7 Phylogeography in Historical Biogeography: Investigating the Biogeographic Histories of Populations, Species, and Young Biotas

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ABSTRACT

Over the past two decades, phylogeography has become an increasingly popular approach to investigating the geography of genetic variation within and among populations, species, and groups of closely related species. Phylogeographic research is uniquely positioned between historical and ecological biogeography, but to date has not incorporated many of the fundamental concepts of the former and, therefore, is susceptible to criticism that it is not a legitimate method in area-based historical biogeography. Here, we review the similarities and differences between phylogeography and area-based historical biogeography; and review concerns regarding the differences. We then summarize one recent approach to reconciling differences that highlights the synergistic and reciprocal strengths of each approach at different stages in the analysis of historical structure within populations, species, and young biotas.

INTRODUCTION

In recent years, the number and variety of new approaches and methods in historical biogeography has grown steadily (summarized by Crisci et al., 2003; see also table 12.2 in Lomolino et al., 2006), but not without debate over the utility and validity of many of them (e.g., Brooks et al., 2001, 2004; Ebach, 2001; Van Veller & Brooks, 2001; Ebach & Humphries, 2002, 2003; Siddall & Perkins, 2003; Van Veller et al., 2003; Siddall, 2005). Much of this recent diversification of historical biogeography can be attributed to a desire to explore aspects of biotic histories that were not considered tractable under the original form of *vicariance* (or *cladistic*) *biogeography*

that emerged in the 1970s (e.g., Nelson, 1974; Crisci et al., 2003). Heated discussions have focused on the range of processes that historical biogeographers should be investigating: e.g., restricted to associations between Earth and biotic histories (Humphries & Ebach, 2004) vs. a full range of vicariance and dispersal histories that underlay the geography of diversification (Brooks, 2004). Additionally, historical biogeography has been challenged on two fronts: first, for not being able to accomplish fundamental tasks such as deciphering the complexity (*pseudo-congruence*) often embedded within a single postulated vicariance event (Donoghue & Moore, 2003), and second, for not yet reaching its potential to contribute to more fundamental questions in ecology and evolution (Wiens & Donoghue, 2004).

One topic of recent debate concerns the role within historical biogeography of *phylogeography,* the extraordinarily popular approach (Figure 7.1a) that began in the late 1980s (Avise et al., 1987). Avise (2000) defined phylogeography as "a field of study concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially those within and among closely related species." The status of phylogeography as a legitimate method in biogeography has been challenged (e.g., Humphries, 2000; Ebach & Humphries, 2002) and, in response, defended (Arbogast & Kenagy, 2001; Riddle & Hafner, 2004). Here, we attempt to clarify unique attributes that have arisen within a phylogeographic paradigm that we believe provide not only a legitimate but an increasingly important component to integrative approaches that provide investigators with the power to address the rich array of patterns and processes involved in the biogeographic histories of populations, species, and young biotas.

PHYLOGEOGRAPHY VS. HISTORICAL BIOGEOGRAPHY

While phylogeographic and historical biogeographic studies overlap in their connections to a variety of macroevolutionary topics (Figure 7.1b), they differ in a number of ways, the most obvious being that phylogeographic studies do not generally extend beyond a Neogene timeframe and typically target a Pleistocene timeframe (Figure 7.1c). As such, phylogeographic approaches have provided a basis for expanding basic questions in historical biogeography into the realms of Quaternary paleoecology and macroecology. Within this timeframe, processes bearing on diversification and distributional dynamics within and among species prominently feature paleoclimate of the Pleistocene (Hewitt, 2004). However, phylogeographic studies often reveal levels of divergence consistent with Pliocene or Miocene timeframes, which require a consideration of the very profound effects of Neogene geotectonics on current landscapes (e.g., Riddle et al., 2000; Mateos, 2005).

