Comparative phylogeography as an integrative approach to historical biogeography

ABSTRACT

Phylogeography has become a powerful approach for elucidating contemporary geographical patterns of evolutionary subdivision within species and species complexes. A recent extension of this approach is the comparison of phylogeographic patterns of multiple co-distributed taxonomic groups, or 'comparative phylogeography.' Recent comparative phylogeographic studies have revealed pervasive and previously unrecognized biogeographic patterns which suggest that vicariance has played a more important role in the historical development of modern biotic assemblages than current taxonomy would indicate. Despite the utility of comparative phylogeography for uncovering such 'cryptic vicariance', this approach has yet to be embraced by some researchers as a valuable complement to other approaches to historical biogeography. We address here some of the common misconceptions surrounding comparative phylogeography, provide an example of this approach based on the boreal mammal fauna of North America, and argue that together with other approaches, comparative phylogeography can contribute importantly to our understanding of the relationship between earth history and biotic diversification.

Keywords
Area cladistics, comparative phylogeography, historical biogeography, vicariance.

INTRODUCTION

In a recent guest editorial Humphries (2000) presented an overview of historical biogeography. He concentrated largely on comparisons of the available methodologies for investigating the relationship between earth history and biotic history. Although Humphries discussed a wide range of biogeographic topics, we believe that his portrayal of phylogeography as a 'chimera of scenario building' and a discipline based in 'dispersal scenarios' was misleading. Of special concern to us was his failure to identify the emerging field of comparative phylogeography (defined broadly as the comparison of geographical patterns of evolutionary subdivision across multiple co-distributed species or species complexes; see Cracraft, 1989; Zink, 1996; Schneider *et al.*, 1998; Avise, 2000; Riddle *et al.*, 2000; Sullivan *et al.*, 2000). This is an important omission because comparative phylogeography shares a common conceptual framework with historical biogeography (Zink, 1996). Comparative phylogeography also permits investigation of biogeographic questions on spatial and temporal scales that are smaller than those typically addressed with other approaches (Avise, 2000), and it often reveals cryptic vicariance in the historical assembly of biotas (e.g. Riddle *et al.*, 2000).

We are writing to suggest that historical biogeography should continue to be a broadly integrative discipline. As such, it should include the perspective of phylogeography, and particularly comparative phylogeography. Using an example based on the boreal mammal fauna of North America we illustrate here: (1) the utility of phylogeography in elucidating contemporary patterns of evolutionary subdivision within species and species complexes and (2) the value of comparative phylogeography in providing novel insights into the relationship between earth history and biotic diversification.

PHYLOGEOGRAPHY IN THE BROAD CONTEXT OF BIOGEOGRAPHY

The goal of 'phylogeography' (Avise *et al.*, 1987) is to characterize the phylogenetic deployment of genealogical lineages across the geographical landscape. As such, phylogeography is a subdiscipline of biogeography in which the primary units of analysis are monophyletic clades that are inferred from phylogenetic analyses. This typically entails the use of one or more molecular markers when intraspecific population phylogeny is being examined, but in principle, any set of phylogenetically informative characters could be used. The most commonly used molecular marker for the first generation of phylogeographic studies has been animal mitochondrial DNA (mtDNA), although other markers, most notably plant chloroplast DNA, have also been used. Several features of animal mtDNA

