

BOOK REVIEW

The ontogeny of molecular ecology

A review of Molecular Ecology by Joanna R. Freeland

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Any successful scientific discipline has an ontogeny, often as follows: conception, a gestational period preceding a formal birth or christening, a relatively innocent childhood, an exuberant adolescence complete with growing pains, a gradual intellectual maturation during early and middle adulthood, solidification of accepted ideas with advancing age, and sometimes eventual senescence perhaps followed by rejuvenation or transformation (e.g. via a Kuhnian revolution). Signal events often mark transitions between a science's various life history stages.

Molecular ecology (ME) was conceived in the 1960s following a blind date arranged by an unlikely matchmaker (protein electrophoresis) between two strangers: laboratory genetics and outdoor natural history. The initial courtship was tempestuous but it led finally to a supportive marriage and to the birth of an offspring displaying hybrid vigour. For this chimerical neonate, the early 1970s were a time of wide-eyed adventure as the field began using its new laboratory toys to explore nature's unanticipated troves of genetic variation. These years were also a time of childlike naiveté when ME's practitioners could still pretend that a small number of allozyme markers adequately characterized whole genomes with respect to genetic distances or heterozygosities (for example), or that a definitive resolution of the selection-neutrality debate would emerge simply from statistical analyses of molecular variation patterns.¹

Periodically since the late 1970s, ME has undergone a series of growth spurts each typically stimulated by the introduction of a new laboratory technique. Youthful exuberance was on display as the adolescent field became infatuated with a succession of alluring partners: RFLP analyses, DNA fingerprinting, RAPD assays, PCR-based sequencing of mitochondrial and then of nuclear loci, microsatellite profiling, assessments of gene expression via microarrays, and several others. Each flirtation was exciting

at the time, and several of the romances expanded into rewarding relationships that continue today. Intellectual growth also accompanied each fling, as molecular ecologists were forced to develop appropriate methods to analyse, interpret, and in general to capitalize upon each new class of genetic information.

A developmental right of passage occurred in 1992 when the field launched its flagship journal, *Molecular Ecology*. Some of the discipline's first edited volumes (e.g. Hoelzel 1992) and authored textbooks (Hoelzel & Dover 1991; Avise 1994) also appeared at about that time. However, future historians may conclude that ME's emergence from adolescence did not begin until early in the 21st century when the genomics era finally was entered, and when a second-generation of molecular ecologists — fully steeped in the notion that integrating genetic and ecological perspectives on nature was both desirable and necessary — had reached a critical mass.

My ruminations (above) on ME's early ontogeny were prompted by the appearance in 2005 of Joanna Freeland's *Molecular Ecology*, which followed closely on the heels of at least three other ME textbooks published in 2004 (see Table 1). Does this proliferation of classroom treatises (among the first intended for wide audiences) mean that the field has reached another developmental milestone? Yes, I believe that it does — but first I should comment specifically on Freeland's text.

Freeland uses a comfortable, matter-of-fact writing style to canvass the current scope of the field for 'upper-level undergraduate and postgraduate students, as well as researchers who may be relatively new to molecular ecology.' In two opening chapters, she introduces several classes of molecular markers and what each can reveal about genetic variation. She then devotes the six remaining chapters to ecological applications for molecular markers in the following contexts: (i) single populations, e.g. with respect to quantifying genetic variation, assessing effective population sizes and demographic bottlenecks, and estimating inbreeding; (ii) multiple populations, e.g. in characterizing population structure, quantifying gene flow, conducting assignment tests, and identifying spatial

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Table 1 Product details: a consumers' thumbnail guide to four recent textbooks in molecular ecology

Parameter or topic	Freeland 2005	Beebe & Rowe 2004*	Lowe <i>et al.</i> 2004	Avise 2004
Technical parameters				
Page length	388	346	326	684
Number of chapters	8	10	7	9
Number of references (approximate)	680	530	1100	4400
Glossary	yes	yes	yes	no
Appendices	no	yes	yes	no
Boxes (with details and asides)	yes	no	yes	yes
Review questions (and answers)	yes	no	no	no
Topics given primary coverage				
Overview and scope of field	Chap. 1	Chap. 1	Chap. 1	Chap. 1
History of field	little	Chap. 1	little	Chap. 2
Molecules, lab methods (descriptions)	Chap. 2	Chap. 2, Appendix	Chap. 2	Chap. 3
Data analyses (method descriptions)	dispersed	Appendix	dispersed	Chap. 4
Forensics, wildlife identification	dispersed	Chap. 3	—	Chap. 5
Parentage, behavioural ecology	Chap. 6	Chap. 4	—	Chap. 5
Population genetics, structure	Chaps. 3, 4	Chaps. 5, 7	Chaps. 3–5	Chap. 6
Phylogeography	Chap. 5	Chap. 7	Chap. 5	Chap. 6
Speciation and hybridization	little	little	Chap. 6	Chap. 7
Phylogeny, systematics	little	little	little	Chap. 8
Conservation genetics	Chap. 7	Chap. 8	scattered	Chap. 9
Empirical case studies	many, dispersed	many, dispersed	Chap. 7	many, dispersed
Microbial ME	little	Chap. 9	little	dispersed
Transgenic organisms in ME	Chap. 8	Chap. 10	—	—
Overall major strength of book	simplicity	simplicity	procedures	breadth, depth
Audience (subjective opinion)	begin.–intermed.	begin.–intermed.	intermed.	begin.–advanced

