

BOOK REVIEW OF PHYLOGEOGRAPHY: THE HISTORY AND FORMATION OF SPECIES
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A genealogical view of geographical variation

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Introduction

John Avise and coworkers coined the term 'phylogeography' in 1987 when presenting their ideas on the potential of combining intraspecific gene trees based on mitochondrial DNA (mtDNA) with geographical information to infer historical processes. Phylogeography has since become an influential field of evolutionary biology. For instance, in the year 2000, 32 papers in *Molecular Ecology* used 'phylogeography' in either the title or as a keyword, and two 'special issues' on phylogeography have been produced (April 1998 and March 2001). With this explosion of interest, the time is right for a summary of what has been accomplished. It is fitting that John Avise, one of the most prominent and prolific phylogeographic researchers, should be the first to do this in *Phylogeography: The History and Formation of Species* (Avise 2000a).

Phylogeography is 'a field of study concerned with the principles and processes governing the geographical distributions of genealogical lineages, especially those within and among closely related taxa' (Avise *et al.* 1987). Simply put, any situation where the phylogenetic relationships of a genetic trait can be estimated and overlain on a map is a phylogeographic study, although most workers employ animal mtDNA markers. The challenge of phylogeography is to use genealogical and geographical information to infer the demographic and historical processes that shaped the evolution of lineages.

Avise begins *Phylogeography* by contrasting the field of phylogeography with other subdisciplines of evolutionary biology, in order to define its scope and highlight its distinctiveness. Phylogeography is proposed to be the bridge uniting micro- and macroevolutionary perspectives by

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integrating population genetics, ethology, and demography with phylogenetics, palaeontology, and historical biogeography. More specifically, phylogeography is that subdiscipline of biogeography which deals with historical relationships within and between closely related species, in contrast to the use of deeper phylogenies in classical historical biogeography (Nelson & Platnick 1981). This difference in historical depth entails an intellectual shift, because the study of gene genealogies within and among closely related species is within the scope of coalescent theory, a rapidly developing branch of population genetics. Finally, phylogeography complements conventional ecogeography (e.g. Allen's rule, which notes that homeotherms in colder climates tend to have shorter appendages) by focusing on the historical links among populations, rather than shared adaptations.

Phylogeography is an ambitious attempt to review the findings and directions of a field that has witnessed rapid empirical development and spurred much theoretical work. The book is organized into three sections, each containing two chapters. The first section defines the field of phylogeography, reviews the genesis and development of mtDNA as the marker of choice in phylogeographic research, and provides an accessible, graphical depiction of those elements of coalescent theory that are most pertinent to phylogeography. The second section of the book offers a thorough review of intraspecific phylogeographic studies in animals. Human phylogeography is given its own chapter, with the goal of reviewing the 'strengths and limitations of molecular phylogeographic appraisals' in a single species. Readers expecting a thorough review of human evolution will be disappointed, but the chapter accomplishes its stated goal. The third section of the book explores the contribution of phylogeographic approaches to higher level questions in evolutionary biology. Speciation, regional biogeography, and concordance among data sets are given special emphasis. Finally, at 97 pages and roughly 1370 references, the bibliography is the longest part of the book, and is itself a contribution because of its scope and completeness.

The findings of phylogeography

Nearly a quarter of *Phylogeography* (77 pages) reviews the empirical results of studies on diverse animal taxa. This is the subject of chapter four, which begins by introducing the five categories of phylogeographic pattern first presented by Avise *et al.* (1987). These categories identify landmarks in a continuum of differentiation, from deeply divergent clades generated in allopatry (Category I) to weakly divergent, sympatric haplotypes (Category IV), and situations in-between (Categories II, III, and V). They are not mutually exclusive; for example, a taxon possessing a Category I pattern on a large scale may display a Category IV pattern within the divergent clades. Though artificial, this framework is useful for conceptualizing the range of possible outcomes of a phylogeographic study (e.g. Patton *et al.* 2000; p. 268). This was especially true in 1987, when the field was nascent and less intuitive to workers.

