

In the light of evolution X: Comparative phylogeography

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Phylogeography is the study of the spatial arrangement of genealogical lineages, especially within and among conspecific populations and closely related species (10). Ever since its inception in the late 1970s (11, 12) and mid-1980s (13), the field has sought to extend phylogenetic reasoning to the intraspecific level, and thereby build empirical and conceptual bridges between the formerly separate disciplines of microevolutionary population genetics and macroevolutionary phylogenetics. In the early years, phylogeographers relied on data from restriction-site surveys of mitochondrial (mt) DNA to draw inferences about population structure and historical demography, but stunning improvements in molecular techniques (14, 15) and extensions of coalescent theory and other analytical methods (16) later broadened the field's scope dramatically (17). Phylogeographic perspectives have transformed aspects of population biology, biogeography, systematics, ecology, genetics, and biodiversity conservation. One aim of this colloquium was to bring together leading scientists to address the current state of phylogeography as the discipline enters its fourth decade. The broader goal was to update a wide audience on recent developments in phylogeographic research and their relevance to past accomplishments and future research directions.

Many of the advancements in phylogeography have entailed comparative appraisals of one sort or another (18). (See refs. 1–9 for papers from previous colloquia in the series and Box 1 for an overview of the series.) Papers in Section I of this colloquium emphasize the word "comparative" in a spatial sense, where the phylogeographic assessments entail various species (sometimes generally codistributed) that may be representative of particular kinds of environmental settings, such as oceanic versus continental realms. Section II deals with comparative phylogeography in a genomic sense. Nonrecombining cytoplasmic genomes have been the standard workhorses of genealogical analyses, but in principle the primary library of

evolutionary histories is ensconced in nuclear genomes that are increasingly accessible to scrutiny. Section III focuses on comparative phylogeography in a taxonomic sense, emphasizing how phylogeographic findings have impacted ecological and evolutionary thought in a diversity of organismal groups. Section IV focuses on comparative phylogeography in a conceptual sense by addressing the place of phylogeography in relation to various allied disciplines in the biodiversity sciences. Several papers in these proceedings inevitably overlap in their sectional assignments because (for example) disparate taxa tend to inhabit different environments, and because the researchers assembled here had a diversity of phylogeographic objectives, data types, and analytical approaches.

Comparative Phylogeography in a Spatial Sense

Phylogeographers have roamed the planet in their quest to identify patterns that might typify organisms occupying diverse environmental regimes. Understanding the biotic response to past challenges provides a compass for contemporary and future challenges. Brian Bowen et al. (19) summarize a vast literature on phylogeographic findings for the world's oceans. At face value, the oceanic realm might seem to be featureless and relatively free of impediments to gene flow. Nevertheless, many migrant species in the sea (such as marine turtles, and some cetaceans and pelagic fishes) display phylogeographic patterns, implicating physical barriers as promoters of both intraspecific genetic breaks and subsequent allopatric speciation events (properly viewed as stages along a temporal continuum). For marine taxa more generally, a wide variety of phylogeographic outcomes implies the operation of other evolutionary processes as well, such as sympatric or ecological speciation in some cases, environmental effects from historically shifting climates, and the important role of organismal behavior and natural history in shaping current phylogeographic

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Box 1. In the Light of Evolution. In 1973, Theodosius Dobzhansky penned a short commentary titled “Nothing in biology makes sense except in the light of evolution” (35). Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have been neglected, misunderstood, or purposefully misapplied. Biodiversity—the great variety of life—is an exuberant product of the evolutionary past, a vast support system for the contemporary human endeavor (aesthetic, intellectual, and material), and a rich legacy to cherish and preserve for the future. Two challenges, as well as opportunities, for 21st century science are to gain deeper insights into the evolutionary processes that foster biodiversity and to translate that understanding into workable solutions for the regional and global crises wrought by seven billion people. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and applied fields, including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought extend into learned realms that are traditionally the domain of philosophy and religion. The central goal of the “In the Light of Evolution” series has been to promote the evolutionary sciences through state-of-the-art colloquia and published proceedings. Each installment has explored evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the “In the Light of Evolution” series has aimed to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually vital as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences. The organizers and founding editors of the “In the Light of Evolution” series (J.C.A. and F.J.A.) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory these colloquia are dedicated. May Dobzhansky’s words and insights continue to inspire rational scientific inquiry into nature’s marvelous operations.

motifs. Empirical phylogeographic patterns in the sea have also illuminated the evolutionary role of biodiversity hotspots and the historical dispersal routes that enhance global biodiversity.

