

Comparative phylogeography: concepts and applications

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Introduction

This special issue of *Molecular Ecology* celebrates the birth of phylogeography 10 years ago (Avise *et al.* 1987). Because the discipline has deep roots in historical biogeography and population genetics, phylogeography was heralded as a bridge linking the study of micro- and macroevolutionary processes. The initial and still dominant infrastructure for this bridge has been mitochondrial DNA (mtDNA) analyses which have permitted genealogical traces to be followed across the genetic boundaries between populations, species and higher taxonomic levels. In his personal reflection, Avise (1998) documents the explosive growth of phylogeography in the decade since its inception and notes many of the hallmark studies that have provided the empirical and conceptual link between systematics and population genetics. Celebrations are often times of renewal, and thus this special issue of *Molecular Ecology* aims not only to review the past but also to present a blend of theoretical and empirical papers with the hope of invigorating the field.

Phylogeography and its predominant reliance on (animal) mtDNA has led to a body of descriptive data that are impressive in terms of their sheer comparative scope. For example, comparisons of mtDNA divergence between sister taxa of North American birds (Bermingham *et al.* 1992; Klicka & Zink 1997), South American rodents and marsupials (da Silva & Patton 1998) and frogs and reptiles across the Australian Wet Tropics (Schneider *et al.* 1998) have significantly discounted Late Pleistocene models of speciation and suggested that many species pairs are older than previously appreciated. Several articles in this issue presage the potential of *comparative* phylogeographic analyses and demonstrate that the shift from RFLP-based assays to direct determination of DNA nucleotide sequence has permitted increasingly fruitful cross-taxa comparisons of evolutionary history. In turn, we project that comparative phylogeographic analysis will permit detailed studies of landscape evolution, including the dispersal of taxa through a region, speciation, adaptive radiation, and

extinction; in other words, investigation of the fundamental links between population processes and regional patterns of diversity and biogeography. The (typically) slower evolutionary rate of chloroplast DNA (Schaal *et al.* 1998) has limited the contribution of plants to phylogeography and our nascent knowledge of landscape evolution. We anticipate that plant phylogeography will increase in importance, thus refining our interpretation of historical landscape assembly and maintenance, as our understanding of the mutational basis of microsatellite evolution improves and permits this class of molecular markers to be used in comparative context.

Certainly one clear empirical success of mtDNA-based phylogeography has been the improved description of the geographical distribution, phylogenetic relationships and genetic distances among evolutionary lineages of animals, leading, in turn, to a better understanding of regional biogeography and areas of endemism. Articles presented in this issue summarize and discuss the evolutionary landscapes of North America (Bernatchez & Wilson 1998), lower Central America (Bermingham & Martin 1998), Amazonia (da Silva & Patton 1998), Europe (Taberlet *et al.* 1998), the Australian Wet Tropics (Schneider *et al.* 1998) and Hawaii (Roderick & Gillespie 1998; see also Fleischer *et al.* 1998). These studies demonstrate the importance of combining molecular phylogeographic evidence with independent information on landscape history obtained from geology, palaeopalynology, etc. Of course there is a long way to go. One of the many challenges lying ahead is the comparative phylogeographic description of marine species, owing in part to the vast and disjunct geographical scale of many marine populations (Shulman & Bermingham 1995; Palumbi 1997). Meeting this challenge will undoubtedly provide contrasts and insights as sharp as those emerging from comparisons of temperate and tropical terrestrial evolutionary landscapes.

Comparative phylogeographic analyses can contribute to broader studies of ecology and evolution in a number of ways. First, phylogeographic analysis can identify historically and evolutionarily independent regions that can be considered as natural replicates amongst which generalizations about specific processes can be tested statistically. For example, the evolutionary response to selection gradients can be compared across

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different historical isolates. Second, phylogeography can provide an evolutionary and geographical context for the species comprising ecological communities, thus permitting determination of historical and spatial influences on patterns of species richness (Ricklefs & Schluter 1993). Third, an understanding of historical responses to changes in the landscape and the identification of evolutionarily isolated areas can inform conservation strategies (Moritz & Faith 1998).