Avise then provides an extensive review of the literature, and attempts to identify the phylogeographic category that best characterizes different taxonomic groups. Literally hundreds of studies are touched upon, often in a sentence or two, with an emphasis on vertebrates (consistent with Avise's interests, but also reflecting a bias in the literature). The breadth of this survey comes at the expense of detail in individual studies. Nevertheless, anyone conducting a phylogeographic study is provided with a useful context within which to interpret his or her results. For example, we learn that it is common to discover that small bodied (less mobile) terrestrial mammals exhibit deeper phylogeographic structure than large bodied (more mobile) mammals. Herpetofauna are seen to be sharply differentiated, in part due to their limited dispersal abilities, yet avian species display a wider range of phylogeographic structures than we may have expected, given their great dispersal potential. As anticipated, freshwater fish are far more differentiated than marine fish, highlighting the role of physical barriers in the development of genetic lineages. Invertebrates are too heterogeneous to fit into a single category, but their phylogeographic patterns are often predictable from their natural histories; for instance, marine species with planktonic larvae typically exhibit far less phylogeographic structure than sedentary terrestrial insects. None of these patterns are especially surprising, and in general these results agree with what we learned from other markers, such as allozymes.

Unfortunately, Avise does not explain the theoretical importance of determining the category most commonly associated with these groups of organisms, and there are many exceptions to the generalities identified by Avise. This is because phylogeographic patterns are the product of life history, demographic, and historical factors, not taxonomic grouping. For instance, the Tiger salamander complex (*Ambystoma tigrinum*) possesses shallow divergence for mtDNA (Shaffer & McKnight 1996), despite the fact

that many species in the genus, and amphibians in general, possess deep phylogeographic structure (the lack of diversity in Tiger salamanders is probably due to a post-Pleistocene range expansion). Because phylogeographic patterns are species-specific, it may have been more useful to summarize the literature by some predictor of phylogeographic pattern, such as dispersal ability. Alternatively, if one suspects that historical (monophyletic) groups share inherited attributes that are predictors of phylogeographic pattern (such as the low gene flow typical of amphibians), then one could generalize across such groups. However, two of the groups considered by Avise (herpetofauna and invertebrates) are not historical, and therefore at best function as poor surrogates for some undefined life history feature.

Evolutionary biology and natural history often inform one another (see also Greene 1986), and Avise shows high regard for organismal natural history when interpreting phylogeographic data. The review of marine turtle phylogeography exemplifies this interaction. Marine turtles are long-lived and extraordinarily mobile, and do not exhibit large amounts of phylogeographic structure. Nevertheless, mtDNA analysis has been useful in confirming the demographic autonomy of rookeries (breeding beaches), and in providing evidence that nonbreeding oceanic aggregations frequently consist of turtles from multiple rookeries. Here, mtDNA studies were greatly informative, but let us not forget that scientists investigating the lives of sea turtles helped frame the questions; imagine the results of a naive phylogeographic study that focused sampling on nonbreeding aggregations rather than rookeries.

Finally, this review of the results of the phylogeographic studies helps direct future research by identifying gaps in our knowledge. Clearly, plants demand more consideration, as do all nonvertebrate groups. Also, there is a North American bias in phylogeographic research. Expanding work to other regions (e.g. Asia) and biomes (e.g. the tropics) is an important next step.

Coalescent theory

Tools developed over the last decade permit molecular sequences to be obtained for population samples, allowing segments of DNA, rather than populations, to be the units of analysis. The estimation of population parameters (such as effective population size or divergence times) using sequence data is the domain of coalescent theory, which offers a probabilistic treatment of how the properties of gene genealogies are related to the demographic and genetic attributes of the population from which they were sampled. As phylogeographic studies use genealogical information, it is appropriate for Avise to dedicate a chapter to the topic of how haplotype trees are related to demographic history. Emphasizing mtDNA, Avise discusses how the rate of coalescence is related to parameters such as population size

and the variance in the number of offspring. These principles are then extended to spatially structured populations, with a discussion of how the amount of population subdivision, the extent and timing of gene flow, and the time elapsed since population separation, are related to properties of the gene tree, such as the attainment of monophyly by populations. Avise also shows how the principles of coalescent theory can be extended to nuclear gene trees. Statistical analyses of phylogeographic data such as nested clade analysis (reviewed in Templeton 1998) are presented, offering an example of how the geographical distribution of lineages can be quantitatively interpreted in a coalescent-based framework. The chapter is not a mathematical introduction to coalescent theory, but offers an excellent overview on how demography shapes gene trees. However, some statistical applications of coalescent theory, relevant to phylogeography, are not given much space in the book. In particular, maximum likelihood methods are a conspicuous omission. Below, we discuss the importance of these coalescent-based approaches.