suit it particularly well for examining geographical distributions of evolutionary lineages. First, the mtDNA genome of animals is typically inherited in a uniparental (matrilineal) fashion and thus has an effective population size one-fourth that of the nuclear genome (Avise *et al.*, 1987). Secondly, the mtDNA genome has a relatively rapid rate of molecular evolution (Brown *et al.*, 1982). These features of the mtDNA genome lead to: (1) non-reticulating (bifurcating) gene trees and (2) rapid geographical sorting and genetic divergence of populations in the absence of gene flow. As a result, phylogeographic studies using mtDNA usually provide more resolution of intraspecific patterns of geographical variation than non-molecular methods (Avise, 2000). Two decades of empirical and theoretical research have also provided a large body of knowledge on the rates at which various regions of the mtDNA genome evolve in animals (Brown *et al.*, 1979, 1982; Irwin *et al.*, 1991; Hillis *et al.*, 1996; Arbogast & Slowinski, 1998; Fleischer *et al.*, 1998). In many cases this information can be used to estimate dates of evolutionary divergence and to develop generalized temporal frameworks for evaluating competing biogeographic hypotheses (Zink & Slowinski, 1995; Hillis *et al.*, 1996; Klicka & Zink, 1997; Gibbons, 1998; Arbogast & Slowinski, 1999).

Since phylogeography was first introduced (Avise *et al.*, 1987), it has been used primarily to examine geographical structuring of gene lineages within single species. Typically individuals are sampled from throughout the geographical range of a species, and the mtDNA genome is characterized for each individual, either through restriction fragment analysis or direct sequencing. The resulting haplotypes are then used to infer a phylogeny, or gene tree, which reflects the evolutionary relationships of the individuals and populations sampled. By combining the resulting gene trees with the geographical location from which each individual was sampled, one can elucidate the geographical distributions of major gene lineages (monophyletic clades) that comprise the gene tree. The application of likelihood and coalescent methods (e.g. Kuhner *et al.*, 1995; Wakeley & Hey, 1997; Wakeley, 1998; Beerli & Felsenstein, 1999), and approaches such as nested clade analysis (Templeton, 1998), allow one to interpret the resulting phylogeographic patterns within the context of evolutionary and biogeographic models. As a result, phylogeography is a powerful approach for investigating a wide range of issues related to biogeography, including the relative roles of gene flow, bottlenecks, population expansion, and vicariant events in shaping geographical patterns of genetic variation.

In many cases, phylogeographic analyses have revealed cryptic and deeply divergent evolutionary lineages that are not reflected in the current taxonomy, and nominal species are often found to be poly- or paraphyletic (Patton & Smith, 1996; Arbogast, 1999a; Demboski *et al.*, 1999; Avise, 2000; Riddle *et al.*, 2000). In such cases, use of current taxonomy leads to an underestimate of the role of vicariance in structuring biotas, and causal connections between earth history and biotic diversification remain unrecognized (Cracraft, 1994; Riddle *et al.*, 2000). In this context it is unclear to us why Humphries (2000) views phylogeography as an inherently dispersalist approach. In fact, in several of the examples he cites to support his contention, the primary mechanism proposed by the original authors to explain observed phylogeographic patterns was vicariance, not dispersal. For example, both Wooding & Ward (1997) and Arbogast (1999a) proposed that vicariance, in the form of forest fragmentation associated with glaciation, divided ancestral populations of the American black bear and northern flying squirrel, respectively. Perhaps the evidence of more recent (post-Wisconsinan) northward recolonization of populations from southern boreal forest refugia, also discussed by Wooding & Ward (1996) and Arbogast (1999a), leads to semantic confusion. However, this type of range expansion does not imply dispersal in the sense used in historical biogeography, i.e. dispersal as long distance movement across a pre-existing environmental barrier. We believe that range expansion and long-distance dispersal should be treated as two distinct phenomena, and we see no reason that the phylogeographic approach is inherently 'dispersalist'.

COMPARATIVE PHYLOGEOGRAPHY

For more than a decade researchers have realized that the comparison of geographical patterns of genetic variation among multiple co-distributed taxa (comparative phylogeography) has strong parallels with historical biogeography (Cracraft, 1989; Riddle, 1996; Zink, 1996). For example, 'Drawing an analogy from historical biogeography… one could test whether co-distributed taxa have congruent phylogeographic patterns of genetic variation, which might be predicted if a given area has but a single history' (Zink, 1996). In both historical biogeography (e.g. Wiley, 1988) and comparative phylogeography (Avise, 2000), the most parsimonious explanation for multiple taxonomic groups that exhibit common spatial patterns of evolutionary subdivision is that they have a shared biogeographic

history. In other words, a common set of historical vicariant events has geographically structured a group of ancestrally co-distributed organisms in a similar way.

