

BOOK REVIEWS

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THE LIFE AND TIMES OF PLANT SPECIES: FROM METAPOPOPULATIONS TO MUTATIONAL MELTDOWN¹

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Flowering plants are among the most species-rich groups of organisms, and there are few habitats on earth that they have not been able to invade. Close to a quarter of a million species have now been described, with countless more that have become extinct since the early Cretaceous, when the angiosperms are thought to have originated. What is the key to understanding their ecological and evolutionary versatility? Is the principal mechanism responsible for angiosperm diversification simply ecological adaptation to the countless environments suitable for plant life? You would think that after two centuries of experimental work on plant evolution (reviewed in Langlet 1971) and the early lead taken by geneticologists and biosystematists, providing a wealth of information about local adaptation and reproductive isolating mechanisms respectively, we would have clear answers to these questions, but surprisingly we do not. Many important questions concerning the evolutionary processes responsible for speciation, which have been the focus of research on other groups, are only just beginning to be addressed rigorously in plants.

What are species and why do they exist? What is the ecological basis of speciation? How important is adaptation for speciation? Can phylogenies inform us about the mechanisms of speciation? What is the genetic architecture of reproductive isolation and how rapidly does it evolve? And of special importance for botanists, do the distinctive features of plants such as immobility, hermaphroditism, and modular growth influence morphological evolution and speciation in ways fundamentally different from most animals? Certainly when this last issue was raised in the mid 1980s by Leslie Gottlieb (1984), it stimulated controversy (Coyne and Lande 1985), but unfortunately not much in the way of relevant data has emerged until recently (e.g., Bradshaw et al. 1998). Our failure to obtain satisfactory answers to these questions and the paucity of studies on plant speciation over the past three decades are surprising, given the historical development of plant evolutionary biology.

Historical Perspectives

Botanists were the first to recognize the power of the reciprocal transplant technique, with Jens Clausen, David Keck and William Hiesey of the Carnegie Institute providing a foundation for experimental studies of local adaptation in the

middle of the twentieth century. During the 1950s and 1960s, the biosystematic approach, led by Ledyard Stebbins, Verne Grant, and Herbert Baker, amassed a huge amount of information on chromosomal evolution, polyploidy, crossing relationships, and the regulation of recombination, all directly relevant to speciation. In the 1960s, with the development of population biology, field experiments were routinely used for testing ecological and evolutionary hypotheses, with John Harper and Tony Bradshaw being the most influential. Curiously, despite this early impetus few modern workers have directly linked ecological studies of the adaptive divergence of populations to the evolution of reproductive barriers. As a result we still know remarkably little about the genetics of reproductive isolation and even less about the ecological mechanisms driving speciation, even in the most intensively studied plant model systems.

Evidence for the limited interest in the ecology and genetics of plant speciation can easily be seen by thumbing through issues of *Evolution*, particularly over the past 30 years. Very few papers on speciation mechanisms are evident and instead studies on mating-system evolution, phenotypic plasticity, and the quantitative genetics and selection of life-history traits are far more prevalent. Although several of these topics are relevant to speciation, few researchers linked their findings to issues of speciation and plant diversification in general. Perhaps some evolutionary botanists were satisfied that most of the important questions on speciation mechanisms had been solved by Stebbins and colleagues, and that constructing phylogenies was a more satisfying pursuit. Many others were clearly attracted to testing predictions of the flood of theoretical models on sex allocation and the evolution of mating systems that appeared in the 1980s and 1990s. Certainly it was discouraging to hear the groans that were often the hallmark of meetings on speciation in the 1970s–1980s, when the occasional plant person invited had the temerity to raise polyploidy, selfing, or apomixis as complications to species concepts, or theories on speciation that seemed to many botanists to be derived largely from studies of fruit flies. You might have thought that comments like “Oh, they’re just plant problems,” and the implication that such exotic behavior was largely irrelevant to the “big picture” being painted for diploid outcrossing organisms, might have emboldened botanists to grasp the nettle and get down to work. But until recently it seemed to have had the opposite effect, as botanists grumbled on the sidelines about “animal chauvinists” and the apparent indifference of many zoologists to plants.

¹ *The Origin, Expansion, and Demise of Plant Species*. Donald A. Levin. 2000. Oxford University Press, New York. 230 pp. HB \$70.00, ISBN 0-19-512728-5; PB \$30.00, ISBN 0-19-512729-3.

The Author and His Book

Now at last a brave soul, Don Levin, has indeed grasped the nettle and provided a synthetic treatment of studies on the ecology and genetics of plant species, with a significant component devoted to speciation. His book, *The Origin, Expansion and Demise of Plant Species* (hereafter *OEDPS*) represents the first book to be written on the topic for 30 years and it is likely to be snapped up by plant evolutionists starved for a modern treatment and eager to move on from the now rather dated works by Jens Clausen (1951)—*Stages in the Evolution of Plant Species*—and Verne Grant (1971)—*Plant Speciation*. *OEDPS* is certainly a timely volume that corresponds to a recent flurry of research, as well as several books on various aspects of speciation that have recently appeared (Arnold 1997; Howard and Berlocher 1998; Schluter 2000).

Don Levin is well qualified to write a book about plant evolution. He is widely recognized as one of the leading workers in the field, and along with Janis Antonovics, Michael Clegg, and Subodh Jain largely founded what could be thought as the “North American Wing” of plant population biology in the 1970s & 1980s. Levin’s papers greatly influenced my own thinking as a student in the 1970s. At that time it was hard to pick up a copy of *Evolution* or *The American Naturalist* that did not contain interesting new work by Levin on a wide range of topics from pollination biology to plant defenses. His studies on *Phlox* represent some of the most imaginative experimental work on the demographic genetics of plant populations, and his classic review of gene flow in seed plants (Levin and Kerster 1974) is one of the most widely cited papers in plant evolutionary biology. With his background and with the bold claim on the cover that *OEDPS* “provides a new synthesis of evolutionary biology and ecology,” it was with some anticipation that I first sat down to find out what Levin had to say about this important but neglected topic.

