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Chapter 1

Twenty-five key evolutionary insights from the phylogeographic revolution in population genetics

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Abstract

An overview is provided of 25 novel perspectives that the field of phylogeography has brought to scientific studies of population genetics and speciation. A unifying theme is that microevolution can be described as an extended genealogical process played out in space and time, and reflecting the oft-idiosyncratic biological and environmental factors that have impinged on historical population demography. Most of the empirical and conceptual methods of phylogeography depart considerably from conventional equilibrium approaches, and they are helping to reorient and extend traditional population genetics in realistic directions that emphasize historical demography and genealogy.

Keywords: phylogeography, genealogy, gene trees, demography, speciation

Introduction

Phylogeography is a relatively young discipline concerned with the principles and processes governing the geographic distributions of gene lineages, especially within and among closely related species (Figure 1). The phylogeographic revolution, inspired by mitochondrial (mt) DNA analyses that were introduced nearly three decades ago, has transformed the study of population genetics and speciation in several ways. In particular, this ongoing reformation has drawn closer empirical and conceptual connections between microevolutionary genetics and phylogenetic biology.

Here I substantiate these claims by compiling more than two dozen salient insights about microevolution that seldom (sometimes never) were an explicit part of the fabric of population genetics in the pre-phylogeography era. The entries in this list appear in a sequence generally consistent with the underlying train of logic, rather than necessarily in order of importance or date of development. Many concepts in the list are nested or partially overlapping, yet each qualifies for inclusion by virtue of having been quite unorthodox when

introduced. More importantly, most of these insights from the field of phylogeography will (I suspect) prove to be enduring truths about microevolutionary processes in nature.

This list provides a brief overview and historical backdrop, and is intended to encapsulate phylogeography's principal contributions. Thus, for each of the 25 entries, I have cited just one key reference that either was seminal in the history of ideas or is particularly informative as a more recent review. For much fuller treatments of all topics considered, readers should consult Avise (2000) and the extensive primary literature that it summarizes.

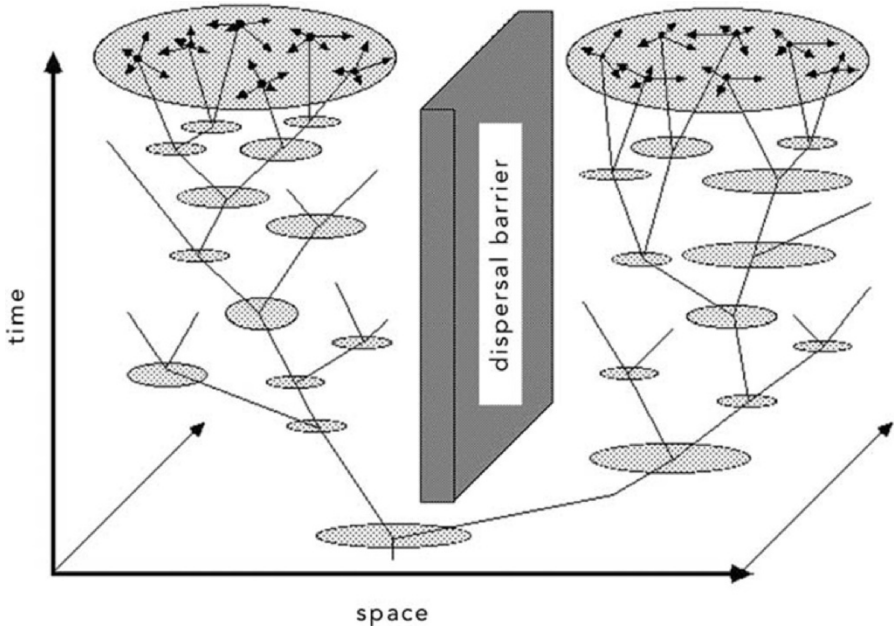


Figure 1. The axes of phylogeography are space and time, across which gene genealogies are scrutinized (modified from Avise 2000).