Brett Riddle (20) summarizes an equally large scientific literature for species that occupy terrestrial or semiterrestrial regimes on continental landmasses. The author identifies phylogeographic hotspots, usually ecological transition zones that are focal points for study. Previously these hotspots were primarily in the northern hemisphere and proximal to well-equipped laboratories, but success and improved technology have inspired a diaspora to geographic settings around the world. Here, as might generally be expected, range contraction-expansion episodes and dispersal from and into Neogene and Quaternary refugia played major roles in shaping the current-day arrangements of phylogeographic lineages for many continental taxa. The classic vicariance-dispersal paradigm, that generated heated debate

and much research in the previous century, is transforming into a more nuanced and multifactorial perspective on why lineages are distributed as we observe them today.

Ivan Prates et al. (21) use a case-history approach to reveal how historic climate and habitat changes affected three broadly codistributed lizard species in Amazonia and the Atlantic Forest of the Neotropics. This study finds partial congruence in phylogeographic patterns that can be attributable to shared historical influences plus similarities in life history and environmental needs. However, the authors then go much further by embracing the close link between phylogeographic pattern and historic population demography to deduce that these taxa had species-specific population demographies in their recent past. These demographic parameters (in conjunction with ecological niche models related to climate change) forecast very distinct population trajectories over the next 60 y for these three environmentally sensitive lizard species.

Remote oceanic archipelagos offer especially intriguing evolutionary studios for studying phylogeographic processes on isolated chains of islands that originated (typically in sequential temporal order) via hotspot volcanism. These midoceanic islands offer a proverbial *tabula rasa* in which every species has origins elsewhere, and community composition is stilted by the filter of dispersal ability. Several such oceanic archipelagos are scattered around the world’s oceans, in most cases with the islands being displaced unidirectionally by plate tectonic movements, as if on an evolutionary conveyor belt. Kerry Shaw and Rosemary Gillespie (22) review comparative phylogeographic findings for diverse taxa on six such oceanic archipelagos. They focus especially on the “progression rule,” which predicts that older genealogical lineages should map to older islands within an archipelago, with progressively younger lineages mapping to progressively younger islands within each such island chain. Shaw and Gillespie find support for the progression rule in some cases (notably in the Hawaiian archipelago), but less so on some others. The authors also highlight the precedence effect, whereby the success of initial colonizers makes it more difficult for subsequent colonizers to establish. The general trend—as well as particular exceptions to it—are both highly informative about dispersal and speciation processes in these distinctive environmental settings. As noted here and by Riddle (20), the simplified evolutionary arena of oceanic islands can reveal phylogeographic patterns that are obscured in a more complex continental setting.

Comparative Phylogeography in a Genomic Sense

Throughout the early phylogeographic era, cytoplasmic genomes (mtDNA in animals and chloroplast DNA in plants) provided the bulk of empirical genetic information for phylogeographic reconstructions. However, a long-appreciated fact is that these cytoplasmic genomes represent only a minuscule fraction of a species’ total hereditary pedigree, the vast majority of which is ensconced in nuclear DNA. Early attempts to extract useful phylogeographic information from the nuclear genome met mostly with failure because of technical difficulties coupled with sex-based genetic recombination. In recent years, this situation has changed (to an arguable degree) because of the ongoing technological revolutions in next-generation sequencing and “big-data” genomics. How might phylogeographic inferences be impacted as new technologies extract more and more genetic information from loci in the recombining nuclear genome?

Each species has its own true phylogeographic past (extended intraspecific pedigree) through which its various loci have been transmitted and which therefore constitute a plethora of gene genealogies. For any species, genealogy and historical population

demography are like opposite sides of the same coin: intimately connected. Coalescent theory offers a robust conceptual framework for translating the empirical phylogeographic structure of a "gene tree" (such as that provided by mtDNA) into inferences about a population's demography history. Although the population pedigree of any species in effect contains (or consists of) multitudinous quasi-independent nuclear gene trees, the actual degree to which a given pedigree constrains the topologies of multiple unlinked loci has received rather scant attention. John Wakeley et al. (23) address this issue using population genetic models and computer simulations. By focusing attention on extreme demographic events (the occurrence of very large families in a pedigree and on strong selective sweeps in the population's recent past), the authors conclude that "only rather extreme versions of such events can be expected to structure population pedigrees in such a way that unlinked loci will show deviations from the standard predictions of population genetics, which average over population pedigrees" (23).