Species’ Histories

At the outset it is important to point out that *OEDPS* is not really a book about plant speciation per se. Rather, it is a book about plant microevolution, with a focus on the species as the fundamental evolutionary unit. *OEDPS* covers considerably more ground than the two previous books on plant speciation and capitalizes on recent interest in small populations and species endangerment by covering not only the origin and spread of species, but also their demise and ultimate extinction. Thus, the central unifying theme of *OEDPS* is the dynamics of species history, with four sequential stages in the lives of plant species identified and described: (1) birth or origin; (2) expansion; (3) differentiation and loss of cohesion; and (4) decline and extinction. *OEDPS* is structured around these themes; the underlying premise being that species are dynamic entities with their evolutionary histories determined by interactions between their biological attributes and an environment that changes in both space and time. This is not an especially deep insight. However, this sequential approach does represent a novel way of dealing with the evolutionary biology of plant species and provides a straightforward structure to the book. An important caveat is that the simple trajectory implied by the four

stages identified by Levin oversimplifies considerable complexity and leads to a rather linear view of species’ histories. Real species often experience repeated cycles of expansion and decline corresponding to fluctuations in their environments, and these can have important evolutionary consequences.

OEDPS comprises nine chapters, each of which is well supplied with figures and tables mostly reprinted from the literature. The volume contains no new experimental data or data analysis and represents a synthesis of mostly recent research on the ecology and genetics of plant species. Those interested in how phylogenetic approaches can inform us about species delimitation and mechanisms of speciation will be disappointed as there is little on these topics. Only one of the 37 figures in the book involves a phylogenetic tree and this is used for character mapping. Despite the claim made on the cover that this work contains “insights from theory,” a weakness of this volume is the almost complete absence of theoretical approaches that could have helped to provide the conceptual underpinnings for individual chapters and motivate key questions.

The first chapter of *OEDPS* sets up the basic historical framework of the book and provides a brief synopsis of the tangled history of species concepts, concluding with a proposal for a new one (more about that below). Chapters 2 and 3 deal with the ecological and genetic bases of speciation, respectively. Separating these topics struck me as rather artificial because the demographic and genetic characteristics of populations are obviously not independent of one another, as Levin’s own work on *Phlox* has shown. Chapter 4 is about the geographical scale of speciation and contains a critique of geographical speciation and an alternative proposal concerning the most probable “unit of speciation” in plants. Chapter 5 focuses on the spread of new species and covers diverse topics, including the nature of range expansions, long-distance dispersal, genetic bottlenecks, and the factors governing range limits. Chapter 6 traces the differentiation and ultimate loss of “species cohesion” through chromosomal and ecological race formation. Subjects such as hybrid zones and character displacement are also dealt with here. The decline and extinction of species are covered in Chapter 7, with a central focus on the genetic and demographic consequences of small population size. The work winds down with a brief chapter on species in *statu nascendi* in which Levin proposes that incipient species often fail to become fully fledged entities because of various forms of “ecological and reproductive interference” from progenitors. The book concludes with a review of species duration times and how rates of speciation may differ among life forms, families, and community types. A common theme in this discussion is that ecological opportunity is a key ingredient in governing speciation rates.

Breadth versus Depth

The broad perspective of Levin’s “life and times” approach to plant species biology is both the main strength and weakness of this work. On the one hand, the wide range of possible issues that relate to species dynamics enables Levin to cover enormous territory, and few recent areas in plant

ecology and genetics do not turn up somewhere in this book. Levin has always had a penchant for integrating “hot topics” into his research and this book covers the full gamut from metapopulations to mutational meltdown. Certainly as a primer on plant microevolution or ecological genetics the work succeeds admirably. The bibliography is excellent and one of Levin’s obvious strengths is his knowledge of the literature. Unfortunately, by sacrificing depth for breadth many of the chapters lack a clear focus and often give the impression of being composed of a catalogue of short snippets of research selected to support a particular argument, or just because they are fashionable. Another annoying feature of this book is Levin’s frequent habit of making general statements without relevant supporting evidence. For example, in a section entitled “Nonadaptive Radiation” in Chapter 2 it is stated that “Nonadaptive radiation may accompany adaptive radiation as independent evolutionary transitions or nonadaptive radiation may arise through the genetic correlations of unselected traits and selected traits” (p. 37). This is followed by a discussion of *intraspecific* variation in color polymorphisms of floral traits in island populations of *Nigella degenii* and *Pedicularis dasyantha* in Greece and Norway, respectively. These patterns involve a few polymorphic genes, probably result from genetic drift, and certainly do not constitute a “nonadaptive radiation,” if indeed this concept has any merit at all, which I doubt.