First, the information contained in gene genealogies can be analysed quantitatively by using coalescence theory, taking the analysis a step further than the pictorial representation of gene trees on geography. For example, the finding that samples from different geographical regions form reciprocally monophyletic groups might suggest that there is no gene flow between these regions. Use of coalescent theory by Slatkin (1989) confirmed the intuition that moderate to high levels of gene flow are inconsistent with such a pattern; however, the analysis also showed that if gene flow is low, no matter how large the samples, reciprocal monophyly would still be attained with high probability. Thus, reciprocal monophyly can refute high levels of gene flow among phylogroups, but low levels of gene flow cannot be ruled out. Information contained in the topology of an inferred tree can also be used to estimate migration rates (Slatkin & Maddison 1989), effective population size (Fu 1994), and to test the hypothesis of population expansion (Nee *et al.* 1996).

A second set of developments allows estimation of population parameters without the need to infer a single best gene genealogy. Instead, likelihoods of parameter values are estimated over a range of genealogies. Conceptually, this can be thought of in the following way. If we knew the true genealogy for a sample of DNA segments, we could estimate the likelihood of the data over a range of parameter values (e.g. different population sizes) and obtain a maximum likelihood estimate. However, because the true genealogy is not known with certainty, an alternative is to compute the likelihood of parameters for every possible genealogy; we could then consolidate this information into a likelihood distribution where the contribution of all genealogies is considered. The technical challenge is to explore the huge number of trees compatible with a data set. Markov-

Chain Monte Carlo algorithms are one possible solution. These methods explore a subset of gene genealogies in a way that generates a likelihood surface with the same shape as the one that would be obtained if all genealogies were inspected. This is achieved by sampling topologies in proportion to their likelihoods, such that unlikely topologies do not contribute as much to the likelihood surface as more likely topologies. Notice that this represents a different computational problem from the search for optimal trees, familiar to most systematists; the goal here is not to find the optimal tree, but to sample from the universe of trees a subset which allows an accurate inference of properties of the entire set of topologies. Examples of these novel coalescent approaches include methods that estimate the direction and amount of gene flow (Beerli & Felsenstein 1999; Bahlo & Griffiths 2000), effective population size (Kuhner *et al.* 1995) and the rate of population growth (Kuhner *et al.* 1998).

Another important development is the extension of coalescent theory to different types of data, such as microsatellite and single nucleotide polymorphism (SNP) variation. This may seem counterintuitive, as gene genealogies cannot be inferred for such markers because they do not carry enough information. However, their prior history can still be modelled because they undergo genealogical transmission, so the distribution of alleles within and among populations can be modelled by the coalescent to make inferences about population parameters. These studies differ from the Avise approach in that no explicit genealogy is inferred; instead, genealogical principles are used to interpret the distribution of alleles. Methods for estimating gene flow (Beerli & Felsenstein 1999) and the time of population divergence (Nielsen *et al.* 1998) are examples.

Coalescent-based likelihood inference methods bring with them changes and challenges to phylogeographic research. An advantage of coalescent methods is that they can be modified to make less restrictive assumptions, and allow statistical testing of hypotheses. For example, a method for inferring divergence times initially assumed populations to experience no gene flow subsequent to separation (Nielsen *et al.* 1998), but has now been extended to provide joint likelihood estimates of gene flow and time of divergence (Nielsen & Slatkin 2000). This likelihood framework allows for a statistical test of two hypotheses; population separation with no gene flow vs. an ancient population separation with ongoing gene flow. However, users of these likelihood-based methods must be aware that although simulations provide guidelines for how much searching is needed to adequately generate the likelihood surface, requirements will differ among data sets. Researchers will thus have to spend some time exploring their data before settling on a final answer.