Phylogeography gained much of its current popularity by providing a linkage, via molecular population genetic and phylogenetic analyses, between those disciplines concentrating on population and species responses to relatively recent evolutionary processes or paleoclimatic events in Earth history with those that have traditionally been more concerned with the association between biological diversification and geological events in Earth history. This "microevolution/macroevolution"

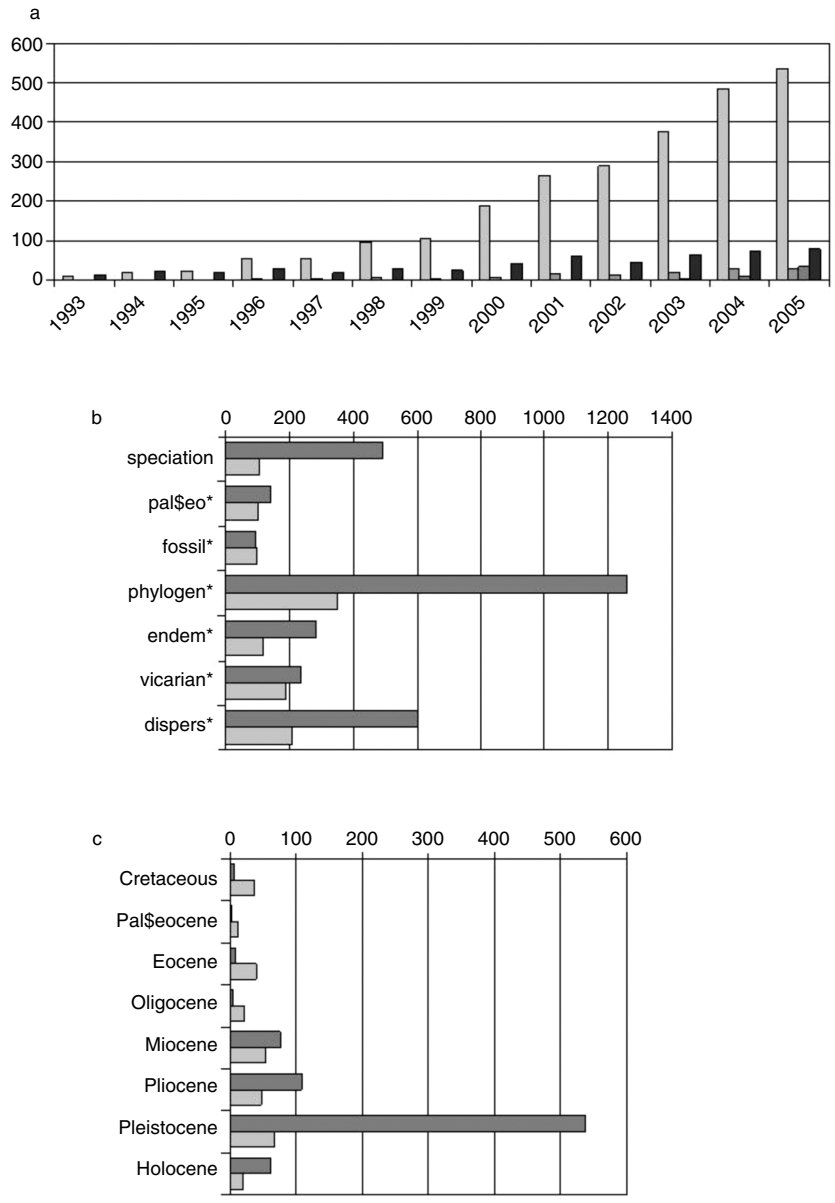

FIGURE 7.1 Several comparisons between phylogeography and historical biogeography based on title, abstract, and keyword searches on the ISI Web of Science, 1993–2005. (a) Total number of hits using, from left to right in each year, "phylogeograph*", "comparative phylogeograph*", "statistical phylogeograph*", or "historical biogeograph* not phylogeograph*. In graphs (b–e), searches were performed using either "phylogeograph* and [the term on the graph]" (dark grey bars) or "historical biogeograph* not phylogeograph* and [the term on the graph]" (light grey bars). (See text for discussion).