To date, several studies have found evidence of phylogeographic congruence among co-distributed taxa (e.g. Avise, 1992; Schneider *et al.*, 1998; Walker & Avise, 1998; Arbogast, 1999b; Demboski *et al.*, 1999; Riddle *et al.*, 2000). In each case, the observed patterns of phylogeographic congruence suggest that the taxa examined have a long-standing geographical association with one another and have attained a common pattern of geographical subdivision as a result of being subjected to the same environmental history. As such, it would be appropriate to construct a general area cladogram (representing a single history of place) based on congruence among the area cladograms derived from phylogenetic analyses of the multiple co-distributed taxa (Sullivan *et al.*, 2000). In contrast, other studies (e.g. Bowen & Avise, 1990; Lamb *et al.*, 1992; Zink, 1996) have demonstrated a lack of phylogeographic congruence among co-distributed taxa. Such incongruent phylogeographic patterns suggest that the species examined do not have shared biogeographic histories. In these cases it would be inappropriate to attempt to construct an area cladogram, because any congruence among single-taxon area cladograms would be the result of chance rather than a reflection of a single history of place (Sullivan *et al.*, 2000).

As an example of how the comparative phylogeographic approach can provide novel insights into the relationship between earth history and biotic history, we illustrate here a comparison of the phylogeographic structure of five forms (species or species complexes) of North American mammals (Fig. 1). These co-distributed mammals are all ecologically associated with the boreal forest biome of North America, yet they exhibit a variety of life-history strategies and dispersal abilities. Based on current taxonomy, these five forms do not exhibit similar patterns of geographical subdivision, i.e. they are comprised of a variable number of species (1–3), and the locations of interspecific distributional boundaries within each form, when present, tend not to occur in the same locations. Thus, taxonomy suggests that these boreal mammals do not have shared biogeographic histories. However, when the mtDNA-based phylogeographic structure of each of these five forms is compared, a different picture emerges. Each of the five forms is characterized by a Pacific Northwest phylogeographic discontinuity that separates a Pacific Coastal (PC) lineage from a more widespread interior continental (CON) lineage. This area of the Pacific Northwest is characterized by a high incidence of hybridization (between nominal species and subspecies) in a diverse array of animals, and it has been considered an important 'suture zone', or zone of secondary contact between previously isolated biotas (Remington, 1968). In the larger mammals, e.g. the American black bear and marten (which have greater potential dispersal distances than the smaller mammals), an overlap of PC and CON lineages appears in the Pacific Northwest and northern Rocky Mountains. The marten is unique in having populations in the southern Rockies that are part of the PC lineage. The delineation between the PC and CON lineages appears more abrupt in the smaller mammals. In addition to the PC–CON phylogeographic break, two of the groups (*Tamiasciurus* and *Clethrionomys*) possess additional phylogeographic discontinuities (Fig. 1), the implications of which are discussed elsewhere (Arbogast, 1999b; Arbogast *et al.*, 2001). It is worth noting that the biogeographic history of *Clethrionomys* appears to be considerably more complex than that of the other boreal mammals exemplified here.