Twenty-five primary revelations

1. Cytoplasmic genomes add a new hierarchical level to population genetics

In diploid organisms, nuclear genomes typically exist as two copies per somatic cell and are transmitted across generations in a single-copy (haploid) molecular fashion. By contrast, mitochondrial and other cytoplasmic genomes

[such as chloroplast (cp) DNA (see also Petit & Vendramin, this volume)] exist as populations of molecules within each somatic and germline cell, and usually are transmitted from parent to offspring as multiple copies. This realization led to a novel research arena directed toward the intra-individual population dynamics of cytoplasmic genomes in somatic cells and germlines – a newly recognized level in the population genetic hierarchy (Birky *et al.* 1983).

2. Germline bottlenecks in mtDNA numbers attend mitochondrial inheritance

Notwithstanding concept #1 (above), the vast majority of mtDNA variation is apportioned among (not within) individual animals, even in local populations. Thus, an individual typically displays a single predominant cytoplasmic genotype that often differs clearly in DNA sequence from other conspecifics. Coupled with experimental findings from pedigree analyses (Hauswirth & Laipis 1982), this observation indicates that relatively small effective population sizes often characterize the intracellular pool of mtDNA molecules that transmits from one generation to the next through animal germlines. Thus, significant heteroplasmy (the joint appearance of two or more mtDNA genotypes within an individual) is normally a transient condition lasting only a small number (i.e. tens or perhaps hundreds) of organismal generations. This discovery carries a huge pragmatic benefit: within-individual sequence heterogeneity seldom seriously compromises mtDNA's utility for genealogical assessments at proximately higher levels in the biological hierarchy (e.g. local demes and geographic populations).

3. DNA repair mechanisms can influence molecular evolutionary rates

A traditional paradigm of molecular evolution is that genes with conserved function evolve slowly. The mitochondrial genome, with its central role in cellular energy metabolism, was thought to be a paradigm if not the epitome of functional conservatism. Thus, early reports that animal mtDNA evolves rapidly (about 5-10x faster than single-copy nuclear DNA) came as a great surprise (Brown *et al.* 1979). Subsequent studies showed that mtDNA sequence evolution is concentrated at synonymous sites and non-coding regions of the molecule, as might be expected. However, a totally unexpected factor contributing to mtDNA's rapid evolution was also intimated and later confirmed: a severe deficiency of DNA repair mechanisms within the mitochondrion.

4. Some DNA sequences in sexual species show asexual inheritance

This notion was not entirely novel because mammalian Y-chromosomes were long known to be paternally inherited, and cytoplasmic genomes such as

mtDNA were assumed to be transmitted maternally. Nonetheless, explicit analyses of cytoplasmic gene sequences and their transmission genetics through organismal pedigrees soon confirmed mtDNA's maternal inheritance at the molecular level. This validation compelled the field of population genetics to reconsider the ramifications of asexual inheritance in sexually reproducing organisms. In particular, it prompted the field to more fully embrace the notion that asexual genomes exist and are transmitted across successive generations without the normal complications of intermolecular recombination otherwise attendant with sex (Hutchinson *et al.* 1974).

5. Matrilineal histories within species can be recovered

The rapid pace of mtDNA sequence evolution in animals, coupled with the molecule's maternal inheritance, meant that species display a wealth of non-recombining markers suitable for deciphering the matriarchal component of an extended organismal pedigree (Wilson *et al.* 1985). Population geneticists thereby were afforded unprecedented access to genealogical information at the intraspecific level.

6. A gene tree is a recognizable component of a population pedigree

Considerations of matrilineal ancestry pioneered the gene-tree concept. Animal mtDNA consists of about 37 functional genes, but the entire non-recombining mitochondrial genome can be considered a single locus from a genealogical perspective. Like the traditional phylogenies of higher-level systematics, an intraspecific gene tree for mtDNA is hierarchically branched and non-reticulate. The gene-tree notion can also be extended to particular sequences in the nuclear genome, at least in principle (Tajima 1983). Thus, the term gene tree gained a generalized definition: the genealogical history of any defined segment of DNA. Such gene trees are real and discrete components of population pedigrees (Figure 2).