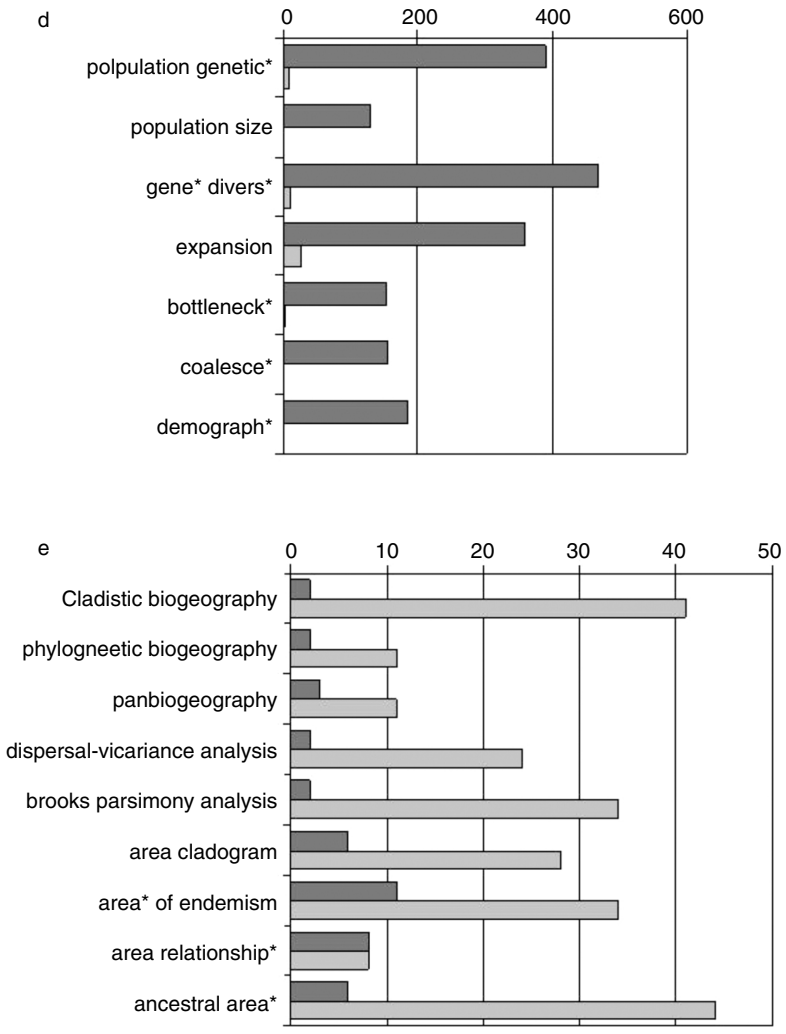

FIGURE 7.1 (Continued)

character should position phylogeographic-based research in a prominent role as historical biogeographers increasingly incorporate questions traditionally of great interest in ecology and evolutionary biology (e.g., Brooks, 2004; Wiens & Donoghue, 2004; Riddle, 2005). Several features, however, suggest a strong disconnect between phylogeography and much of the rest of historical biogeography. First, although phylogeography, since its inception, has been considered as a bridge between traditionally separate macroevolutionary and microevolutionary (Figure 7.1d) regimes (Avise, 2000), phylogeographic studies increasingly explore dispersal and population connectivity within ongoing or very recent ecological arenas (see any recent issue of the journal *Molecular Ecology* for examples). Within these studies, historical

biogeographic explanations are included as but one alternative or one level in a spatio-temporal hierarchy of explanations. Increasing sophistication of coalescent-based analytical methods and capabilities to sample different (particularly rapidly evolving) partitions of an organism's genome (e.g., mitochondrial vs. nuclear) has driven much of phylogeography in the direction of population genetic analyses of very recent events in the history of a population or species and has led to the introduction of the concept of *statistical phylogeography* (Knowles, 2004; Templeton, 2004). For example, the goal of nested clade phylogeographic analysis (Templeton, 2004) is to differentiate between the influences of population structure (processes that determine gene flow among extant populations) and population history (vicariance, long-distance dispersal, etc.) in determining current patterns of genetic diversity across the geographic range of a species.

A second indication of a disconnect between phylogeography and historical biogeography is the near lack in phylogeography of reference to an array of terms, concepts, and methods that are central to the rest of historical biogeography (Figure 7.1e). Despite the explosive popularity of phylogeographically based studies, very few incorporate the concept of an *area of endemism,* which is the fundamental unit of analysis in much of the rest of historical biogeography. A search on ISI Web of Science, 1993–2005, revealed a total of 2,495 studies with "phylogeograph*" in title, abstract, or keywords, yet a search for "phylogeograph* and area* of endemism" (Figure 7.1e) revealed only 11 papers, three of which referred to a single study. Likewise, "phylogeograph* and area cladogram" produced only six hits. Clearly, phylogeographic studies rarely are designed to incorporate the conceptual framework that predominated in historical biogeography over the past three decades. For this reason alone, it should not be surprising that researchers operating within a more traditional cladistic biogeographic framework have expressed a concern about the legitimacy of phylogeography within historical biogeography (Humphries, 2000; Ebach & Humphries, 2003; Humphries & Ebach, 2004).