The congruent PC–CON phylogeographic break of these boreal forest mammals suggests that they have responded in a concerted fashion to vicariance in the environmental history of the region. Had the mtDNA phylogeographic patterns of these animals not been investigated, the importance of vicariance in structuring this biota would likely have been overlooked. Several authors (e.g. Rogers *et al.*, 1991; Wooding & Ward, 1997; Arbogast, 1999a, b; Arbogast *et al.*, 2001) have proposed that historical episodes of fragmentation, contraction and subsequent expansion of boreal forest associated with Pleistocene glacial cycles could produce the observed phylogeographic pattern. Both the fossil record (Kurtèn & Anderson, 1980) and levels of mtDNA sequence divergence (Fig. 1) are consistent with a Pleistocene divergence of the PC and CON lineages. However, given the cyclic nature of Quaternary glaciation and associated changes in the distribution of boreal forest (Rogers *et al.*, 1991; Brown & Lomolino, 1998), it is also plausible that a series of glacially related vicariant events, each fragmenting the boreal forest habitat of North America in a similar way, may have produced similar phylogeographic patterns at different times. If this were the case, the similar phylogeographic patterns might lead to the inappropriate conclusion that these taxa have shared biogeographic histories, when in fact they do not. The roughly clock-like rate of evolution of vertebrate mtDNA provides an initial perspective on whether the PC–CON division in each of the five forms of boreal mammals occurred contemporaneously. Levels of mtDNA sequence divergence between the PC and CON lineages of the five forms vary (Fig. 1), which suggests that the groups may have diversified at different times in the
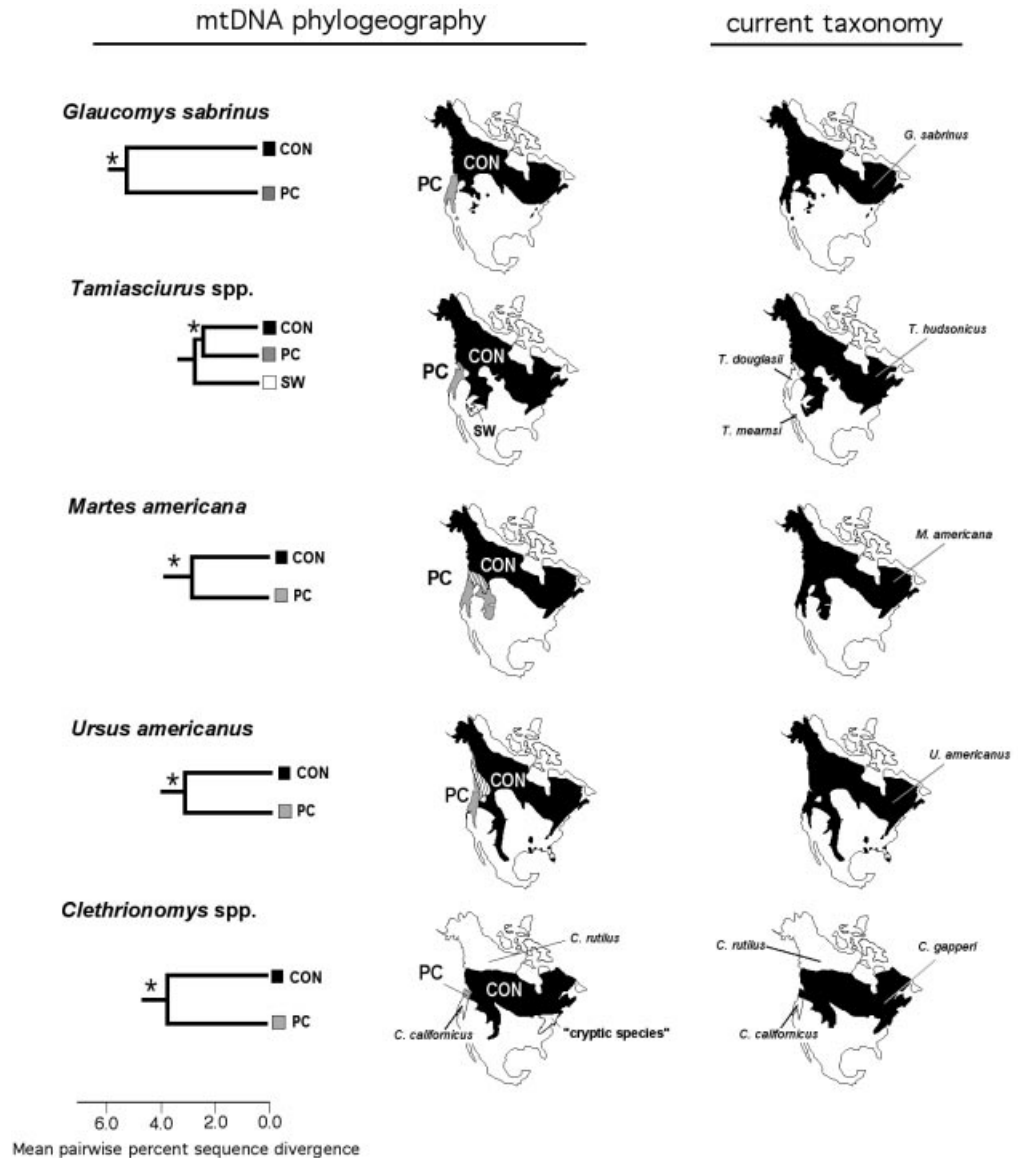
mtDNA phylogeography | current taxonomy