Phylogeography can be (and has been) criticized for being overly reliant on a single gene system, mtDNA, as a marker of evolutionary descent. The pitfalls, including effects of selection, inadvertent amplification of pseudogenes, interspecific hybridization etc., can often be avoided by thoughtful molecular and numerical analyses and by testing for phylogenetic congruence across nuclear and mitochondrial genes. However, the utility of nuclear gene (e.g. intron) sequences in population-level phylogenetics appears to be limited by the substantially greater coalescent time (and associated variance) of nuclear genes as compared to mitochondrial genes, and the potential for reticulate evolution among nuclear alleles due to recombination. Nonetheless, phylogeographers will come to rely increasingly on nuclear markers, and statistical in addition to phylogenetic analyses, as attention turns to joint study of the demographic and phylogenetic histories of species.

Under some conditions, particularly where genetic divergence is limited and there is substantial homoplasy and among-site rate variation, or both, it may be inappropriate to use tree-based analytical methods even for mtDNA (Smouse 1998). But where even part of a tree or network can be estimated reliably, overlaying the tree on geography can provide insights into history that are difficult to obtain in any other way (Templeton 1998). The obvious link between coalescence models (Hudson 1998) and empirically estimated gene trees has refined phylogenetic analysis as the field increasingly incorporates this rapidly developing area of population genetics theory. Already, it is apparent that gene trees can provide estimates of (long-term) effective population size, mutation rate and gene flow (see papers in Harvey *et al.* 1996). The result should be strong inference regarding the history of a taxon's spread across a landscape and the presence of continuing migration between populations.

One area where phylogeographic interpretations (including some of our own) have been weakest relates to the timing of cladogenetic events. Phylogeographers often assume that nucleotide substitution rates are approximately homogeneous with respect to taxon, lineage, and time, and thus use branch points in a phylogeny to estimate the relative chronology (or absolute time) of separation among lineages. Yet molecular rate constancy has been tested against well-dated fossils or vicariant events in only a few cases, including several species

distributed across the K–Ar-aged Hawaiian Islands (Fleischer *et al.* 1998). More typically, phylogeographers have extrapolated molecular rates from point estimates relating a presumed date of separation with molecular divergence between taxa. The faith that many phylogeographers appear to place in molecular clocks would be disquieting were it not for the advent of a number of statistical and phylogenetic approaches that permit measures of molecular divergence to be tested for rate heterogeneity. Notwithstanding these tests, robust temporal estimation in phylogeographic reconstructions would be improved by utilizing two or more unlinked genetic markers and determining from each set of data whether the relative times since cladogenesis are congruent.

Therefore, the major challenges that we see in the future are:

- 1 To utilize unlinked molecular markers and develop improved analytical approaches for testing for evolutionary congruence, or lack thereof, between nuclear and organelle genes.
- 2 To incorporate new developments in coalescence theory, particularly as they apply to nonequilibrium populations, into phylogeography and, more generally, to increase the statistical rigour of the field.
- 3 To increase the precision with which the timing of cladogenetic (separation) events can be estimated.

Improvements in these areas, some of which are evident from studies in this issue, will improve substantially the power of phylogeography to test hypotheses derived from species biogeography, speciation, earth history, etc.

In conclusion, phylogeography seeks to test the congruence between the evolutionary, demographic and distributional histories of taxa against the particular geological and ecological setting of a region and to determine the chronology of evolutionary diversification. Comparative phylogeography describes the evolution of landscapes and permits analysis of the effects of history and geography on organismal community structure at both local and regional levels. Knowledge concerning the different ages of biotas and their areas of extent and the different rates of species origin and extinction will enhance our understanding of the processes responsible for the origin and maintenance of communities and, perhaps, make some contribution to our efforts to conserve biodiversity.

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