In our opinion, new likelihood methods complement, rather than replace, the simpler methods described by Avise. Simultaneous use of different methods allows an

understanding of the conditions under which methods differ, and provides an internal reference to verify results. Simple methods, such as Watterson's estimator of effective population size (Watterson 1975), Tajima's (1989) statistic for detecting whether populations are under selection or in nonequilibrium conditions (e.g. recent expansions), or plotting an inferred gene tree onto a map, will remain fundamental because they provide a useful, intuitive description of the data.

Concordance and discordance

One of the clearest lessons from coalescent theory is that independent DNA segments can traverse different transmission routes. A gene tree is thus a realization of one genealogical pathway, and may not reflect population-level divergences. Introgressive hybridization, natural selection, retention of ancestral polymorphisms, and other evolutionary forces all conspire to generate discordances among loci. Similarly, when comparing the phylogeographic patterns of different species from the same region, extinction and dispersal can obfuscate the detection of among-species vicariant patterns. Bearing such problems in mind, Avise attributes particular significance to concordance among data sets, because concordance increases our confidence that a particular pattern is of general biological interest. This is the topic of chapter five.

Avise identifies four aspects of genealogical concordance. The first is concordance among sequence characters within a gene, which leads to high nodal support (e.g. as measured by bootstrapping) and increases our confidence in inferred clades. The second is concordance among gene genealogies within a taxon, such as between mtDNA and nuclear genes. There currently are few data of this nature, in part because of the technical and biological hurdles involved in generating nuclear sequence data, such as the extra work of separating alleles in heterozygotes, the possibly lower phylogeographic resolution because of the increased coalescence times of nuclear genealogies, and the prospect of recombination. Avise paints a gloomy picture for nuclear phylogeographic studies, but the problems are not insurmountable (Harrison 2001). The generation of gene trees for multiple loci is important for phylogeography because a single genealogy may not accurately reflect the historical and demographic processes experienced by populations. In humans, for instance, mtDNA and Y-chromosome markers provide different estimates of population subdivision, which may reflect differences among the sexes in effective population size or historical migration patterns (Seielstad *et al.* 1998). The bias towards mtDNA as a phylogeographic marker is reflective of its power and ease (e.g. lack of recombination, fast rate of evolution, and low effective population size relative to nuclear DNA). However, the additional information provided by multilocus data, such as more accurate

parameter estimates or the detection of demographic differences among sexes, implies that they are important to phylogeographic studies.

Two other aspects of genealogical concordance are discussed by Avise: concordance in the geography of gene-tree partitions across multiple codistributed species, and concordance of gene-tree partitions with other biogeographic data. These two aspects are the launching pad for an extended treatment of regional phylogeographic studies. Avise surveys the studies on many species in the southeastern US, small mammals of lowland Amazonia, South American cats, plants of the Pacific Northwest of the US, the trans-Arctic interchange of marine organisms following the disappearance of the Bering land bridge, vertebrates of the eastern Australia rainforests, marine taxa across the Isthmus of Panama, and birds and arthropods on the Hawaiian volcanic conveyor belt. Such multispecies research programmes provide convincing examples regarding how earth history has influenced intraspecific diversification.

Discordance between phylogeographic patterns and other data is only briefly discussed by Avise. Discordance can be viewed as phylogeographic noise, for instance when a nuclear gene differs from a mtDNA gene because of the retention of ancestral polymorphism. More interestingly, discordance can be viewed as an opportunity for studying other evolutionary forces. In fact, Karl & Avise (1992) provided one of the first examples of this, where they argued that concordant phylogeographic structure in nuclear and mtDNA restriction fragment length polymorphisms, when compared to a relative lack of differentiation in protein-coding loci (allozymes), was evidence of balancing selection at those loci in the American oyster, *Crassostrea virginica*. More generally, under the assumption that independent loci from a taxon share the same demographic history, significant discordances can be evidence of selection. Thus, phylogeographic studies offer a 'null model' for the study of geographical variation, providing a historical context for comparison with the distribution of other genetic, ecological, morphological or behavioural traits. Remaining theoretical challenges are to determine the number of loci needed to generate a reliable historical null model, and to assess when discordance results from stochastic (nonselective) processes alone; these important theoretical questions are not treated in the book.

