691-08817-9 (alk. paper).

Key words: coalescent theory; kin selection; metapopulations; population genetics.

In his book entitled *Genetic structure and selection in subdivided populations,* Rousset covers many aspects of the mathematics of the single-locus population genetics of structured populations. The primary approach is the mathematics of coalescent theory; however, the subjects covered go well beyond this, including providing a useful definition of inclusive fitness and a detailed discussion of effective population size. As such, it is a valuable book, and one that I am glad I have on my shelf. That said, it is a book for the technician. A student attempting to learn the mathematics of population structure using this book will be disappointed. The problem does not lie in the math, which is nicely laid out, but rather in the writing, which at times is cryptic. Scattered throughout the book are examples of non-parallel construction, e.g., the discussion of hard selection leads seamlessly into a discussion of stepping stone models with soft selection without ever informing the reader that the transition has been made. The result of this difficult writing is that frequently one is left with needing to understand the equations in order to interpret the text. As I said, the math is reasonably well laid out, so this is not an impossible order, but it may not be the best way to learn the math in the first place.

One of the more important insights in this book is the development of the ''direct fitness'' approach to ''inclusive fitness.'' I have never been a huge fan of kin selection approaches to modeling because in most cases it is more productive to use a multilevel selection perspective. Nevertheless, much has been gained using a kin selection approach, and it has to be recognized as a valuable theoretical approach. Inclusive fitness, however, has always been especially problematical. In particular, as inclusive fitness is usually expressed (an individual accrues fitness by helping a relative), partitioning fitness becomes a difficult accounting problem. If I help my sister raise her baby it still is only one baby (unit of fitness?). Do I get some of that fitness, and if so, do I take it away from my sister? If not, do we get to count it as $1 + r$ babies? Using this formulation, making the math work out is difficult or impossible, a fact reflected in the paucity of studies that actually measure inclusive fitness. Rousset resolves this problem in a simple and correct manner: his ''direct fitness'' approach. Under this approach the fitness of an individual is measured using only those factors directly influencing that individual's fitness. Thus, in the example above, if I help my sister, her fitness increases and I gain nothing directly. Hamilton's rule still applies because the increase in my sister's fitness raises the average fitness of our kin group (the benefit portion of the equation) offsetting the effort on my part that lowers my direct fitness (the cost portion of the equation). Since the averaging for the kin group would be weighted by relatedness, Hamilton's equation is once again recaptured. In my opinion, Rousset is correct on this. The direct fitness approach is the only meaningful way to deal with inclusive fitness type problems. What is interesting about this is that it is a group selection approach. Indeed, it is the group selection approach originally pioneered by Bruce Griffing (1977. Selection for populations of interacting genotypes. Pages 413–434 *in* Edward Pollak, Oscar Kempthorne, and Theodore B. Bailey, Jr., editors. *Proceedings of the International Conference on Quantitative Genetics, August 16–21, 1976*. Iowa State University Press, Ames, Iowa) in his analysis of direct and indirect effects in crop plants. To see that this is a group selection approach, recognize that in the example above, my sister gets an increase in fitness because I help her, and my direct fitness declines. My act of altruism makes evolutionary sense because it increases the fitness of my (kin) group.

An important consequence of adopting the group selection approach is that the group and individual traits are most correctly considered to be separate traits that may have a genetic correlation that is different than predicted based on additive theory. For example, Griffing (as cited above) reasoned that individual level traits (yield for a crop plant) would be negatively genetically correlated with group level traits (yield per hectare for a population). The reasoning is that selection on individual plants to increase yield will favor those plants that can aggressively sequester nutrients at the expense of their neighbors, whereas selection at the population level would favor those populations that most efficiently shared resources. The logical consequence of this reasoning is that if an approach is adopted that uses multilevel selection allowing only partially correlated group and individual traits, then the evolutionary outcome becomes a competing rates problem. The problem with this outcome, in turn, is that an evolutionarily stable strategy (ESS) approach that works well for selective forces acting on a single trait will not work in general for such multilevel selection problems. Consider the situation where the ESS under pure individual selection is complete selfishness, and the ESS under pure group selection is complete altruism. Where a population will lie on this continuum under the combined forces of group and individual selection will depend on the relative strength of the two forces, the relative heritabilities of the group- and individual-level traits, and the correlation between them.