Levin’s basic approach in most chapters is to begin by providing a brief, one or two paragraph narrative account about the way he sees a particular stage in the life of plant species. The rest of the chapter is then spent marshaling bits of empirical data to support his viewpoint. Chapters end with short overview sections which often record the obvious: “Species are composed of populations of various sizes and with various levels of genetic variation” (p. 39) or, more disconcertingly, announce facts that the reader is sometimes hard pressed to find solid evidence for earlier in the chapter. For example, in Chapter 8 he concludes that “The probability of a peripheral incipient species surviving is a positive function of the ecological and genomic disparities between it and its progenitor. In essence the progenitor “selects” divergent derivatives and “rejects” the others when the two are in contact” (p. 170). This is an interesting idea, but I could find no clear evidence anywhere in the book that it actually occurs. Levin’s sermon-like writing style could give the uncritical reader a false sense of security about the strength of the evidence supporting his pronouncements. Rarely does he use a truly Darwinian approach, giving equal weight to evidence for and against his ideas. In fact, my main concern about *OEDPS* is Levin’s failure to distinguish known facts from wishful thinking. Many of our most cherished evolutionary stories fail us when they are looked at more carefully (e.g., industrial melanism, see Coyne 1998) and my guess is that although this book may stimulate some, it will frustrate many others because of its lack of depth and critical analysis.

The Ecogenetic Species Concept

What new ideas or proposals emerge from Levin’s synthesis, and are they likely to impact future work in plant species biology? Levin introduces a brand new species con-

cept in *OEDPS*, thus rendering Schemske’s (2000, p. 1072) recent tongue-in-cheek plea that new species concepts should be “limited to one per century” stillborn. The Ecogenetic Species Concept is presented on pp. 10–11: “The limitations of any species concept notwithstanding, I am obliged to employ one, since this book deals with origin and fate of species. I propose that each species has a unique way of living in and relating to the environment and has a unique genetic system—that is, that which governs the intercrossability and interfertility of individuals and populations. I will refer to this as the “Ecogenetic Species Concept.” At this point the reader can be excused for wondering how this differs from the biological species concept. However, Levin goes on to distinguish ecogenetic species in terms of both their genetic systems and a range of ecological characteristics. This leads to the inevitable conclusion that “ecogenetic species occupy different niches” (p. 10). The melding of ecological and genetic criteria is obviously appealing; however, it is not at all clear how much ecological differentiation would be required for separate ecogenetic species to be recognized. After all, ecological races of species occupy different niches, but I assume these would not be accorded ecogenetic species status unless they were intersterile and hence, biological species. To make matters worse, Levin’s suggestion that “good ecogenetic species may hybridize” and that “most taxonomic species are likely to be equivalent to ecogenetic species” thoroughly confuses the issue of circumscription and left me doubtful as to whether this new species concept will be widely adopted by plant evolutionary biologists. Levin’s thinking on species concepts has evolved during the course of his career, I prefer his earlier papers on the topic with their clear focus on the origins of reproductive isolation (e.g., Levin 1978).

Spatial Scale of Speciation

The geographical context in which speciation occurs is a central focus of debate and Levin devotes Chapter 4 to this topic. He is dubious about phylogenetic and biogeographical interpretations of the scale of speciation, primarily because history can obscure the spatial relationships of progenitor and derivative and because of the assumption that progenitor species must lose their identities during the splitting of lineages, as some cladists like to argue. Ever since Harlan Lewis’s influential studies on speciation in *Clarkia*, the budding-off of peripheral isolates has appealed to plant population biologists and most have rejected the straightjacket of the monophyly rule as being inconsistent with known speciation mechanisms. Not surprisingly, Levin also favors microevolutionary considerations in his treatment over those that emphasize phylogenetic species concepts.

A curious omission from this chapter is any detailed consideration of sympatric speciation, which receives just a short paragraph with no mention of polyploidy. Although polyploidy is briefly mentioned intermittently throughout the book, the absence of a thorough population-genetic treatment framed in the context of sympatric speciation struck me as a missed opportunity. Too often, debates over the occurrence of sympatric speciation fail to take into account that this form of speciation can and does occur very commonly in plants

through polyploidy. This omission is all the more surprising because Levin's minority cytotype exclusion principle (Levin 1975) is a valuable contribution to theories on polyploid speciation, as is evident from recent experimental work on this topic (Husband 2000).

In addition to polyploidy, geographical speciation through the divergence of ecologically and geographically distinct races has been viewed as a primary mode of speciation in plants (Clausen 1951; Grant 1971). Building on his earlier paper in *Systematic Botany* (Levin 1993), Levin rejects geographical speciation because "a manifold change across a large population system is unlikely because there is no effective mechanism to bring it about" (p. 62). He argues that the absence of both uniform selection across the range of an ecological race and pervasive gene flow would prevent "the collective evolution of a race." Instead, Levin turns his attention to the local population as the unit of speciation, but also finds this wanting "given the vulnerability of single populations to extinction, the traditional premise that local speciation occurs within single isolated populations is not readily supported" (p. 73). As a way out of this dilemma, he then introduces another spatial construct "I propose that the unit of speciation often, perhaps usually, is a metapopulation" (p. 73).

Aside from the problems of determining the boundaries of metapopulations and whether the metapopulation concept is even appropriate for certain plant groups (see Eriksson 1997), I fail to see how Levin can so easily reject the local population as the primary unit of speciation. As he so cogently argued in his 1993 paper, this is the arena in which reproductive isolation first evolves and ecological divergence begins. I agree with Levin that a metapopulation perspective can be a valuable framework for studying gene flow and population divergence, especially in plant species with ephemeral population systems. However speciation, like any other evolutionary process, first begins through the conversion of variation that resides within local populations to differences between populations. Moreover, I am not convinced that the earlier proponents of geographical speciation necessarily viewed this process as occurring because geographical or ecological races are, as Levin claims, "somewhat cohesive breeding communities whose populations evolved collectively" (p. 61) through uniform selection. This seems to me to distort what they had in mind. The proponents of geographical speciation did not invoke the idea of "collective evolution," but simply recognized that once adaptations arise in local populations they have the capacity to spread, forming distinctive ecological or geographical races. Of course not all races are transitional stages on the inexorable pathway to fully fledged species, but where reproductive isolation develops between them it is hard to see why the resulting entities would not be classified as good biological or even "ecogenetic species."