7. Gene trees in sexual species are multitudinous and non-isomorphic

For sexually reproducing organisms, a matrilineal gene tree represents only a minuscule fraction of a species' hereditary history. More than 99% of that total history resides instead in nuclear genes whose alleles have been transmitted along multi-generation genealogical pathways involving both genders. Due to Mendelian segregation and independent assortment, the realized transmission histories of unlinked DNA sequences inevitably differ from locus to locus. Thus, gene trees for unlinked loci are highly unlikely to be strictly isomorphic (identical in branching structure). This insight led to the notion that any pictured cladogram summarizing historical relationships of populations or species is actually a much-simplified representation of an

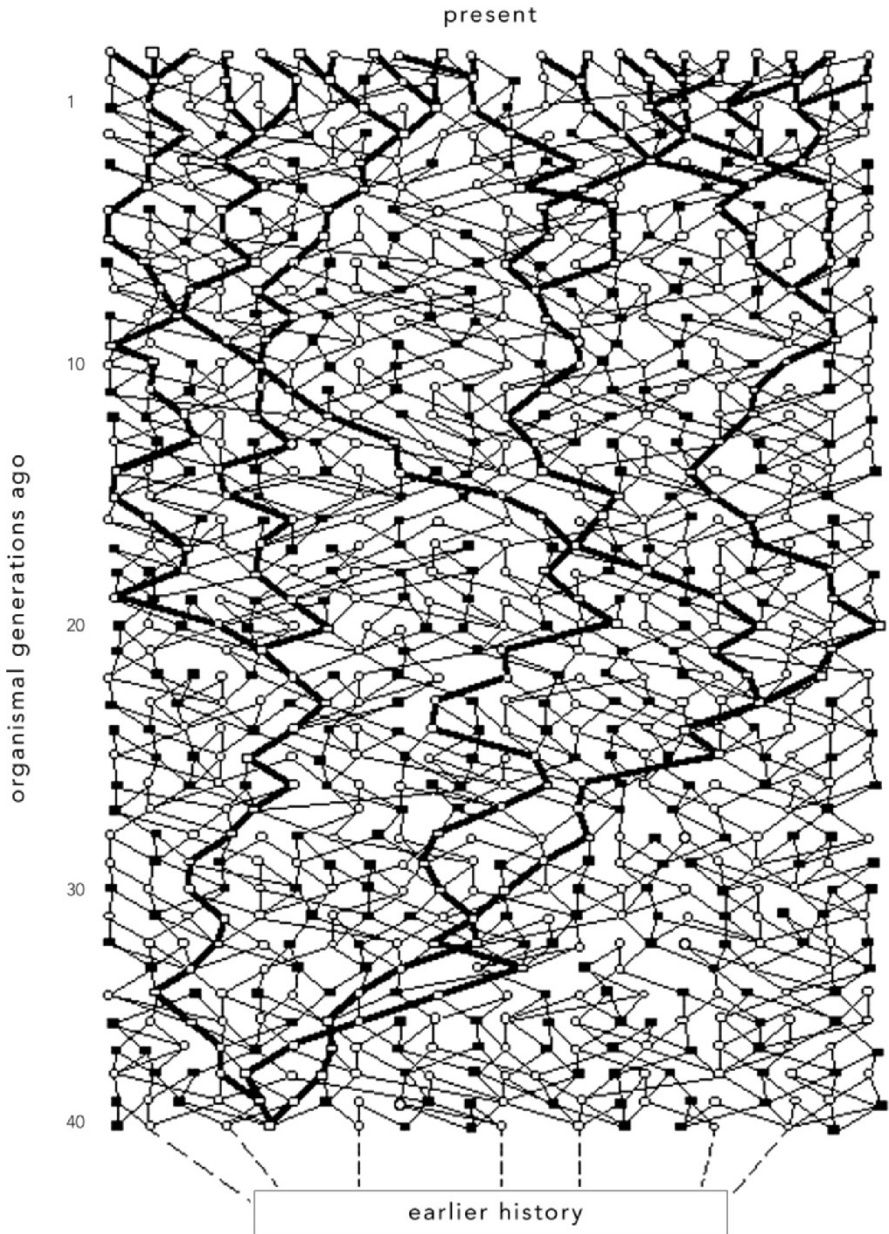


Figure 2. Highlighted in heavy lines is one (among multitudinous) gene trees within an organismal pedigree across 40 generations. Note how the lineages coalesce to shared ancestors (modified from Avise 2000).

underlying statistical ‘cloudogram’ of quasi-independent gene trees with a variance (Maddison 1997).