Speciation and the species problem

In the last chapter of the book, Avise offers a personal perspective on what coalescent thinking can contribute to questions above the intraspecific level, such as speciation and phylogeny reconstruction. Particular attention is given to the integration of genealogical thinking and species concepts, as phylogeographic approaches have become an

important element of the systematist's toolbox (e.g. Wheeler & Meier 2000). Phylogenetic species concepts (PSCs), in particular, emphasize the importance of historical relationships over reproductive criteria (the focus of biological species concepts, or BSCs). Whereas the heavy emphasis of the book on phylogeographic structure might lead one to expect that PSCs would be perceived as a useful way of recognizing groups of organisms, Avise argues strongly against this use of phylogeographic data (see also Avise 2000b). Avise's opinions stem from what coalescent theory tells us about the behaviour of gene trees. For instance, species may not be reciprocally monophyletic when divergence is relatively recent (e.g. Brown bears, *Ursus arctos*, are paraphyletic with respect to Polar bears, *U. maritimus*; Talbot & Shield 1996). Thus, to Avise, the PSCs represent an 'overly simplified caricature of organismal phylogeny.' Advocates of the BSC, like Avise, see reproductive isolation as fundamental because it prevents reticulate evolution. In fact, reproductive isolation, demography and geography act in concert to mold the cloud of realized gene genealogies, and from this perspective Avise argues the BSC and the PSC are not as antithetical as many believe (see also de Queiroz 1998). This perspective is likely to be unpopular in some systematic circles, yet Avise's population genetic perspective presents a formidable case for their reconciliation. On the other hand, the contrasting of PSCs and BSCs does not consider other influential species concepts. For example, the evolutionary species concept (Wiley 1978, 1981) and the cohesion species concept (Templeton 1989, 2001) could be employed in a manner consistent with the integration of phylogenetic, isolation, and adaptive criteria. Nevertheless, phylogeographic approaches have invigorated systematics and are used extensively in the identification of species boundaries, especially in morphologically conservative groups. Such an approach has been particularly helpful in identifying cryptic species, many of which fit the criteria of the BSC (e.g. Wake 1981; Jockusch *et al.* 2001), and in making informed determinations regarding allopatric groups (e.g. Nielson *et al.* 2001).

Phylogeographic analysis can do more than identify the geographical structuring of lineages; it can often distinguish between hypotheses about the intraspecific diversification process. For example, phylogeographic studies have been important in testing models of ecological speciation (Orr & Smith 1998). In these cases, the phylogeographic pattern functions as a null model against which the distribution of ecotypes can be compared. For example, Schneider *et al.* (1999) found two well defined, allopatric phylogroups in the tropical lizard *Carlia rubrigularis*. Two ecotypes are present in both phylogroups, parapatrically distributed across sharp open/closed forest ecotones. Comparison with the mtDNA tree suggests that the open forest ecotype evolved independently within each phylogroup, and experiments with clay models identified predation as

a possible selective force promoting the evolution of the open forest ecotype. In this case, the phylogeographic analysis provided evidence that the open forest ecotype had evolved more than once. This example illustrates how phylogeographic tools can be used to study natural selection on phenotypic traits (e.g. Smith *et al.* 1997; Taylor *et al.* 1997; Losos *et al.* 1998), a topic to which Avise does not dedicate much attention.

The duration of speciation events is a theme Avise devotes considerable attention to, especially with respect to the hypothesis that Pleistocene climatic fluctuations played an important role in species formation in songbirds. One approach used to estimate the typical age of species is to calculate divergence times among sister taxa under the assumption of a molecular clock. Such an approach does not 'correct' for the intraspecific phylogeographic structure within ancestral species, and thus overestimates divergence times. For instance, Avise reports that 71% of songbird sister species are found to have evolved during the Pleistocene when intraspecific variation is factored out, as compared to 31% when it is not. Such calculations assume that phylogroups are incipient taxa, and that extinction is not a serious confounding factor. The challenge of using genetic divergence to infer the age of population differentiation is an active area of research, recently reviewed by Edwards & Beerli (2000). These authors make it clear that population genetic and coalescent approaches are needed to accurately infer population divergence times from estimates of genetic differentiation.