New Species as Invaders

The factors influencing the spread of new species following their origin and the ecological and genetic constraints on range limits are important topics that have not received much attention from plant evolutionists. In Chapter 5, Levin tackles

these issues by reviewing information from two main sources: contemporary plant invasions involving successful weed species, mostly polyploids, and the postglacial migration of trees during the Holocene. These rather disparate ecological groups are used because they provide almost the only data available to assess the spatial and temporal dynamics of species' expansion. Levin's review of the mechanisms involved in the spread of species is valuable and his discussion of the potential role of gene flow in limiting adaptation at range margins, as Haldane (1956) originally proposed, will hopefully stimulate badly needed empirical work in this area. Up to now this issue has been largely dominated by theory (see Case and Taper 2000), and it remains to be seen how important gene flow really is at range limits in plants, particularly in perennials where populations at geographical margins are often predominantly asexual, limiting opportunities for much evolution to occur, let alone gene flow.

There are problems with Levin's use of successful plant invaders as surrogates for how new plant species are likely to spread following their origin (Chapter 5). First, humans have either deliberately or inadvertently played a major role in determining the spread and current geographical distributions of most plant invaders. This is certainly not the case for most neospecies. Second, invaders of alien territory generally do not face competition from close relatives, or their pests and diseases. However, these factors could be important in the spread of new species and, indeed, this is a major theme in Chapter 8. Finally, the life-history traits that characterize many successful invaders (e.g., rapid growth rates, high reproductive capacity, proficient dispersal) would seem to limit the generality of using them as models for most new species. While presumably aware of these issues, Levin seems undeterred as he asks rhetorically "can we learn something about the potential for neospecies invasions from the literature on invasive plants? The answer is definitely yes" (p. 90). I am much less confident. To me the term invasion usually implies rapid population growth leading to extensive geographical spread following introduction (lag phases aside). Only a very small number of "successful" speciation events seem likely to spawn plants that behave like the infamous Cheat Grass *Bromus tectorum* in the northwestern United States, a species that Levin uses to provide insight into the spread of neospecies (pp. 80–81).

Because of my own interest in invading species, I found this chapter one of the most interesting, but Levin's treatment of this topic would have been a lot more balanced had he also dealt with the behavior of new species with more local distributions. One wonders how many speciation events result in situations such as those involving the ill-fated *Stephanomeria malheurensis*. This species went extinct less than 20 years after it was discovered, partly because Cheat Grass invaded the only location in which it was known. Less successful species, including *S. malheurensis*, are briefly covered in Chapter 8, but they should have been discussed in this chapter to counter the impression given that most new species are invaders, which they certainly are not. Perhaps most neospecies like most plant introductions are ephemeral, and our perception of both is biased because we only study the "success" stories.

Species Extinction

Chapter 7 is a good review of recent work in plant conservation biology and will be useful for students interested in the ecology and genetics of small populations. Although Levin covers inbreeding depression at some length, his artificial separation of the genetic and demographic aspects of species decline leads to an important omission. There is no mention of the potential demographic costs of inbreeding depression, surely one of the main hazards of small population size. It would be interesting to know how often such demographic problems result from homozygosity at numerous mildly deleterious genes influencing various life-history stages. Indeed, this is just part of the more general problem that we currently know little about how much of the wide-fitness variation that occurs in plant populations is governed by such mutational effects. Since the intensity of inbreeding depression varies considerably with life-cycle stage and environment, it is important that a detailed understanding of the demographic costs of this variation be determined. Some discussion of these issues and suggestions on how we might proceed in the future would have been useful.

I was disappointed that Levin chose not to elaborate on his earlier suggestion that through the accumulation of many mildly deleterious genes of small effect “plant populations may be particularly vulnerable to extinction via mutational meltdown” (p. 73). I am not aware of any convincing experimental data on mutational meltdown in plant populations. Eckert et al. (1999) recently reported a similar drift-induced phenomenon involving genes of large effect resulting in the abolition of sex in geographically marginal populations of *Decodon verticillatus*, a clonal aquatic plant. However in this case, loss of sex is selectively neutral since ecological factors also prevent sexual recruitment and asexual clones perform as well as sexual clones. It would have been better if Levin had articulated why he believes that plants may be especially prone to meltdown and what kinds of research would be needed to obtain evidence on this potential cause of plant extinction.

The evolutionary significance of interspecific hybridization always seems to stir the emotions of botanists, eliciting different viewpoints and frequent swings in the popularity ratings (Heiser 1973; Ellstrand et al. 1996; Arnold 1997; Schemske 2000). Levin has always had an interest in hybridization, and in this chapter he deals with one of his favorite recent topics—the role hybridization plays in the extinction of plant species (p. 152–155). Levin’s perspective can be viewed as the flip side of Harlan and de Wet’s (1963, p. 499) compilospecies concept, in which genetically aggressive species were thought to plunder vulnerable congeners of their heredities and by doing so increased their own ecological amplitude. Now, with conservation biology all the rage, the focus has switched from the plunderer to the plundered and Levin sets alarm bells ringing that plant species may be under threat through this insidious form of “genetic pollution.” He is not alone in this concern (Rhymers and Simberloff 1996).