Under the assumption of additive gene action, the division of kin selection into group and individual components provides little insight. Thus, given the additive gene-centered approach of this book, it is hardly surprising that Rousset does not discuss the competing rates issue for ESS. However, he does do a good job of examining ESS methodologies in detail. Given that ESS has proven to be a fruitful approach for a broad range of problems, this detailed examination is quite welcome. Of particular interest is his discussion of convergence stability and evolutionary stability. Unfortunately this is one section where the writing gets in the way of the mathematics, requiring an understanding of the math before the sections can be interpreted. Suffice it to say that convergence stability is the tendency for a population to evolve towards an ESS, and evolutionary stability is the tendency for a population to stay at an ESS once it has arrived at that point. Rousset goes on to discuss the ramifications of these different aspects of stability in detail.

The models presented in this book are all fundamentally single-locus models. This important assumption of ''bean bag'' genetics is reasonable, and works well in panmictic populations. In a large panmictic population, genes are sufficiently mixed that the main effects of alleles will be reasonable estimates of their fitness, and complications such as epistasis can be ignored or relegated to ''environmental variance.'' Thus, in a large panmictic population, single locus deterministic models provide a reasonable descriptor of evolutionary change.

In metapopulations, by their nature, genes do not mix sufficiently that simple main effects of genes describe gene action, and models that ignore genetic interactions are bound to fail (Wade, Michael J., and Charles J. Goodnight. 1998. The theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. *Evolution* **52**:1537–1553). The single-locus additive dominance model is an approximation that is sensitive to the assumption of panmixia and fails when this assumption is violated. Subdivided populations are of interest because they violate this assumption. Because of the focus on additive gene action (or at most dominance) in this book, the models will remain disappointing as a means of explaining selection and evolution in subdivided populations.

The basic problem is that populations are complex systems with extensive interactions, including both genetic interactions and interactions among individuals. Within a single population, such complex systems may reveal none of their complexity. Indeed, for statistical reasons epistasis will frequently not be detectable within a single population, and interactions among individuals will be sufficiently close to random that they will not contribute to within-population evolution. The tremendous success of quantitative genetics is likely due to the fact that the range of variation within populations and the enforced random mating of selection experiments make the additive linear models of quantitative genetics excellent for describing selection within populations. A second aspect of complex genetic systems is that when simple models fail they have a tendency to fail spectacularly. Importantly, the failures often come when the parameter space is extended beyond the range for which the original model was intended, and beyond the range in which the underlying assumptions are valid. Even nonrandom mating within a single population makes the validity of the linear additive model questionable (Falconer, D. S. 1985. A note on Fisher's ''average effect'' and ''average excess.'' *Genetetical Research* **46**:337–347). Population structure can only make this worse. For example, epistasis in structured populations can have the added effect of making the effect of an allele on the phenotype unpredictable. Thus, directional individual selection acting in different populations becomes a force causing population divergence as different alleles are favored in the different populations. Population structure is an extreme deviation from panmixia, and a situation in which we should expect simple additive models to collapse. Thus, although the linear-additive approach that is the basis of the models the Rousset develops is adequate and appropriate for single populations, they should not be extended to model evolution in metapopulations because the underlying assumptions of the approach have been violated. In short, it is unlikely that Rousset's models adequately describe evolution in metapopulations.

Thus, in summary, I find that this book to be an excellent and even definitive source for the mathematics of single-locus theory in subdivided populations. As such it deserves a place on the shelf of mathematically inclined evolutionary biologists. It is not, however, the last word on evolution in structured populations. A thorough understanding of evolution in structured populations will not occur until the mathematical machinery for understanding complex genetical systems has been fully embraced by the biological community.

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