Cladistic biogeographers have correctly criticized phylogeography for its failure to incorporate the most important constructs of late twentieth-century historical biogeography, including the frequent reliance in phylogeographic studies on single-taxon approaches to differentiate between dispersal and vicariance histories. Nevertheless, we believe that the criticism that phylogeography is weighted toward the production of ad hoc dispersal scenarios (and thus resurrects a failed paradigm in biogeography) has discounted two areas of growth in phylogeography: statistically rigorous population genetic methods for assessing population geographic structure and history, and the emerging popularity of comparative phylogeographic approaches.

Many of the methods incorporated into statistical phylogeography (Knowles, 2004; Templeton, 2004) are normally used to address hypotheses about the geographic structure and history of populations. These include post-Pleistocene range expansion of a single species out of one or more glacial-age refugia (Hewitt, 2004), the prevailing direction of gene flow via dispersal between two or more geographically separated populations within a single species (Zheng et al., 2003), and the relative contributions of historical and extant population processes in structuring geographical population genetic architecture (Templeton et al., 1995). These

approaches incorporate a rich theory based on population genetic principles (migration, drift, selection, effective population sizes) to differentiate, for example, between either long-term occupancy of a current and widespread geographic distribution, or recent range expansion from a previously smaller distribution. As such, they rely on a very different set of acceptance or rejection criteria to test historical hypotheses. In contrast, area-based methods in biogeography usually rely on examination of phylogenetic relationships across an *a priori* chosen set of areas of endemism, and many further arenas using discordance with a general area cladogram to suggest that the biogeographic history of taxa across a set of areas of endemism is at odds with an underlying vicariant history.

However, as the timeframe for development of biotic patterns across a landscape or seascape deepens, the likelihood that molecular genetic architecture within geographically isolated populations or closely related species sorts into discrete *reciprocally monophyletic* clades increases as well. Indeed, many phylogeographic studies are informative about events in biotic and Earth history several million years prior to the Pleistocene (Figure 7.1c), and often serve to refine the boundary between intraspecific and interspecific diversity through discovery of cryptic species or biogeographic events (ISI Web of Science search, 1993-–2005, using "phylogeograph* and cryptic" revealed 148 studies). Of course, the pace of transformation of an ancestral *phylogroup* into two or more reciprocally monophyletic phylogroups is strongly associated with population genetic parameters that influence the rate of sorting of ancestral polymorphism and fixation of new mutations. This prevents the establishment of a universal metric across organisms for the timeframe within which we expect to discover reciprocally monophyletic phylogroups. Even so, one can identify the threads of an empirical, conceptual, and analytical bridge between phylogeography and the rest of historical biogeography at the nexus between population genetic and phylogenetic patterns of divergence among geographically structured populations.

FROM SINGLE-TAXON TO COMPARATIVE PHYLOGEOGRAPHY

Much as historical biogeographers did several decades ago, practitioners of phylogeography have increasingly recognized the need to examine congruence across multiple, co-distributed taxa to differentiate general events (e.g., vicariance or geodispersal; Lieberman, 2004) from taxon-specific events (e.g., long-distance dispersal and speciation of peripheral isolates; Bermingham & Moritz, 1998; Arbogast & Kenagy, 2001; Riddle & Hafner, 2004). *Comparative phylogeography* is defined, in part, as "the geographical comparison of evolutionary subdivision across multiple co-distributed species or species complexes" (Arbogast & Kenagy, 2001). The implication of phylogenetic subdivision produces conceptual affinities with area-based historical biogeography and, indeed, comparative phylogeographic studies often address vicariance vs. dispersal issues in a straightforward phylogenetic fashion. However, these studies also investigate population histories from a statistical phylogeographic approach when gene lineages in isolated populations have not yet