Compilospecies were popular when I was at graduate school, and hybridization was frequently invoked to account for all manner of variation that seemed to turn up when congeners were sympatric, as they often are. Several botanists,

unwittingly using group selection arguments, even proposed that the evolutionary benefits resulting from novel variation indicated that hybridization was part of the “adaptive systems” of plants (Rattenbury 1962; Raven 1977). However, the reality is that we have remarkably little data from natural plant populations on actual rates of hybridization, based on marker-gene analysis, and even less ecological information on hybrid establishment and fitness. Thus it is difficult to assess the ecological consequences of hybridization and how often it impairs fitness. The loss of some ovules to hybridization may not be infrequent for some congeners, but the critical issue is whether this reduction in reproductive potential has any significant influence on fertility, recruitment, and population viability. How commonly do hybrids and introgressants actually replace parental forms? My guess is that hybridization will prove to be a fairly insignificant factor in the extinction of plant species, except in the case of a few island endemics. Finding that neutral marker alleles have “contaminated species purity” hardly seems cause for concern, unless of course there is clear evidence that they accompany the loss of morphological integrity and species-specific adaptations.

Concluding Remarks

How well does *OEDPS* address some of the critical questions in plant speciation? Unfortunately, for those interested in key topics such as the ecological basis of adaptive radiation and speciation or the genetics of reproductive isolation, *OEDPS* will be a disappointment. The section on “Adaptive Radiation” (pp. 32–34) is barely two and a half pages long, not much more than the section on “Nonadaptive Radiation” mentioned earlier. Similarly, those interested in Levin’s views on the continuing debate over the relative importance of major versus minor genes in adaptation and speciation will have to be satisfied with a brief treatment of this topic. It begins with the disconcerting declaration that “I will not evaluate the merits of each of the views” (p. 40), but Levin never explains why, beyond the fact that both types of genes are obviously involved, a point that is not really at issue among the protagonists. Thus, this is not a book that provides many new insights about the details of speciation mechanisms in plants.

Alternatively, *OEDPS* will be useful for those looking for an up-to-date review of recent work in plant ecological genetics. The book can be used as a springboard into the literature and does contain several proposals that are likely to stimulate discussion, especially in graduate seminars. The species-history approach adopted by Levin is valuable because it points to obvious areas where we lack information, such as the timing of species origins, the nature of species spread, range limits, and the causes of extinction. As Levin points out, microevolutionists have written little about the evolutionary history of species, preferring instead to focus on contemporary processes amenable to experimental analysis. I would guess that many of today’s botanists working diligently at the population level on their favorite model systems have no clue about the age of the species involved, nor very much about their evolutionary history beyond perhaps their location on a molecular phylogeny. *OEDPS* should force

plant ecological geneticists to consider how history may have shaped plant phenotypes, in addition to the proximal ecological and genetic factors that are usually the subject of their attention.

The arrival of new books on various aspects of speciation seems likely to stimulate research on plant diversification and it will be interesting to see if papers on the mechanisms driving plant speciation start to appear regularly in *Evolution*. Perhaps in another 30 years, botanists will finally have enough data to explain the exceptional ecological and evolutionary diversity of the angiosperms. But perhaps this is just more wishful thinking.

LITERATURE CITED

- Arnold, M. L. 1997. Natural hybridization and evolution. Oxford Univ. Press, New York.
- Bradshaw, H. D. Jr., K. G. Otto, B. E. Frewen, J. K. McKay, and D. W. Schemske. 1998. Quantitative trait loci affecting differences in floral morphology between two species of monkey-flower (*Mimulus*). *Genetics* 149:367–382.
- Case, T. J. and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species borders. *Am. Nat.* 155:583–605.
- Clausen, J. 1951. Stages in the evolution of plant species. Cornell Univ. Press, Ithaca NY.
- Coyne, J. A. 1998. Not black and white. *Nature* 396:35–36.
- Coyne, J. A., and R. Lande 1985. The genetic basis of species differences in plants. *Am. Nat.* 126:141–145.
- Eckert, C. G., M. E. Dorken, and S. A. Mitchell. 1999. Loss of sex in clonal populations of a flowering plant, *Decodon verticillatus* (Lythraceae). *Evolution* 53:1079–1092.
- Ellstrand, N. C., R. Whitkus, and L. H. Rieseberg. 1996. Distribution of spontaneous plant hybrids. *Proc. Natl. Acad. Sci.* 93: 5090–5093.
- Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248–258.
- Gottlieb, L. D. 1984. Genetics and morphological evolution in plants. *Am. Nat.* 123:681–709.
- Grant, V. 1971. Plant speciation. Columbia Univ. Press, New York.
- Haldane, J. B. S. 1956. The relation between density regulation and natural selection. *Proc. R. Soc. Lond. B. Biol. Sci.* 145:306–308.
- Harlan, J., and J. M. J. de Wet 1963. The compilospecies concept. *Evolution* 17:497–501.
- Heiser, C. B., Jr. 1973. Introgression reexamined. *Bot. Rev.* 39: 347–366.
- Howard, D. J., and S. H. Berlocher 1998. Endless forms: species and speciation. Oxford Univ. Press, New York.
- Husband, B. C. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. *Proc. R. Soc. Lond. B* 267:217–223.
- Langlet, O. 1971. Two hundred years of of geneecology. *Taxon* 20: 653–722.
- Levin, D. A. 1975. Minority cytotype exclusion in local plant populations. *Taxon* 24:35–43.
- . 1978. The origin of isolating mechanisms in flowering plants. *Evol. Biol.* 11:185–317.
- . 1993. Local speciation in plants: the rule not the exception. *Syst. Bot.* 18:197–208.
- Levin, D. A., and H. W. Kerster. 1974. Gene flow in seed plants. *Evol. Biol.* 7:139–220.
- Rattenbury, J. A. 1962. Cyclic hybridization as a survival mechanism. *Evolution* 16:349–363.
- Raven, P. H. 1977. Systematics and population biology. *Syst. Bot.* 1:284–316.
- Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization. *Annu. Rev. Ecol. Syst.* 27:83–109.
- Schemske, D. W. 2000. Understanding the origin of species. *Evolution* 54:1069–1073.
- Schluter D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, New York.