8. Phylogenetic reasoning is quite relevant at the intraspecific level

Traditional wisdom in systematics had been that phylogenetic principles apply only above the taxonomic rank of species, i.e. that they have no meaning in the supposedly reticulate realm of intraspecific evolution. The gene-tree concept, prompted by studies of mtDNA, challenged this dogma by clarifying the principle that particular DNA sequences do in fact have genealogical (phylogenetic) histories of transmission within a species pedigree also (Avise 1989a). Furthermore, gene trees (or at the least, unrooted genealogical networks) can often be empirically recovered when the complications of sex-mediated recombination are absent or minimal. So, historical gene genealogies can be estimated from suitable molecular data using phylogenetic algorithms, and such historical representations aptly lend themselves to description by traditional macro-phylogenetic concepts such as clades, outgroups, and synapomorphic (shared-derived) characters (provided that these terms are now interpreted to apply explicitly to features of the gene tree *per se*).

9. Individuals can be treated as ‘operational taxonomic units’ (OTUs)

The basic data of traditional population genetic analysis consist of allelic or genotypic frequencies in population samples, with the populations themselves often prespecified by criteria such as geography or suspected reproductive relationships. Although such collective empirical data can always be used to estimate genetic relationships among suites or assemblages of individuals, an undesirable element of circular reasoning underlies the exercise, and much useful information on particular specimens is lost. Both the circularity and the information loss are removed entirely when *individuals* are treated as the basic units of analysis in genealogical reconstructions (Avise *et al.* 1979). Since the advent of phylogeography, this ‘individual as OTU’ approach is now included routinely in phylogenetic appraisals of mtDNA (and some nuclear loci).

10. Intraspecific genealogy and historical demography are intertwined

At the intraspecific level, concepts of genealogy and historical population demography are inextricably associated. Precise mating relationships of individuals, coupled with generation-by-generation means and variances in individual reproductive success, describe the extended pedigree of a population, thereby defining the genealogical pathways that were available for allelic transmission. Any gene tree is one realized subset, or historical sample,

from this constellation of pathways (Figure 2). As such, each gene tree is an ineluctable reflection of historical population demography. This realization gave rise to ‘coalescent theory’ (Hudson 1990), a burgeoning discipline in mathematical population genetics that seeks to uncover and formalize the relationships between historical population demography and the structure of intraspecific gene genealogies.

11. Evolutionary effective population sizes of most animal species are relatively small

In most surveyed animal species (especially those that are relatively abundant today, and whose populations are characterized by high historical levels of gene flow), estimated evolutionary effective population sizes (N_e values over the long term) have proved to be orders-of-magnitude smaller than contemporary census numbers (N). This conclusion stems from coalescent theory as applied to the surprisingly shallow intraspecific gene trees for such species, as evidenced in empirical mtDNA data sets (Avise *et al.* 1988). Two explanations are likely, the first probably being of greater importance: a) population-demographic histories *per se*, such as occasional bottlenecks in population size, or large variances among females in reproductive success; and b) rare ‘selective sweeps’ that purge existing variation as selectively advantageous mutations course through a species to fixation. Either way, gene lineages that survived for current observation have been historically squeezed through many fewer ancestors than otherwise might have been supposed, thereby constraining what would otherwise be greater temporal depths in intraspecific mtDNA gene trees.

12. Cytonuclear associations matter

The joint availability of molecular data from nuclear and cytoplasmic (e.g. mitochondrial or chloroplast) loci prompted an important new research area dealing with ‘cytonuclear’ patterns. Of special interest is how natural selection and other biological factors interact to produce the non-random associations (cytonuclear disequilibria) often observed between uni-parentally and bi-parentally inherited alleles in particular populations or species (Asmussen *et al.* 1987).