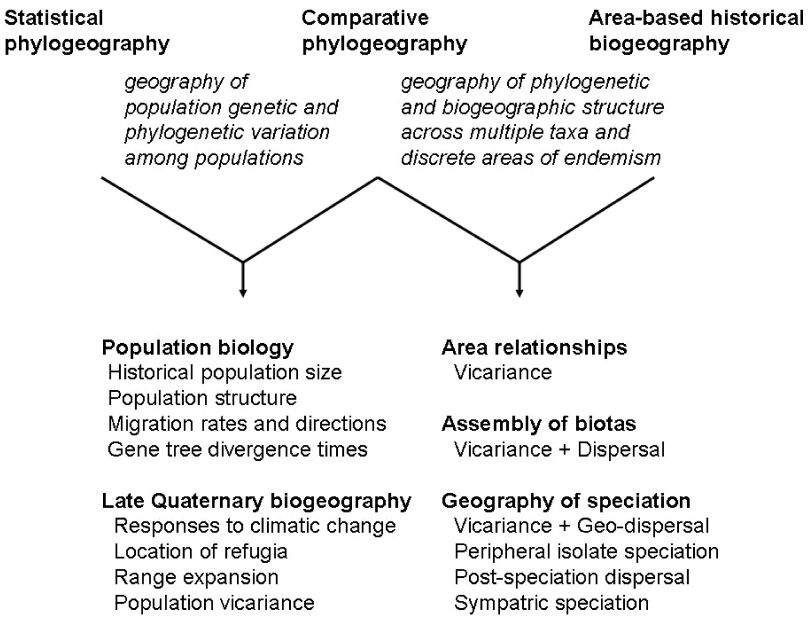

FIGURE 7.2 A depiction of objectives and questions most appropriately addressed within the conceptually and analytically different arenas of statistical phylogeography, and area-based historical biogeography (see text for discussion), and illustrating the "bridging" position of comparative phylogeography.

sorted to a state of reciprocal monophyly (e.g., Rocha et al., 2002; Wares, 2002; Bremer et al., 2005; Lourie et al., 2005). Given the ability of comparative phylogeography to incorporate methods and approaches from both statistical phylogeography and area-based historical biogeography, it promises to form the basis for developing more robust linkages between these approaches (Figure 7.2) than currently exist.

As with area-based historical biogeography, comparative phylogeography offers a predictive framework in which an initial pattern of congruence across co-distributed taxa can be continually updated through addition of new co-distributed taxa and re-evaluation of patterns and explanations. An excellent example involves the postulated existence of a Pleistocene seaway across the Baja California Peninsula of Mexico. Flooding of the midpeninsula has been hypothesized since 1921, but was first invoked to explain genetic discontinuities among peninsular species by Upton & Murphy (1997). Studying the side-blotched lizard (*Uta*), Upton & Murphy (1997) marshalled supportive evidence from the distribution and genetics of marine organisms in adjacent oceanic and gulf waters. They hypothesized a date of about 1 million years for the existence of this seaway separating the Peninsular North and Peninsular South areas (Figure 7.3). A comparative phylogeographic analysis of co-distributed mammalian, reptilian, and amphibian taxa provided evidence for a congruent break between southern and northern populations (Riddle et al., 2000) in the vicinity of