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GENEALOGIES AND GEOGRAPHY: DECIPHERING RECENT EVOLUTIONARY HISTORY¹

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Evolution is change over time via descent with modification. Lineages with independent pathways of descent and modification give rise to differentiated populations, species, and ultimately higher taxa. Unfortunately, except in organisms with very short generation times, there is rarely an opportunity to observe the process of evolution directly, to track changes in diverging lineages as they become distinct. To gain insights into change over time, evolutionary biologists attempt to infer historical events and processes from current patterns of genetic variation. These patterns can, in principle,

reveal the signatures of historical events, including recent changes in population size (bottlenecks or expansions), gene flow (vicariance events or recent admixture), and natural selection (environmental change). However, the ongoing influence of natural selection, gene flow, and genetic drift erases these signatures, moving populations toward new equilibria that reflect the current balance of evolutionary forces rather than the consequences of historical events. In fact, both recent history and current ecology are important determinants of observed patterns of variation, but distinguishing their relative impact is rarely straightforward (Endler 1982).

Studies of spatial (geographic) patterns of variation and their interpretation have contributed in important ways to the development of evolutionary biology. These contributions

¹ *Phylogeography*. J. C. Avise. 2000. Harvard University Press, Cambridge, Massachusetts. viii plus 447 pp. HB \$49.95, ISBN 0-674-66638-0.

represent two very distinct traditions, which focus attention on different spatial and/or taxonomic scales and place different emphasis on historical versus current ecological determinants of spatial pattern. Historical biogeography is the study of the geographic distributions of species and higher taxa. Distributions are explained in terms of vicariance events and dispersal; such explanations, in turn, depend on detailed knowledge of geological history and phylogenetic relationships (Nelson and Platnick 1981). Current ecology is not often considered as an important determinant of observed distributions. (In contrast, "ecological biogeography" attempts to explain distributions in terms of the current physical and biotic environment [Brown and Lomolino 1998]). A second tradition within evolutionary biology (population and evolutionary genetics) has focused on patterns of geographic variation within species, especially on clines and abrupt spatial discontinuities. These patterns are most often explained in terms of a balance among current evolutionary forces, for example, between natural selection and gene flow (Endler 1977). Studies of intraspecific patterns have often downplayed the importance of historical influences and emphasized current ecology; debates about hybrid zone origins (secondary contact versus primary intergradation) have brought this distinction into sharp focus (Harrison 1990).

Our ability to assess patterns of genetic variation has improved dramatically in recent years, and the new methods of analysis have revolutionized what we can learn about evolutionary history. The latest revolution has followed the introduction of PCR and the widespread use of DNA sequencing as a method for generating data on population-level variation. This revolution has been accompanied by the elaboration of theory for examining the statistical properties of genealogies (coalescent theory), which has provided a conceptual framework for the accumulating data (Hudson 1990). DNA sequence data make very clear that genealogies grade into phylogenies and that we can trace pathways of descent across species boundaries. One of the leaders in this recent revolution has been John Avise, who in 1987 coined the term "intraspecific phylogeography" (Avise et al. 1987) to describe a new discipline that focused on variation within species but searched for historical explanations for geographic patterns. Now Avise has authored a book entitled *Phylogeography*, in which he describes the discipline as "concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially those within and among closely related species" (p. 3). Phylogeography, according to Avise, provides "an empirical and conceptual bridge between the traditionally separate disciplines of population genetics and phylogenetic biology" (p. 36). He contrasts phylogeography with ecogeography, which he views as a discipline that emphasizes "patterns produced by contemporary selection" (p. 7). Thus, Avise adopts the historical perspective from phylogenetics and historical biogeography and applies it to patterns of variation that traditionally have been the province of evolutionary geneticists preoccupied with the impact of ongoing selection, drift, and gene flow.

Eight years before introducing the term "phylogeography," Avise together with Robert Lansman and colleagues at the University of Georgia published two important papers

in which mtDNA genealogies defined by restriction endonuclease cleavage sites were used to examine the distribution of variation within species of small mammals (Avise et al. 1979a,b). In that same year, Wes Brown and Allan Wilson published a classic paper in which they compared restriction enzyme cleavage maps of four species of primates (Brown et al. 1979). Their data suggested that mtDNA has a rate of evolution ten times greater than that for nuclear genes. They concluded (correctly) that "mtDNA will be an extremely useful molecule for evolutionary biologists to use in assessing relationships among species and populations that diverged rather recently. . .".

In the intervening two decades, sequencing of mtDNA genes (and even entire genomes) has become commonplace. During this period, Avise has been a pioneer in the application of molecular markers in population and evolutionary biology. Throughout an enormously productive career, he has shown a consistent interest in defining and interpreting intraspecific patterns of variation and attempting to understand what they tell us about the evolutionary history of lineages. He has also focused on genealogical relationships between recently diverged populations or species, emphasizing the importance of ancestral polymorphism and random lineage extinction as determinants of relatedness and time to common ancestry. The Avise laboratory has been the source of a continuous stream of detailed empirical studies, most of which have focused on vertebrates. Avise has also authored a remarkable number of papers that develop a descriptive conceptual framework in which to interpret data from molecular ecological and molecular evolutionary studies.