*previously reviewed in Hinten 2006.

footprints of genetic drift and natural selection; (iii) phylogeography, including discussions of intraspecific networks and gene trees, molecular clocks, coalescent processes, and cursory treatments (unfortunately so) of speciation and hybridization; (iv) behavioural ecology, involving genetic assessments of parentage, breeding behaviours and mating systems, extended kinship, sex-biased dispersal, and other topics such as molecular forensic analyses of dietary habits; (v) conservation genetics, including treatments of molecular taxonomy, DNA barcoding, inbreeding and outbreeding depression, captive breeding programmes, and biotic translocations; and (vi) special topics in wildlife forensics, agriculture, and fisheries.

Freeland's book has an ecological more so than molecular orientation, meaning that it is stronger on biological applications than on laboratory techniques or population genetic analyses. Thus, depending on the audience, a major strength of this textbook — its relative simplicity — is simultaneously its primary limitation. Beginners will find the treatment straightforward and nonintimidating, but advanced students and researchers may yearn for deeper insights into the many fascinating nuances and caveats of ME analyses in actual practice. This is not meant to be an indictment of Freeland's effort, because trade-offs between accessibility and profundity are almost inevitable in any

entry-level textbook. Indeed, for its intended purpose this is an excellent work that provides an informative and highly readable introduction to the field.

Three other ME textbooks were published one year earlier, and their salient features are summarized in Table 1. Because I authored one of these volumes, it would be inappropriate for me to express here my personal opinions on the books' relative merits. However, in considering these four volumes, what impressed and surprised me most is their remarkable likeness in terms of overall formats and topics covered (albeit at different depths and breadths). This suggests that the field of ME has, for better or worse, reached a considerable level of consensus regarding its current approaches and ambit.

Commonalities among these four textbooks include the following. Each treatment begins with an introductory chapter outlining the field. Each devotes one early background chapter (or an appendix) to basically the same array of laboratory methods, and each describes (either in a focused chapter or dispersed across the text) standard suites of population genetic parameters and data analysis methods. Each textbook devotes a chapter or major portion thereof to traditional genetic analyses of population structure, and another such chapter to the special genealogical orientation of phylogeography. Three of the four books

devote a full chapter to conservation genetics. Similarly, three of the four deal extensively with genetic analyses in the context of behavioural ecology, and with genetic analyses in various aspects of wildlife forensics. The four ME textbooks also display some notable differences (Table 1). For example, only two of them explore the history of the field, only two treat speciation and hybridization at appropriate length, and only one also includes extensive coverage of supraspecific phylogeny and systematics (two topics traditionally reserved for textbooks in molecular evolution rather than molecular ecology).

The near-simultaneous appearance of these four ME textbooks suggests that the field may have graduated to a very early stage of adulthood. The discipline is now well established, has a recognizable persona, and is projecting its appeal to a broader audience. While celebrating this ontogenetic maturation, perhaps it is time also to reflect that ME is not yet close to all that it can be or is likely to become, even in the near future. As evidenced by the field's recent textbooks, ME's empirical successes to date have mostly involved what molecular markers (often neutral) can reveal about the behaviours, genetic relationships, and natural histories of a wide variety of organisms, and the accomplishments are impressive indeed. Relatively scarce, however, are other imaginable categories of ME studies, such as those that draw informative links between molecular genotypes and adaptive phenotypes, or how such causal connections might play out on natural ecological stages.