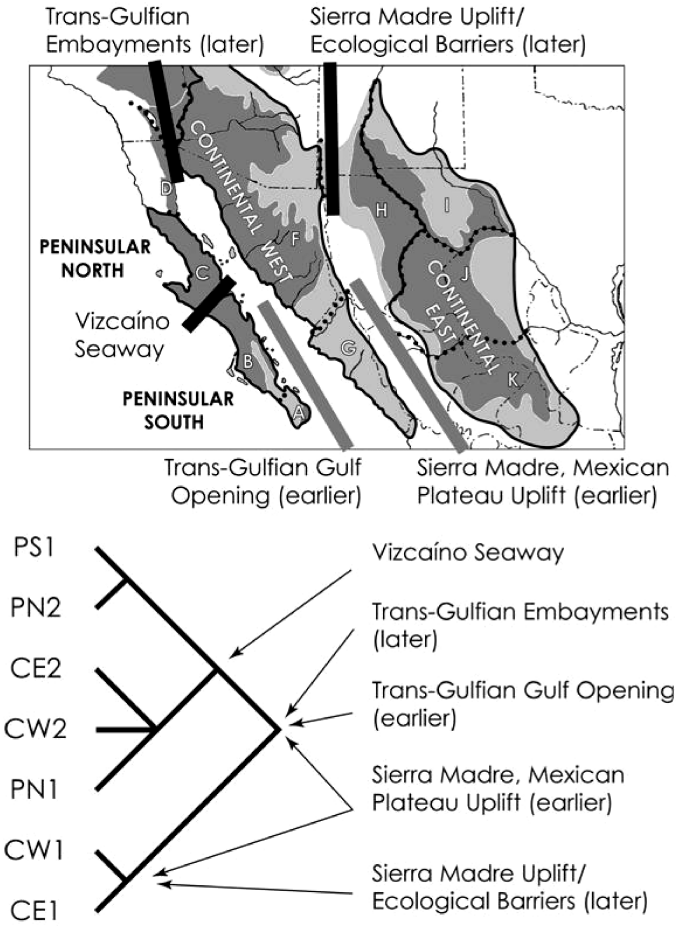

FIGURE 7.3 Summary diagram from a recent study using a step-wise approach to integrate phylogeographic and historical biogeographic analyses into a comprehensive analysis of biotic history in the warm deserts of western North America (summarized in text). The map shows areas of distribution (A–K), areas of endemism (Peninsular South, Peninsular North, Continental West, Continental East), and several postulated Neogene vicariant events. The area cladogram is a secondary BPA tree summarizing postulated historical events across these areas of endemism. (See Riddle & Hafner 2006a, b for details).

the postulated "Vizcaíno Seaway," which was consistent with evidence available at that time from additional reptilian (Upton & Murphy, 1997; Rodriguez-Robles & De Jesus-Escobar, 2000) and avian (Zink et al., 2001) taxa. Subsequently, various studies have confirmed the geographic generality of this southern vs. northern split in a wide variety of taxa, including more reptiles (Murphy & Aquirre-Leon, 2002; Lindell et al., 2005), spiders (Crews & Hedin, 2005), and marine fish (Bernardi et al., 2003; Riginos, 2005). Grismer (2002) has challenged invocation of a Pleistocene transpeninsular seaway, citing a lack of geological evidence (reviewed

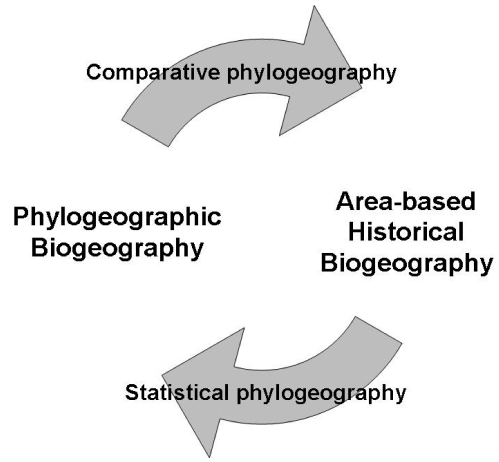

FIGURE 7.4 Illustration of one depiction of the synergistic and reciprocal nature of phylogeographic biogeographic and area-based historical biogeographic perspectives and approaches, in which comparative and statistical phylogeography provide the hypothesis generating and hypothesis testing bridges, respectively, between the two approaches.

in Jacobs *et al.* 2004). Grismer (2002) further maintains that abrupt ecological changes in the midpeninsula are sufficient to explain genetic differentiation of terrestrial species. New evidence for marine fish (Riginos, 2005) provides particularly compelling support for a former seaway. Whereas an incomplete seaway, perhaps plugged with an active volcanic field or an abrupt ecological shift, would have limited dispersal of terrestrial forms up and down the peninsula, this would not account for disjunct marine distributions (Hafner & Riddle, 2005). The specific timeframe in which such a seaway might have existed (e.g., Lindell et al., 2005; Riginos, 2005) and alternative explanations for north/south divergence across taxa (Grismer 2002; Crews & Hedin, 2006) are being actively explored. Nevertheless, this case study illustrates the value of a comparative phylogeographic approach in providing an appropriate framework for developing, recognizing, and testing hypotheses of historical divergence in a co-distributed biota. One weakness of the framework for addressing the generality of this pattern at this stage would be recognized clearly by area-based historical biogeographers: it reduces to only a two-area statement of area-relationships, which is meaningless within a cladistic biogeography framework that requires a minimum of three areas for postulating historical relationships — although panbiogeographers would consider it an acceptable general track.