13. Key behavioral and demographic parameters can differ between the genders

Several parameters relevant to intraspecific gene genealogies often show fundamental asymmetries between the genders. For example, males are the primary dispersers in many animal species, females so in others. In many plant species, seed propagules to which cytoplasmic genomes are confined

may be far less dispersive than pollen granules that typically carry nuclear genes only. In both animal and plant taxa, variances in individual reproductive success often differ between the sexes. In general, matrilineal genetic markers in conjunction with those from nuclear loci have opened many novel opportunities to empirically assess the population genetic consequences of such gender-associated biological asymmetries (Melnick & Hoelzer 1992).

14. Conspecific populations are genealogically allied yet often highly distinctive from one another

Molecular data from mtDNA are especially useful in revealing phylogeographic structure of populations within a species. An important realization is that these historical population structures can range along a continuum from evolutionarily (temporally) shallow to deep (the latter being especially true for species that have had severe restrictions on historical gene flow). Within a species, the most distinctive deeper units (the major matrilineal branches) sometimes are referred to as intraspecific 'phylogroups' (Avise & Walker 1998). Such phylogroups often, but not invariably, are also apparent in appropriate assays of nuclear genes, in which case they may warrant potential recognition as evolutionarily significant units for purposes of taxonomy or conservation efforts (see concept # 20 below).

15. Principles of genealogical concordance assess the depth and strength of phylogeographic structure

Not all phylogeographic population structures are equal in magnitude. To distinguish the historically deep from the shallow population separations, four distinct aspects of phylogeographic concordance are employed (Avise & Ball 1990). Each examines the level of agreement or consensus among multiple classes of information: across multiple sequence characters within a single gene tree (aspect 1 of genealogical concordance); across multiple gene trees within a species (aspect 2); across multiple species within a regional biota (aspect 3); and across multiple categories of data, such as molecular genetics and historical geography (aspect 4). By hard criteria, only when concordance has been demonstrated in at least some (preferably several) of these various aspects is it proper to conclude that the available data register salient evolutionary separations among the conspecific populations examined.

16. The number of phylogroups per species usually is small

In most vertebrate species and many invertebrate and plant species surveyed to date, the number of highly distinctive intraspecific phylogroups is small

or modest – typically only about 1-5 per taxonomic species (Avise & Walker 1999). This observation, coupled with the finding that cytoplasmic gene sequences even in closely related biological species usually tend to be readily distinguishable, suggests that historically distinctive units identified in molecular-genetic analyses often conform quite well both in composition and number (at least within an order-of-magnitude) to the arrays of taxonomic species recognized in more traditional biological classifications. Thus, when judged from the newer vantages and criteria of molecular phylogeography, traditional non-molecular systematists generally seem to have done an excellent job in identifying and classifying salient historical discontinuities in the biological world.

17. Intraspecific phylogroups are nearly always allopatric

Because individuals can be considered OTUs in gene-genealogical analyses (concept #9), there is no logic demanding that major branches in gene trees must be allopatric. Empirically, however, most such intraspecific phylogroups have proved to be non-overlapping or nearly so in geographic distribution (and when this is not the case, secondary overlap often seems to be the most plausible explanation). Furthermore, these phylogroups are often spatially arrayed in coherent regional patterns such that they can be thought of as corresponding roughly to what was implied under the traditional concepts of subspecies, incipient species, or (in more recent literature) ‘evolutionarily significant units’ (Moritz 1994).

18. The geographic distributions of intraspecific phylogroups usually make biogeographic sense

In specific instances, the spatial arrangements of major branches in intraspecific gene trees usually orient well with known or suspected biogeographic agents, such as obvious environmental barriers to historical gene flow, or the locations of Pleistocene refugia. Indeed, the primary aim of most phylogeographic studies has been to employ gene-tree data to help recover and interpret the genealogical history of conspecific populations and closely related species in the context of historical geography and other relevant factors. In recent years, this approach often has been extended to multiple codistributed species, thereby revealing the composite histories of regional biotas. This type of endeavor has blossomed into a new subdiscipline in its own right that can be termed comparative phylogeography (Avise 1992).

19. Species’ natural histories also impact phylogeographic patterns

In addition to vicariant historical factors associated with changes in the physical environment, endogenous biological factors – species’ ecologies,

behaviors, and natural histories – play key roles in shaping phylogeographic patterns (Avise 2000). To mention just one example, highly dispersive marine fishes, as a rule, have proved to show far less phylogeographic population structure than most of their freshwater counterparts when sampled across ranges of comparable size.