Phylogeography and phylogenetics

Phylogeography most commonly uses gene trees to make inferences about intraspecific demography and diversification. In the final chapter, Avise shifts to a discussion of how intraspecific phylogeographic principles can inform the study of diversification at deeper taxonomic levels. We are reminded that even if we correctly infer the gene genealogy, the recovered topology may be incongruent with the species tree because of horizontal transfer of genes, introgressive hybridization, or stochastic lineage sorting (Maddison 1997). Considerable attention is given to addressing the common misconception that gene trees for species with ancient divergences should be congruent with the species tree (if inferred correctly), since sorting leads to reciprocal monophyly in the descendant taxa. This is not the case, because if the time between speciation events is short relative to the species' effective population sizes, there is a high probability that stochastic sorting of lineages will generate a gene tree that is discordant from the species tree, no matter how much time has elapsed since the divergence took place. Moore (1995) has shown that for the separation times typical of avian species, mtDNA trees will generally have the same topology as the species tree; however, cases in

which groups of species have diverged from a common ancestor within a narrow time interval could be difficult to resolve (e.g. Patton & Smith 1994). Rough estimates of the effective population size of ancestral species could be helpful, placing a limit on the minimal divergence times that we can hope to resolve (Edwards & Beerli 2000). Avise's presentation suggests that the connections between demography and phylogeny require more consideration from workers in phylogenetic biology.

Another link between phylogenetics and phylogeography concerns the methodologies used to recover gene trees from DNA sequences. Phylogenetic inference is not covered by Avise. Although this omission is reasonable because there are several good resources on phylogenetic methods (e.g. Swofford *et al.* 1996), certain questions related to phylogenetic inference may have deserved further attention. Throughout the book, the trees used to interpret phylogeographic patterns are assumed to be known, and their topology was the point of departure for the inference of the processes that shaped them. It is important to ask how much the uncertainty inherent in phylogenetic inference influences the outcome of phylogeographic analyses, and to consider how this can be accounted for. At least two approaches illustrate how this problem can be addressed. Coalescent methods can estimate population parameters without assuming that a genealogy is known (see section on coalescent theory), and Templeton *et al.* (1992) have developed parsimony-based methods that infer a set of plausible cladograms, rather than a single inferred topology.

Conservation and biodiversity

Conservation biologists are interested in phylogeography because of the information conveyed about individual species and regional biotas. In *Phylogeography*, Avise reviews how phylogeographic analysis can help identify management units (MUs) and evolutionarily significant units (ESUs) within species (see also Moritz 1994). An MU is defined as a population (or group of populations) showing significant differences in the frequency of neutral alleles (e.g. allozymes or mtDNA haplotypes) from other populations. Some species may possess dozens of MUs. ESUs are essentially MUs that are also monophyletic for mtDNA, which suggests a deeper separation than an MU. Such distinctions have helped fisheries biologists identify stocks for management purposes (e.g. Ovenden 1990; but see Taylor & Dizon 1999).

The use of phylogeographic analysis to identify regional biotas is another exciting possibility focused upon in *Phylogeography*. In this case, phylogeographic analysis is carried out on many species to identify concordant patterns (see Concordance and discordance section above). Such research programmes can help to identify biodiversity hotspots, and to prioritize regions for conservation efforts. However, regional studies require years of work and large amounts of

resources, and probably are not practical in many situations. Avise reports the good news is that regional phylogeographic analyses tend to be concordant with traditionally recognized biogeographic provinces and ecoregions, so much of this regional information already exists. Perhaps the biggest contribution of regional phylogeographic analysis to conservation will reside in the gradual uncovering of more cryptic bioregions, such as the association of southern Sierra Nevada herpetofauna with coastal and southern California (reviewed in Macey *et al.* 2001).

Conclusion

John Avise's book will impress upon readers how successfully phylogeography has explored the historical information inherent in mtDNA gene genealogies. The text shows the importance of coalescent theory in the interpretation of intraspecific gene trees, offers a snapshot of the multitude of patterns that have been revealed by the application of this approach, and seeks integration with other fields of historical biology. Avise's focus is on the questions and results of the field, and his clear presentation will be particularly useful to advanced undergraduates, graduate students, and faculty who are struggling to grasp the field and its potential, though even seasoned phylogeographers will find the book useful and informative. Phylogeography is not a 'how-to' book, and readers interested in detailed discussions of methodologies will need to consult other sources, such as Hillis *et al.* (1996) for a review of molecular systematics, and Hartl & Clark (1989) for a review of population genetics.