Given the dominant role that John Avise has played in the development of molecular ecology and molecular population biology, it is not surprising that his latest book is a very personal account. The focus is clearly on the analysis of gene genealogies in the context of geographic distributions and the implications of genealogical patterns for understanding recent population history. There are three major sections in the book; the first provides the historical and conceptual framework, the second summarizes data on intraspecific phylogeographic patterns, and the third examines genealogical concordance (across genes and taxa) and discusses insights into speciation processes derived from phylogeography.

Patterns of variation for mtDNA provide the majority of examples in the book. Avise argues that the "special properties" of mtDNA (maternal inheritance, no recombination, rapid evolution) were essential for the triumph of a genealogical perspective, that "the historical roots of the science are intertwined with empirical studies of animal mtDNA" (p. 35). I would tend to agree with this assessment. Avise reviews data on mtDNA variation in a variety of taxa; these examples clearly illustrate the importance of a genealogical perspective for understanding current population structure and recent evolutionary history. Patterns of mtDNA variation also reveal striking genealogical concordance across taxa in regional phylogeographic studies of both terrestrial and marine species.

The examples used to illustrate genealogical patterns are most often taken from studies of vertebrates. For example, in Chapter 4 (on intraspecific patterns in animals other than humans), 50 pages are devoted to phylogeography of ver-

tebrates, whereas the discussion of patterns in invertebrates (terrestrial, freshwater, and marine) occupies only 12 pages. Plant examples are essentially absent (in part because there have been fewer studies of intraspecific phylogeography in plants). The emphasis on vertebrate examples probably accurately reflects the taxonomic sample in studies coming from the Avise lab. But, one might have hoped for a more extensive comparison of patterns in different major groups. For example, my impression is that conspecific populations and sister species of insects are often less divergent in mtDNA sequences than are corresponding groups in many vertebrate taxa; problems with ancestral polymorphism and random lineage sorting are probably correspondingly greater in insects. The contrast between vertebrates and insects might reflect consistent differences in historical effective population sizes. Larger population sizes in many insects would imply longer times for sorting of ancestral polymorphisms.

The book's intended audience includes ecologists, ethologists, population biologists, conservation biologists, and geneticists who increasingly appreciate the importance of having a historical context for understanding the evolution of trait differences. Avise makes very clear in the Preface that *Phylogeography* is "a simplified and mostly graphical" treatment of the subject. No background in mathematics is necessary; there are very few equations. The book is very readable, very clearly argued, and densely illustrated with schematic diagrams and summaries of data from the literature. Fundamental concepts are explained simply, with generous use of examples, many taken from published papers on which Avise is a co-author. Avise seems at his best when discussing work from his own laboratory group and appears to be less comfortable when he strays from this focus as he does in the chapter on human history.

Phylogeography is an excellent review of concepts that are important for developing a genealogical (phylogenetic) perspective on speciation and on patterns of variation within species. As the nearly one-hundred-page bibliography suggests, it is also a remarkable summary of data that have emerged over the past two decades. Even so, there are some notable omissions, and the book should not be read as a general introduction to methods for inferring population history and microevolutionary process. There is obvious strategic value in limiting the scope of the book (the organization is more transparent, examples can be presented in detail), but the consequence is that the book is primarily a discussion of one approach to solving a set of problems, rather than a discussion of the problems themselves.

Before the introduction of DNA technologies that allow sequence data to be obtained from large samples of individuals, it was difficult to apply phylogenetic approaches to intraspecific patterns of variation. The study of such patterns was the province of population genetics, which focused on spatial patterns and temporal changes in allele frequencies within and between populations. Allele frequency data can be extremely revealing, both for defining spatial patterns of variation and for estimating amounts of variation (genetic diversity). The great advantage of DNA sequences (as opposed to allozymes, RFLPs, microsatellites, etc.) is that they not only provide information on allele frequencies, but also information on the similarity of alleles (from which rela-

tionships among the individual alleles can be inferred). As Avise clearly emphasizes, sequence data potentially allow individual organisms to be characterized as unique haplotypes or genotypes, which can then serve as terminals in phylogenetic analysis, eliminating the need for a priori definition of populations.

However, in his enthusiasm for DNA sequence data (especially mtDNA sequences), Avise appears to turn his back on other methods and approaches, some of which he has employed (and continues to employ) very successfully in his own research. There is, to be sure, a brief (albeit somewhat unorthodox) introduction to branching processes and coalescent theory. There is also a section on estimating gene flow from F_{ST} or private alleles. However, because the focus is *phylogeography*, the recent evolutionary history of populations and species is examined primarily in the context of mtDNA haplotype networks or phylogenies. The naive reader might come away thinking that traditional population genetic approaches have little to offer, when in fact they are an important complement to phylogenetic analysis. Allele frequency data can provide insights into many of the same questions that are addressed in studies of phylogeography. Indeed, one of the great challenges for evolutionary geneticists is to develop better methods for extracting information on evolutionary history from patterns of variation (e.g., linkage disequilibrium) for arrays of single nucleotide polymorphisms. This is particularly true for attempts to understand demographic histories, that is, historical population sizes, population bottlenecks, range expansions, etc. It is true that "phylogeography attempts to build bridges between the traditionally disengaged disciplines of phylogenetics and population genetics" (p. 20), but there is, in fact, rather little population genetics in this book.