Rohan Mehta et al. (24) continue this general theme of the fundamental distinction between gene trees and population (or species) trees, by addressing the probability of monophyly of a gene lineage on a species tree. Although such models (based on neutral coalescent theory) have long been used to calculate the probability that a set of gene lineages is reciprocally monophyletic under the simplest case of a pair of sister taxa, Mehta et al. extend such analyses to probabilities of gene-tree monophyly for genetic studies that span arbitrary numbers of multiple isolated populations or species.

One of several new types of nuclear data stemming from next-generation sequencing involves the recovery of SNPs from many thousands of unlinked nuclear genomic regions, even in non-model species. SNPs are increasingly being used to supplement more traditional phylogeographic datasets based on cytoplasmic genomic sequences or allelic profiles at relatively small numbers of microsatellite loci. Maria Thomé and Bryan Carstens (25) use a case-history approach (involving Brazilian frogs) to illustrate how such molecular information can be used to estimate historic population demographic parameters (such as population size and gene flow) under a wide variety of evolutionary models. Their take-home message is that an objective approach to phylogeographic inference should entail calculating the probability of multiple demographic models, given the data, and then subsequently ranking these models using information theory. The paper's framework also allows the authors to express their own views on the ever-changing epistemology of phylogeographic inference.

Anna Papadopoulou and Lacey Knowles (26) expand on the topic of phylogeographic models by tracing and critiquing the historical emphasis on genealogical concordance in comparative phylogeography. Such concordance generally refers to shared phylogeographic patterns, either across multiple loci within extant species or across particular genes of multiple codistributed species. The authors question whether concordance in general is a uniformly useful criterion for evaluating alternative phylogeographic hypotheses, by emphasizing taxon-specific traits that may predict concordance or discordance among datasets and species. Papadopoulou and Knowles bolster their reservations with case studies illustrating the many possible ways that genealogical discordance (the antithesis of concordance) can arise in particular situations.

Scott Edwards et al. (27) conclude this section by providing an overview of the impact of cutting-edge molecular technologies (such as various expressions of next-generation sequencing) on the trajectory of the fields of phylogeography and phylogenetics

in the genomics era. As empirically illustrated by the authors' comparative genetic research, spanning diverse vertebrate taxa across northern Australia, the emerging discipline of phylogenomics will call for a greater appreciation of reticulation during the evolutionary process, both within genomes in the form of genetic recombination, and across populations and species in the forms of gene flow and introgression. In this important sense, the arenas of comparative phylogeography and interspecies phylogenetics can again be seen as lying along a conceptual continuum of historical evolutionary genetic phenomena, from population-level separations to deeper organismal divergences.

Comparative Phylogeography in a Taxonomic Sense

Because nucleic acids are the universal hereditary material of life on Earth, molecular approaches to phylogeography can in principle be applied to creatures ranging from bacteria to whales and humans. The papers in this section will further illustrate the catholic nature of comparative phylogeography by describing a few chosen examples spanning a wide array of disparate taxonomic groups.

Although microbes have not been a traditional focus of phylogeographic research (mostly for logistical or technical reasons), Michaeline Nelson et al. (28) show how a trait-based approach can enlighten our understanding of microbial biogeography on a global scale. The genetic traits they surveyed involve different pathways for nitrogen cycling in soil microbes sampled from around the world. By analyzing the spatial and taxonomic distributions of such microbial traits, the authors develop an argument for how comparative phylogeographic methods could be highly relevant to predicting the responses of biogeochemical cycles to future climatic and other environmental changes.

Kelly Zamudio et al. (29) make a similar case for vertebrate animals by emphasizing the need to integrate trait (phenotypic) data with molecular genetic data in future phylogeographic appraisals. The authors argue that because phenotypes are the actual targets of selection, they should be assessed in conjunction with other phylogeographic data to illuminate the ecological and evolutionary forces shaping biodiversity. Ever since the time of Alfred Russel Wallace (the founder of biogeography in the mid-1800s), biogeographic appraisals have relied primarily on the spatial distributions of phenotypic attributes. Thus, if the integrative prescriptions of Zamudio et al. are to be followed, the field of comparative phylogeography may in effect partially return to its intellectual biogeographic roots even while simultaneously expanding the latter in new genealogical directions. Bowen et al. (19) and Papadopoulou and Knowles (26) similarly endorse the links between biogeography defined with organismal traits and phylogeography founded on gene genealogies.