20. Phylogeographic units have primary importance for taxonomy and conservation

Biodiversity (which in the final analysis is genetic diversity) is what taxonomy seeks to name and conservation biology seeks to preserve. By describing the spatial distributions of genealogical variety within and among related species, the data of phylogeography can help tremendously in recognizing historical biotic partitions that should be of central relevance both to microevolutionary systematics and to biodiversity preservation (Avise 1989b).

21. Gene trees can differ in topology from population trees and species trees

This statement applies to sexually reproducing species, but not to strictly asexual taxa (where, in principle, one-and-the-same historical transmission pathway characterizes all loci). The fundamental distinction between a gene tree and a species tree in sexual species was unappreciated until fairly recently (Hey 1994). For example, an earlier paradigm in systematics stated that even one synapomorph (shared-derived character) is enough to define a clade. This is patently false (unless ‘clade’ refers solely to a branch in the particular gene tree in question). It is for such reasons that principles of genealogical concordance (concept #15) are important in deciding whether or not deep historical partitions in particular gene trees accurately register genome-wide partitions that should distinguish long-separated populations, intraspecific phylogroups, or species.

22. The phylogenetic status of sister populations or species can itself be evolutionarily dynamic

With respect to gene genealogies, it is no longer adequate to consider recently separated populations or species as having a fixed phylogenetic relationship to one another (Neigel & Avise 1986). Due to lineage sorting across the generations mediated by demographic turnover (organismal reproduction and death), extant populations at any point in time carry only a subset of the lineage diversity of their ancestors, plus newly arisen lineage diversity postdating the vicariant separations. Thus, a common phylogenetic progression for gene trees in recently separated sister taxa is initial

polyphyly or paraphyly, only eventually followed by reciprocal monophyly (Figure 3). The rate at which this genealogical transition proceeds (under neutrality) is a function of population demographic events immediately preceding, during, and following the vicariant split. The transition also takes longer in principle, all else being equal, for autosomal than for cytoplasmic genes, due to a four-fold larger effective population size for genes that are diploid (as opposed to haploid) and inherited biparentally (as opposed to uni-parentally).