The preoccupation with mtDNA sequences is understandable, because the vast majority of data in phylogeography has thus far come from this one molecule. But Avise's apparent pessimism about the ability of nuclear gene genealogies to provide historical insights is puzzling. He comments that "to date, technical and biological hurdles have conspired to hinder retrieval of nuclear gene genealogies within most species" (p. 92). Presumably, "technical hurdles" refers to the difficulty of isolating single alleles. Because many of the organisms we work with are diploid, to sequence individual alleles we must either produce homozygous lines, clone PCR products, design allele-specific PCR primers, or work with sex-linked genes in individuals of the heterogametic sex. Some organisms will be better suited for these approaches than others, raising the possibility that model systems may play a larger role in the future of evolutionary biology. Furthermore, because effective population sizes for autosomal nuclear genes are four times those for mtDNA (mtDNA is effectively haploid and is transmitted uniparentally), we expect random lineage extinction to be slower and ancestral polymorphisms to persist longer, meaning potentially less concordance among nuclear gene genealogies and less correspondence with the "real" population history (Moore 1995). This is the "biological hurdle" to which Avise refers. Nonetheless, nuclear gene genealogies will inevitably inform our understanding of recent population history, because they trace independent pathways of descent for multiple gene re-

gions. If populations or species are not exclusive groups for many or most nuclear genes, that in itself tells us something about population history.

Of course, nuclear gene genealogies will also differ among gene regions because both selection and recombination vary across the genome. Balancing selection will tend to maintain variation in populations and across speciation events, pushing coalescence events farther back in time. In such cases, recent population histories may not be recorded in the pattern of relationships among haplotypes or genotypes. Directional selection will tend to eliminate variation, and recent selective sweeps will erase previously existing patterns of variation. The extent of the genomic region influenced by selection will depend on the strength of selection and the rate of recombination. Thus, different genome regions provide different windows on recent evolutionary history. Although phylogeneticists and population geneticists tend to gravitate to "neutral" markers, gene regions that have experienced a selective sweep some time in the past (in one or both of a pair of geographically or reproductively isolated daughter lineages) are more likely to be free of the confounding influence of shared ancestral polymorphism. Phylogenetic analysis using genes directly involved in reproductive isolation (or tightly linked gene regions) may ultimately prove to be very useful in understanding the recent history of speciation events (Ting et al. 2000).

The conviction that nuclear gene genealogies are unlikely to be informative is particularly disturbing if we are not comfortable with "traditional" population genetic approaches that rely on allele frequency data. We surely cannot afford to rely only on mtDNA, because any single marker provides a very narrow (and potentially biased) window on recent evolutionary history. Distinguishing population effects (bottlenecks or founder effects) from locus-specific effects (selective sweeps) obviously requires data from at least two independent loci. If nuclear gene genealogies provide only limited insights into recent evolutionary history, then we have no choice but to extract information from analysis of allele frequencies at multiple gene loci. It seems strange that Avise includes virtually no mention of microsatellites or of other sorts of markers (RAPDs, AFLPs, SNPs) that might be useful in this endeavor. Perhaps he felt that including this material would dilute the focus on an explicitly phylogenetic approach.

Although phylogeography is a new discipline with a rapidly expanding literature, Avise's book is primarily retrospective, a celebration of how far we have come in the past two decades. Relatively little space is devoted to outlining prospects for the future. In an era when "genomics initiatives" are sweeping university campuses and whole genome sequencing is providing remarkable insights into genome organization and evolution, it might seem a mistake to focus

exclusively on where we have been and not on where we are going. Knowing what the future holds would be particularly interesting for the audience that Avise targets. However, an opposing argument is that in rapidly developing disciplines (like "comparative genomics") it may be pointless for the author of a book to peer into the future, given that the future is likely to have come and gone before the book appears in print.

In spite of the somewhat limited methodological and taxonomic focus, this is an important book. It is an invaluable reference and source of examples for the practitioner, a clear and accessible explication of the science of phylogeography for the student. It admirably summarizes two decades of conceptual and empirical advance in a discipline that attempts to integrate information and methodology from three traditional fields of study: phylogenetics, biogeography, and population genetics. At the same time, the book provides a valuable introduction for scientists from other disciplines (ecology, behavior, conservation biology), who will surely profit from the new perspectives that it provides.

LITERATURE CITED

- Avise, J. C., R. A. Lansman, and R. O. Shade 1979a. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. I. Population structure and evolution in the genus *Peromyscus*. *Genetics* 92:279–295.
- Avise, J. C., C. Giblin-Davidson, J. Laerm, J. C. Patton, and R. A. Lansman. 1979b. Mitochondrial DNA clones and matriarchal phylogeny within and among geographic populations of the pocket gopher, *Geomys pinetis*. *Proc. Natl. Acad. Sci. USA* 76:6694–6698.
- Avise, J. C., J. Arnold, R. M. Ball, Jr., E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reeb, and N. C. Saunders. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annu. Rev. Ecol. Syst.* 18:489–522.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sinauer Associates, Sunderland, MA.
- Brown, W. M., M. George, Jr., and A. C. Wilson. 1979. Rapid evolution of animal mitochondrial DNA. *Proc. Natl. Acad. Sci. USA* 76:1967–1971.
- Endler, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton Univ. Press, Princeton, NJ.
- . 1982. Problems in distinguishing historical from ecological factors in biogeography. *Am. Zool.* 22:441–452.
- Harrison, R. G. 1990. Hybrid zones: Windows on evolutionary process. *Oxf. Surv. Evol. Biol.* 7:69–128.
- Hudson, R. R. 1990. Gene genealogies and the coalescent process. *Oxf. Surv. Evol. Biol.* 7:1–44.
- Moore, W. S. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution* 49:718–726.
- Nelson, G., and N. Platnick. 1981. *Systematics and biogeography: cladistics and vicariance*. Columbia Univ. Press, New York.
- Ting, C.-T., S.-C. Tsaur, and C.-I. Wu. 2000. The phylogeny of closely related species as revealed by the genealogy of a speciation gene, *Odyseus*. *Proc. Natl. Acad. Sci. USA* 97:5313–5316.

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