In support of this last contention, consider the following. In 2001, the journal *Molecular Ecology* announced an editorial decision to group its published articles into seven subject areas, six of which (involving population and conservation genetics; phylogeography, speciation, and hybridization; kinship, parentage, and behaviour; molecular diagnostics; and so on) correspond closely to topics addressed at length in most if not all of the four textbooks described above. The remaining category was entitled 'molecular adaptation and environmental genomics'. From 2001 through 2006, by my count 1456 articles were published in *Molecular Ecology*, only 35 of which (2.4%) involved functional adaptation or environmental genetics (and more than half of those 35 articles appeared in one special issue of the journal — May 2003). These tallies do not necessarily imply that studies of molecular adaptation and functional genomics are rare in an ecological context, but they certainly do indicate that such topics have not been closely identified with the field of ME.

This current state of affairs in ME is ironic because, throughout the molecular revolution of the late 20th

century and continuing today, theoretical and empirical population geneticists have been quite preoccupied with issues of selection vs. neutrality, and frequently bemoan the fact that mechanistic connections between observable genotypes and ecologically relevant phenotypes often remain black boxes. The field of ME became closely associated with 'marker-based analyses' not because neutral markers provide end-all-and-be-all understandings of nature, but rather because such analyses are entirely feasible and can illuminate a plethora of fascinating ecological and behavioural phenomena not always amenable to direct observations. Nevertheless, my point is that ME will become a more mature discipline when it also incorporates ecologically germane information on genotype–phenotype connections. If ME should decide to widen its circle of friends to include fields such as functional genomics and developmental biology, it could quickly expand its intellectual horizons and thereby, perhaps, eventually assume an adult phenotype appreciably different from that of its youth.

Is ME showing any signs yet of diminished vitality? No, I don't think so. Even if the field continues to address only the topical categories summarized in its four recent textbooks, there would still remain a vast natural world (including millions of irresistible species) and countless natural-history questions to investigate using molecular markers. However, with functional genomic approaches rapidly becoming feasible as well, ME also has an opportunity to broaden its scope and maybe even transform itself. Thus, the continued growth of ME seems assured, and a partial mid-life change is at least plausible. Thankfully, however, any ultimate senescence for the field is still a long way off.

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Molecular Ecology publishes papers that utilize molecular genetic techniques to address consequential questions in ecology, evolution, behaviour and conservation. Studies may employ neutral markers for inference about ecological and evolutionary processes or examine ecologically important genes and their products. We also publish articles on technical methods, computer programs and genomic resource development in our companion journal, Molecular Ecology Resources. However, papers that are primarily descriptive and relevant only to the taxon being studied should be submitted to a more specializ... Â Vol 27(24 Issues in 2018) Print ISSN: 0962-1083 Online ISSN: 1365294X Impact Factor: 6.086. For the first time, this study considers in detail the ontogeny of the genet of *L. dortmanna* in oligotrophic lakes of Tver oblast. Detailed characteristics of the following age stages of individuals are given: resting seeds, seedlings, juvenile, young and adult vegetative, latent generative, middle-aged and old generative and quasisenile plants. It is shown that the transition to the juvenile age stage occurs at the end of the first year of life, the virginile age stage lasts two years, and the generative stage of development occurs in the fourth year of life. The change in the growth pattern

Part B: Molecular and Developmental Evolution. Vol.302. P.207-225.Â Facial growth and the ontogeny of morphological variation within and between the primates *Cebus apella* and *Cercocebus torquatus* // Journal of Zoology, London. Vol.254. P.337-357.Â A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton // Journal of Anatomy.Vol.201. No.1. P.211-229. Wagner G.P. & Altenberg L. 1996. The emergence of molecular ecology An unlimited source of data Overview Chapter summary Useful websites and software Further reading Review questions. 2 Molecular Markers in Ecology. Understanding molecular markers Modes of inheritance Molecular markers Overview Chapter summary Useful websites and software Further reading Online activities Review questions.Â Since 2005, when the first edition of Molecular Ecology was published, the field has continued to evolve. As a result, this second edition contains numerous updates and additions that reflect the fast-moving pace of genetic discovery. Perhaps the most significant development in molecular ecology in the past five years has been in the area of ecogenomics. Molecular Ecology publishes papers that utilize molecular genetic techniques to address consequential questions in ecology, evolution, behaviour and conservation. Studies may employ neutral markers for inference about ecological and evolutionary processes or examine ecologically important genes and their products. We also publish articles on technical methods, computer programs and genomic resource development in our companion journal, Molecular Ecology Resources. However, papers that are primarily descriptive and relevant only to the taxon being studied should be submitted to a more specializ...Â Vol 27(24 Issues in 2018) Print ISSN: 0962-1083 Online ISSN: 1365294X Impact Factor: 6.086.