Figure 1 Phylogeographic structure vs. current taxonomy for five North American boreal mammals: the northern flying squirrel, *Glaucomys sabrinus* (Arbogast, 1999a); tree squirrels of the genus *Tamiasciurus* (Arbogast *et al.*, 2001); the American marten, *Martes americana* (Demboski *et al.*, 1999); the American black bear, *Ursus americanus* (Wooding & Ward, 1996; Stone & Cook, 2000); and red-backed voles, *Clethrionomys* (Arbogast, 1999b). Branching diagrams on left summarize estimated levels of mtDNA sequence divergence between PC (Pacific Coastal) and CON (continental) lineages in each group, with corresponding nodes designated by an asterisk. Hatched areas represent regions of geographical overlap between two lineages. SW refers to a south-western mtDNA lineage of *Tamiasciurus* and 'cryptic species' refers to a highly divergent mtDNA lineage within *Clethrionomys gapperi*. Detailed gene trees for each of the five mammal groups can be found in the papers cited above.

past (Zink, 1996; Klicka & Zink, 1997; Strange & Burr, 1997; Walker & Avise, 1998). However, a number of other factors, including differences in ancestral population size and among-lineage mtDNA rate heterogeneity, could also contribute to the differing amounts of mtDNA divergence detected between the PC and CON lineages of the forms (Edwards, 1997; Edwards & Beerli, 2000). Therefore, based on the available data it is difficult to reject a hypothesis of contemporaneous divergence of PC and CON lineages for each of the five forms of boreal mammals. However, by evaluating genetic

divergence across a large number of independent loci in each taxonomic group, it should be possible to differentiate statistically between 'single-event' and 'multiple-event' biogeographic hypotheses (Edwards & Beerli, 2000).

CONCLUSIONS

Comparative phylogeography is a developing field that complements other analytical approaches to historical biogeography, including cladistic approaches aimed at reconstructing the history of place. Comparative phylogeography is not inherently based in dispersal narratives. In fact, one of the major strengths of this approach is that it often reveals previously cryptic vicariance in the historical assembly of biotas (Riddle *et al.*, 2000). In addition, because the phylogenies used in comparative phylogeography are typically based on molecular data, it is possible to test hypotheses within likelihood frameworks and to estimate important biogeographic and population parameters. These include the timing of population separations and speciation events, and the estimation of changes in effective population size over time. All of this information can be evaluated within the context of data that are obtained independently from the geological, climatological, palaeontological and palynological records. Rather than viewing comparative phylogeography as a chimera of scenario building, we see it as a quantitative and integrative approach that allows biogeographers to draw upon diverse sources of information when developing and testing hypotheses that seek to explain the complex relationship between earth history and contemporary patterns of biodiversity.

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