Studies overlaying mtDNA genealogies on geography have dominated phylogeographic research, and this is strongly reflected in the text. However, motivated by the very work that Avise pioneered, the field has the potential to expand beyond its current scope. For instance, newer approaches, such as nested clade analysis (reviewed in Templeton 1998), offer a more formal framework for quantifying genealogical and geographical information in a way that allows the statistical testing of biogeographic scenarios. Moreover, the increased use of nuclear sequence data, the development of multilocus coalescent theory and likelihood approaches for the estimation of population parameters, increased taxonomic breadth and regional scope, and more sophisticated integration with spatial and historical disciplines (such as palaeontology and geographical information systems) lurk on the horizon of phylogeography.

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References

- Avise JC (2000a) *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.
- Avise JC (2000b) Cladists in Wonderland. *Evolution*, **54**, 1828–1832.
- Avise JC, Arnold J, Ball RM *et al.* (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.
- Bahlo M, Griffiths RC (2000) Inference from gene trees in a subdivided population. *Theoretical Population Biology*, **57**, 79–95.
- Beerli P, Felsenstein J (1999) Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics*, **152**, 763–773.
- Edwards SV, Beerli P (2000) Perspective: gene divergence, population divergence, and the variance in coalescence times in phylogeographic studies. *Evolution*, **54**, 1839–1854.
- Fu Y-X (1994) A phylogenetic estimator of effective population size or mutation rate. *Genetics*, **136**, 685–692.
- Greene HW (1986) Natural history and evolutionary biology. In: *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates* (eds Feder ME, Lauder GV), pp. 99–108. University of Chicago Press, Chicago.
- Harrison R (2001) Genealogies and geography: deciphering recent evolutionary history. *Evolution*, **55**, 646–649.
- Hartl DL, Clark AG (1989) *Principles of Population Genetics*. 2nd edn. Sinauer Associates, Inc, Sunderland.
- Hillis DM, Moritz C, Mable BK, eds (1996) *Molecular Systematics*. 2nd edn. Sinauer Associates, Inc, Sunderland.
- Jockusch EL, Wake DB, Yanev KP (2001) Molecular phylogenetic analysis of slender salamanders, genus *Batrachoseps* (Amphibia: Plethodontidae), from central coastal California with descriptions of four new species. *Herpetological Monographs*, **15**, 54–98.
- Karl SA, Avise JC (1992) Balancing selection at allozyme loci in oysters: implications from nuclear RFLPs. *Science*, **256**, 100–102.
- Kuhner MK, Yamato J, Felsenstein J (1995) Estimating effective population size and mutation rate from sequence data using Metropolis-Hastings sampling. *Genetics*, **140**, 1421–1430.
- Kuhner MK, Yamato J, Felsenstein J (1998) Maximum likelihood estimation of population growth rates based on the coalescent. *Genetics*, **149**, 429–434.
- Losos JB, Jackman TR, Larson A, De Queiroz K, Rodriguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**, 2115–2118.
- Macey JR, Strasburg JL, Brisson JA, Vredenburg VT, Jennings M, Larson A (2001) Molecular phylogenetics of western North American frogs of the *Rana boyleii* species group. *Molecular Phylogenetics and Evolution*, **19**, 131–143.
- Maddison WP (1997) Gene trees in species trees. *Systematic Biology*, **46**, 523–536.
- Moore WS (1995) Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution*, **49**, 718–726.
- Moritz C (1994) Defining 'evolutionary significant units' for conservation. *Trends in Ecology & Evolution*, **9**, 373–375.
- Nee S, Holmes EC, Rambaut A, Harvey PH (1996) Inferring population history from molecular phylogenies. In: *New Uses for New Phylogenies* (eds Harvey PH, Brown AJL, Smith JM, Nee S), pp. 66–80. Oxford University Press, Inc, Oxford.
- Nelson GJ, Platnick NI (1981) *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- Nielsen R, Mountain JL, Hulsenbeck JP, Slatkin M (1998) Maximum-likelihood estimation of population divergence times and population phylogeny in models without mutation. *Evolution*, **52**, 669–677.
- Nielsen R, Slatkin M (2000) Likelihood analysis of ongoing gene flow and historical association. *Evolution*, **54**, 44–50.
- Nielson M, Lohman K, Sullivan J (2001) Phylogeography of the tailed frog (*Ascaphus truei*): implications for the biogeography of the Pacific Northwest. *Evolution*, **55**, 147–160.
- Orr MR, Smith TB (1998) Ecology and speciation. *Trends in Ecology & Evolution*, **13**, 502–506.
- Ovenden JR (1990) Mitochondrial DNA and marine stock assessment: a review. *Australian Journal of Marine and Freshwater Research*, **41**, 835–854.
- Patton JL, da Silva MNF, Malcolm JR (2000) Mammals of the Rio Jurua and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History*, **244**, 1–306.
- Patton JL, Smith MF (1994) Paraphyly, polyphyly, and the nature of species boundaries in pocket gophers (genus *Thomomys*). *Systematic Biology*, **43**, 11–26.
- de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: *Endless Forms: Species and Speciation* (eds Howard DJ, Berlocher SH), pp. 57–75. Oxford University Press, New York.
- Schneider CJ, Smith TB, Larison B, Moritz C (1999) A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. *Proceedings of the National Academy of Sciences of the USA*, **96**, 13869–13873.
- Sielstad MT, Minch E, Cavalli-Sforza LL (1998) Genetic evidence for a high female migration rate in humans. *Nature Genetics*, **20**, 278–280.
- Shaffer HB, McKnight ML (1996) The polytypic species revisited: genetic differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. *Evolution*, **50**, 417–433.
- Slatkin M (1989) Detecting small amounts of gene flow from phylogenies of alleles. *Genetics*, **121**, 609–612.
- Slatkin M, Maddison WP (1989) A cladistic measure of gene flow inferred from the phylogenies of alleles. *Genetics*, **123**, 603–614.
- Smith TB, Wayne RK, Girman DJ, Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. *Science*, **276**, 1855–1857.
- Swofford DL, Olsen GJ, Waddell PJ, Hillis DM (1996) Phylogenetic inference. In: *Molecular Systematics* (eds Hillis DM, Moritz C, Mable BK) 2nd edn, pp. 407–514. Sinauer Associates, Inc, Sunderland.
- Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 585–596.
- Talbot SL, Shields GF (1996) Phylogeography of Brown Bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution*, **5**, 477–494.
- Taylor BL, Dizon AE (1999) First policy then science: why a management unit based solely on genetic criteria cannot work. *Molecular Ecology*, **8**, S11–S16.
- Taylor EB, McPhail JD, Schlüter D (1997) History of ecological selection in sticklebacks: uniting experimental and phylogenetic approaches. In: *Molecular Evolution and Adaptive Radiation* (eds