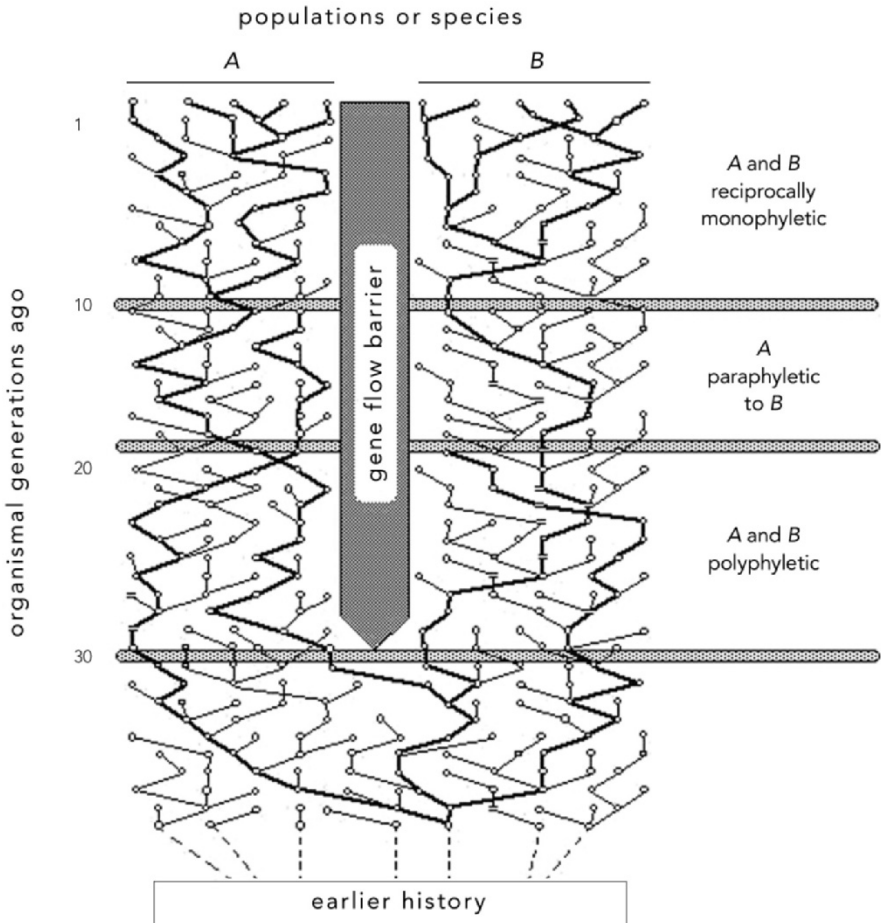


Figure 3. Illustration of the shifting phylogenetic status of a gene tree (heavy lines) through time in two recently separated populations or species.

23. Discordant gene trees and species trees can also characterize ancient taxa

Suppose that two or more successive cladogenetic events occurred long ago but close together in evolutionary time. If evolutionary effective population sizes of the species traversing the relevant nodes in the phylogenetic tree were larger than the internodal times as measured in organismal generations, then lineage sorting may not have proceeded to reciprocal monophyly in all gene trees of the immediate descendents (Tateno *et al.* 1982). Then, a topological discordance between a gene tree and a species tree will become evolutionarily 'locked in' as subsequent lineage sorting results in the eventual fixations of ancestral lineages in derivative taxa. Such idiosyncratic lineage sorting is one of several ways (others include secondary hybridization and various means of horizontal gene transfer) by which gene trees can come to differ topologically from one another and also from the composite species tree.

24. Allopatric speciation is a temporally extended process

A habit in traditional systematics is to view speciation as a point event in time (i.e. as a discrete node in a phylogeny). Although this may generally be acceptable for ancient cladogenetic events (where any temporal durations for speciation are small in comparison to the total time elapsed since), it can be grossly inadequate for recent speciations. By comparing the branching structures of mitochondrial gene trees within and among extant pairs of sister species, and by applying molecular clocks, recent phylogeographic appraisals suggest that the temporal duration of allopatric speciation in many vertebrate taxa averages (albeit with a large variance) about two million years (Avise *et al.* 1998). Such lengthy timeframes cannot be neglected when appraising, for example, the impacts of Pleistocene or more recent events on patterns of biological diversification.

25. Microevolution, like macroevolution, is historical

This catch-all truism sums up many of the phylogeographic insights described above. It is a basic realization that too often was overlooked in conventional population genetics, probably due in large part to that discipline's underlying formal theoretical framework. For reasons of mathematical tractability, many derivations and formulations in traditional population genetics dealt with equilibrium expectations (e.g. between mutation and selection, or genetic drift and migration) in unrealistically simplified contemporary settings (e.g. an 'island model' in which equal-sized populations are all assumed to exchange genes at equal rates). These were always pre-

sented as simplifying assumptions, but the net result nonetheless was a discipline too seldom focused on historical idiosyncrasies and non-equilibrium outcomes that are a *sine qua non* of real-life intraspecific evolution. Phylogeographic perspectives have enriched population genetics by adding an explicit focus on historical genealogy, and thereby drawing the field much closer to allied disciplines such as population demography, biogeography, and phylogenetic biology (Avice *et al.* 1987).

Synopsis

Historical reasoning and phylogenetic analysis have long been central themes of macroevolutionary biology and higher-level systematics, but until recently they had not permeated studies of intraspecific evolution to nearly the same extent. Thus, throughout most of the 20th century, there was a major gulf between the fields of phylogenetic biology and population genetics, to the detriment of both. Phylogeography is helping to bridge this gulf.

Microevolution too is a historical-genealogical process. Indeed, all limbs, branches, and twigs in any phylogenetic tree summarizing species' relationships ultimately consist of generation-to-generation organismal pedigrees through which genes were transmitted. The tools of molecular biology can now provide explicit historical information about genealogical tracings through such extended pedigrees, within as well as among living species. The net result has been the birth and growth of phylogeographic perspectives that promise to forge a useful new synthesis of micro- and macroevolutionary thought.

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