In summary, we believe that a reconciliation of the concern over the validity of phylogeography within historical biogeography must recognize that questions explored under a phylogeographic rubric overlap strongly with those that form the core of the more time-honored, area-based historical biogeography, but also extend beyond the traditional envelope of that discipline. Yes, much of phylogeography is designed explicitly to investigate single-taxon dispersal hypotheses and utilizes

sampling designs and statistical approaches appropriate for addressing questions such as population range expansion, locations of Late Quaternary refugia, and prevailing directions of migration between genetically divergent populations. However, within the multi-faceted phylogenetic and population genetic framework of phylogeography, the development and increasing application of comparative phylogeographic approaches provides a conceptual and empirical bridge between the statistical phylogeography that has arisen from a population genetic arena, and a more distinctly phylogenetic, area-based historical biogeography (Figure 7.2). Explicit attention to building such a synthetic perspective has only recently begun to enter the biogeographic literature.

TOWARD AN INTEGRATION OF PHYLOGEOGRAPHY AND HISTORICAL BIOGEOGRAPHY

Few studies have analyzed phylogeographic data within a cladistic biogeographic framework. Taberlet *et al.* (1998) used an earlier version of Brooks parsimony analysis (primary BPA) to postulate glacial-age refugia and routes of post-glacial colonization among 10 co-distributed taxa in Europe. Bermingham & Martin (1998) used COMPONENT 2.0 to address area-congruence across three genera of Neotropical fish. Hall & Harvey (2002) used a matrix representation with parsimony approach to generate a general area cladogram. The latter study combined a phylogeographic-scale cladogram from a neotropical butterfly genus with area cladograms derived from a wide range of published area cladograms of vertebrate taxa, most of which were not generated from phylogeographic data.

As has been recognized previously (Morrone & Crisci, 1995; Andersson, 1996; Crisci et al., 2003), questions that need to be addressed in a historical biogeographic analysis can be arranged sequentially, beginning with careful attention to the biotic and landscape scope of a study. We have suggested (Riddle & Hafner, 2006a, b) that phylogeographic and historical biogeographic analyses can be employed interactively across a series of sequential steps in an analysis of a biota in which divergence and distributional patterns likely occurred during the Neogene. This protocol and rationale, summarized briefly below, are discussed fully and illustrated by Riddle & Hafner (2006a and Figure 3 therein).

A wide range of studies over the past 25 years collectively have now provided convincing evidence that the appropriate units of analysis in a Neogene timeframe will, in most cases, be derived through phylogeographic-scale data and a phylogeographic sampling design. Phylogeographic-scale data include sequencing or otherwise diagnostic character state variation within rapidly evolving and rapidly sorting DNA partitions. Phylogeographic sampling involves multiple individuals from multiple sites distributed across the geographic range of a taxon. This sampling strategy is necessary to characterize accurately the geographic distribution of what are often morphologically cryptic phylogenetic lineages (i.e., phylogroups or evolutionarily significant units) within and among geographic distributional areas, and to provide an adequate

database for statistical phylogeographic hypothesis testing. In our case study (Riddle & Hafner, 2006a, b), we initially identified 16 distributional areas (10 of which are shown as areas A through K in Figure 7.3) for taxa in 22 clades of mammals, birds, reptiles, amphibians, and plants with decidedly "warm desert" ecological affinities, distributed primarily across the major warm deserts of southwestern North America (Figure 7.3).

Distributional areas are not, by themselves, robustly recognizable as areas of endemism. Additional analysis of the degree of distributional overlap among taxa, as well as recognition of barriers and filter-barriers among areas and phylogenetic and distributional congruence among taxa, are also required (Lomolino et al., 2006). We employed an iterative parsimony analysis of endemicity (PAE) procedure to assess distributional congruence of phylogroups from the 22 cladograms across distributional areas. Based on the scale of resolution available in the phylogeographic data, this resulted in a set of four core warm desert areas of endemism (Figure 7.3).