- Givnish TJ, Sytsma KJ), pp. 511–534. Cambridge University Press, Cambridge.
- Templeton AR (1989) The meaning of species and speciation: a genetic perspective. In: *Speciation and its Consequences* (eds Otte D, Endler JA), pp. 3–27. Sinauer. Sunderland.
- Templeton AR (1998) Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. *Molecular Ecology*, **7**, 381–397.
- Templeton AR (2001) Using phylogeographic analyses of gene trees to test species status and processes. *Molecular Ecology*, **10**, 779–791.
- Templeton AR, Crandall KA, Sing CF (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics*, **132**, 619–633.
- Wake DB (1981) The application of allozyme evidence to problems in the evolution of morphology. In: *Evolution Today, Proceedings of the Second International Congress of Systematic and Evolutionary Biology* (eds Scudder GGE, Reveal JL), pp. 257–270. Carnegie-Mellon University Press, Pittsburgh.
- Watterson GA (1975) On the number of segregating sites in genetical models without recombination. *Theoretical Population Biology*, **7**, 256–276.
- Wheeler QD, Meier R, eds (2000) *Species Concepts and Phylogenetic Theory*. Columbia University Press, New York.
- Wiley EO (1978) The evolutionary species concept reconsidered. *Systematic Zoology*, **27**, 17–26.
- Wiley EO (1981) *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley-Interscience, New York.