Anne Yoder et al. (30) focus on comparative genetic patterns in one particular taxonomic assemblage: congeneric mouse lemurs on the island of Madagascar. Apart from demonstrating the profound phylogeographic ramifications of altered landscapes across recent geological and human timescales, this survey is instructive because it exemplifies the types of comparative phylogeographic analyses that have been applied to many other animal taxa in various regions around the globe, and because it involves an island (as opposed to, for example, an oceanic, continental, or archipelago setting).

In a phylogeographic study of North American bison, Peter Heintzman et al. (31) advocate for a greater emphasis on paleoecology as a major driving force shaping contemporary phylogeographic patterns. Their example involves the purported role of an Ice Free Corridor as a plausible route for dispersal (of humans

and other animals) between Beringia and more southerly areas of North America. Without knowledge of such paleoecological conditions in times past, the authors argue that phylogeographers will remain handicapped in their attempts to interpret the spatial genetic architecture of extant taxa.

Whereas mtDNA has been the traditional molecular workhorse of phylogeographic appraisals in animals, chloroplast DNA has performed the corresponding role in plant studies. Victoria Sork et al. (32) summarize evolutionary lessons learned from comparative analyses of phylogeographic patterns displayed by diverse plant taxa in California. Most plants have several biological features that differ from those of most (not all) animals and that presumably have major phylogeographic and demographic relevance: a sessile growth form, high reproductive output, leptokurtic dispersal through pollen and seeds, intimate interactions with local environmental conditions, and the potential for individual longevity. Sork et al. provide empirical examples of how these botanical features apparently have impacted phylogeographic patterns in "plants" as diverse as oak trees and lichens.

Unsurprisingly, perhaps no single species has received greater phylogeographic attention than *Homo sapiens*. In the final paper of this section, Alexander Harcourt (33) provides a panoramic overview of the phylogeography of our species, beginning with origins on the African continent some 200,000 y ago and continuing with the diasporas of our ancestors from that landmass to eventually occupy the entire world. Included in this paper are the deduced evolutionary dates and specific migration routes used by our ancestors to "people the planet," as well as discussions of the patterns of cultural diversity associated with this phylogeographic history. Harcourt's concise summary of a vast literature on human origins should be of considerable interest to anthropologists and general audiences alike.

Comparative Phylogeography in a Conceptual Sense

One final dimension in which phylogeography can be considered "comparative" is through its interactions with various other

biodiversity disciplines. This general topic has already been addressed by several of the colloquium papers. For example, Bowen et al. (19) explicitly link modern marine phylogeography to traditional biogeographic perspectives on biodiversity in the sea; Wakeley et al. (23), Mehta et al. (24), and others relate phylogeography to historical population demography, coalescent theory, and traditional population genetics; Edwards et al. (27) explicitly weighed and contrasted comparative phylogeography with molecular phylogenetics and phylogenomics; Heintzman et al. (31) and Prates et al. (21), among others, advocated the incorporation of more paleoecology into phylogeography; and several authors touched upon the special relevance of phylogeographic findings for the field of conservation biology. The final paper in this colloquium provides one further example of how comparative phylogeography relates to yet another emerging biodiversity field.

The term "landscape genetics" has blossomed in recent years into a recognizable and popular research arena, purportedly forming a needed bridge between landscape ecology and population genetics (much as the field of phylogeography attempted to bridge phylogenetics and population genetics). Leslie Rissler (34) recounts the relatively recent (as well as deeper) conceptual histories of both phylogeography and landscape genetics, strives to highlight different empirical and intellectual emphases in these two fields, and speculates on some major research areas ripe for further investigation in the emerging era of genomics. Rissler concludes by advocating a union of comparative phylogeography and landscape genetics under the broader umbrella of biogeography, which has always sought to connect ecology and evolutionary biology. The union of comparative phylogeography and biogeography is a theme that emerged in the first contribution (19), was elaborated throughout this colloquium (26, 29, and elsewhere), and is eloquently summarized in this final contribution (34).

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