Once areas of endemism were identified, we selected primary and secondary Brooks parsimony analysis (BPA; Brooks et al., 2001) as an appropriate method for analyzing area relationships across the four core areas. Our experience with the North American warm-desert biota led us to suspect a high level of idiosyncratic responses of taxa to postulated vicariant events and variable rates of historical dispersal across areas, which together are likely to result in high levels of reticulation across areas. Primary and secondary BPA were designed to disentangle reticulation across areas by resolving area cladograms into a set of area relationships derived through postulated vicariance, sympatric speciation, post-speciation dispersal, speciation of peripheral isolates, and extinction events. Our secondary BPA tree (Figure 7.3) is consistent with the Neogene geological history of southwestern North America and provides a realistic depiction of the temporal continuum inherent in the tectonically driven transformation of a landscape (Riddle and Hafner, 2006a, b). Moreover, it provides an objective depiction of major sources of reticulation in the area-relationships depicted on the primary BPA cladogram: the equivalent role of the Continental West area in diversification and dispersal to the west (peninsular areas) and east (Continental East area); and a similarly central role for the Peninsular North area between Peninsular South and Continental West. Recently, Wojcicki & Brooks (2004, 2005) have introduced a new algorithm (PACT = phylogenetic analysis for comparing trees) that builds upon BPA and purportedly "embodies all of the strong points and none of the weaknesses of previously proposed methods of historical biogeography." We eagerly await the availability of this algorithm in a computer program package so that its efficacy can be evaluated against other available approaches. We believe that perhaps the most powerful feature of our five-step approach (Riddle & Hafner 2006a, b) is the heuristic nature of the resulting area cladogram, which provides a number of interesting hypotheses that can then be addressed by turning to a statistical phylogeographic arena. For example, events that might otherwise be interpreted by historical biogeographers based on cladogenetic structure alone as "sympatric speciation" actually comprise two alternative hypotheses: sympatric speciation or embedded allopatric speciation, possibly with subsequent range expansion of one

or both sister taxa. These alternatives can be addressed through a variety of available statistical phylogeographic analyses.

One pattern of great interest in our study involves the population history of taxa on the Baja California Peninsula. While nine phylogroups are currently endemic to the Peninsular South area, another nine occur across both of the peninsular areas. Thus, because of the high level of endemicity in the southern area and a postulated vicariant event that putatively is associated, at least in part, with this pattern (Figure 7.3), we consider either post-barrier range expansion (primarily from south to north) or ancestrally widespread distributions as two alternative hypotheses to explain the currently widespread distribution of the nine taxa across southern and northern areas. Again, these hypotheses are highly tractable by using statistical phylogeographic analyses to assess the likelihood of each alternative. In fact, previous phylogeographic studies of two of these taxa have provided evidence in favor of recent northward range expansion from the Peninsular South area (Zink et al., 2000; Nason et al., 2002). While those studies were conducted within a typical single-taxon phylogeographic framework, the synthetic approach we have presented here illustrates the predictive power of working interactively between phylogeography and area-based historical biogeography. By recognizing the strong signal of endemism and separating the histories of the southern and northern peninsular areas, we have constructed an objective framework for entertaining the hypothesis that post-barrier range expansion has not only been a general feature in the Neogene history of this biota, but is primarily asymmetrical in direction.

FUTURE DIRECTIONS

We foresee a rapid strengthening of the developing bridge between statistical phylogeography and area-based historical biogeography. The explosive growth of single-taxon phylogeographic studies should inevitably lead to additional comparative phylogeographic studies of regions such as our analyses of North American warm deserts (Riddle & Hafner 2006a, b). These, in turn, will allow comparative studies among diverse regions that address questions of deeper temporal scale and broader geographic scale (e.g., Lessa et al., 2003). We anticipate emergence of new tools to optimize the synergism and reciprocal strengths (Figure 7.3) between, on the one hand, population-genetic approaches that examine detailed dynamics of individual taxa in local environments and, on the other hand, area-based historical biogeographic approaches that seek to summarize regional biotic histories.

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