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A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota

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Abstract

In this paper, we develop a five-step approach for analysis of historical relationships among areas of endemism using a set of 22 clades (9 mammal, 7 bird, 4 reptile, 1 amphibian, and 1 cactus) drawn from the warm deserts biota of western North America. As has been suggested in previous studies of portions of this biota, our results suggest a complex biogeographic history, but with substantial support for the influence of several major vicariant events in the diversification and assembly of the aridlands biota. We discuss and demonstrate the reciprocal strengths (and weaknesses) of phylogeography and phylogenetic biogeography for defining areas of endemism, analysing vicariance and dispersal, and dealing with temporal and spatial pseudo-congruence.

Keywords: Historical biogeography; Phylogenetic biogeography; Phylogeography; Vicariance; Dispersal; Brooks parsimony analysis; Parsimony analysis of endemicity; North American deserts

1. Introduction

The goals of historical biogeography are diverse (Crisci et al., 2003). For example *phylogenetic biogeography* (in the sense of Van Veller et al., 2002; not in the sense of Hennig, 1966) seeks to deduce both dispersal and vicariance from an area cladogram, whereas *cladistic biogeography* (Ebach and Humphries, 2002) rejects consideration of

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dispersal explanations. *Phylogeography*, an increasingly popular subdiscipline of biogeography, seeks to understand the geographic distribution of gene lineages embedded within species and among closely related species (Avise, 2000). While much of single-taxon phylogeography has been criticized for its historical narrative and "dispersalist" flavor (e.g. Humphries, 2000; Ebach and Humphries, 2002), proponents of *comparative phylogeography*—"the comparison of geographical patterns of evolutionary subdivision across multiple co-distributed species or species complexes" (Arbogast and Kenagy, 2001)—claim this to be a valid method to sort between vicariant and dispersal histories. Riddle and Hafner (2004) conclude that while phylogeography has been highly successful in achieving the goal of framing microevolutionary questions within a geographic frameworks (e.g. Althoff and Pellmyr, 2002; Knowles and Maddison, 2002), it has to date been less successful in bringing the goals and constructs of historical biogeography into a spatially smaller (e.g. intra-continental) and temporally more recent (e.g. Pleistocene) realm.

Phylogenetic biogeography and comparative phylogeography share several features. For example, phylogenetic biogeography relies on the use of phylogenetic information to construct and analyse area cladograms, which can also be accomplished within a comparative phylogeography framework. Both approaches emphasize the geography of diversification (species or gene lineages), and acknowledge explicitly that real world biotas are complex, with both vicariant and dispersal events likely to have contributed significantly to the historical assembly of biotas. Both disciplines recognize that multiple co-distributed taxa must be analysed in order to sort general from lineage-specific geographic structure (e.g. the "Threes Rule" rule, Brooks and McLennan, 2002). Furthermore, these approaches offer a complementary set of strengths. For example, the high quality of data derived through phylogeographic sampling strategies (i.e. geographically dense and large sample sizes, molecular genetic-based phylogenies) can potentially resolve a single taxonomic species into two or more geographically distinct "cryptic" evolutionary lineages (phylogroups). Recognition of phylogroups can add sensitivity to the mapping of lineages across a set of areas of endemism (if the original was widespread across multiple areas), or within a single area of endemism (which might lead to recognition of multiple embedded areas). Additionally, phylogeographic studies have frequently indicated that the original taxon is paraphyletic or polyphyletic, rendering a previously biogeographically uninformative taxon into one or more clades that are amenable to historical biogeographic analysis. Phylogenetic biogeography—as implemented most recently through primary and secondary Brooks Parsimony Analysis (BPA; Brooks et al., 2001)—provides a hypothesis of general divergence and distributional histories resulting either from vicariance or geo-dispersal (the latter describing the erosion of a barrier, synchronous dispersal of more than one species, re-emergence of a barrier in the same location, and subsequent differentiation of co-distributed taxa in allopatry; Lieberman, 2004), as well as hypotheses of exceptions to the general biotic history (post-speciation dispersal, peripheral isolates speciation, and extinction).

To date, events postulated on the basis of phylogenetic biogeography to result from vicariance, geo-dispersal or some other form of dispersal (e.g. based on a secondary BPA tree) seldom have been evaluated further. Yet, for example, a single postulated vicariant event may have subsumed multiple independent events, a phenomenon termed pseudo-congruence—the false presumption of a single vicariance event when in fact temporally or spatially different events result in a topologically identical pattern of area relationships.

Additionally, a presumed sympatric speciation event might alternatively have resulted from allopatric divergence embedded within a single area of endemism; and tree structure alone may not allow resolution of alternative explanations for taxa that are widespread across two or more areas (e.g. through dispersal from an ancestral area, or from failure of an ancestrally widespread taxon to respond to a vicariant event). However, if one is employing comparative phylogeographic data within the BPA analysis, several sorts of hypotheses should be testable through a return to phylogeographically based analytical procedures (Althoff and Pellmyr, 2002; Knowles and Maddison, 2002; Zink, 2002). For example, alternative explanations for the occurrence of widespread taxa (ancestrally widespread, post-speciation dispersal of individual taxa, or geo-dispersal of biotas) could be approached using predictions derived from a phylogeographic gene genealogy perspective. Spatial pseudo-congruence might be evaluated through a more detailed examination of phylogeographic structure: Is geographic structure within a phylogroup consistent with the contention that a specified barrier was in fact the initiating event leading to isolation and divergence of an ancestrally widespread phylogroup? Temporal pseudo-congruence could be evaluated through critical examination of comparative levels of molecular divergence across co-distributed taxa: Have the taxa diverged within a single time slice across the postulated vicariant feature?

1.1. Delineating a core North American warm deserts biota

1.1.1. Historical development of regional deserts

In his seminal study of the desert vegetation of North America, Shreve (1942) emphasized life-forms and dominant species of arid-adapted plants that indicated relative uniformity within the arid regions, recognizing one cold (Great Basin) and three warm (Chihuahuan, Mojave, Sonoran) deserts (Fig. 1). Although Shreve (1942, p. 211) specifically stated that these deserts are "…like any other great natural region in being without sharp boundaries…" and noted (p. 215) that "it is not yet possible to state…to what extent the differences [among regions] have been influenced by historical factors," he indicated specific borders to homogeneous regions, and included only community succession as a historical process. Over time, and counter to his original intent, the specific boundaries of these supposedly homogeneous areas became accepted dogma.

Axelrod (1979, 1983) stressed the antiquity of some taxa that have been incorporated into what are actually extremely recently formed regional deserts. His model of desert formation imagined desert floras developing in local dry sites during the Tertiary drying trend, drawing arid-adapted species from boreal shrub-steppes, Great Plains grasslands, Mexican highlands, Sinaloan thornscrub, and California chaparral. An exact demarcation between desert and non-desert taxa or regions is not always possible even now. For example, there exists a high degree of distributional overlap between regional deserts and adjacent grassland, chaparral, and thornscrub communities, and even the species included below in a "phylogeographically resolved core subset" of the warm deserts track often extend to various degrees into surrounding cold desert steppes, grasslands, and chaparral.

Semi-deserts attained their maximum area during the early Pliocene and were reduced in area during the moist Late Pliocene and during Pleistocene pluvial intervals. Full regional deserts formed during interglacials, and reached their maximum extent following the Wisconsinan glacial during the warm interval variously referred to as the altithermal, xerothermic, hypsithermal, or climatic optimum. Thus, sister taxa in alternate regional

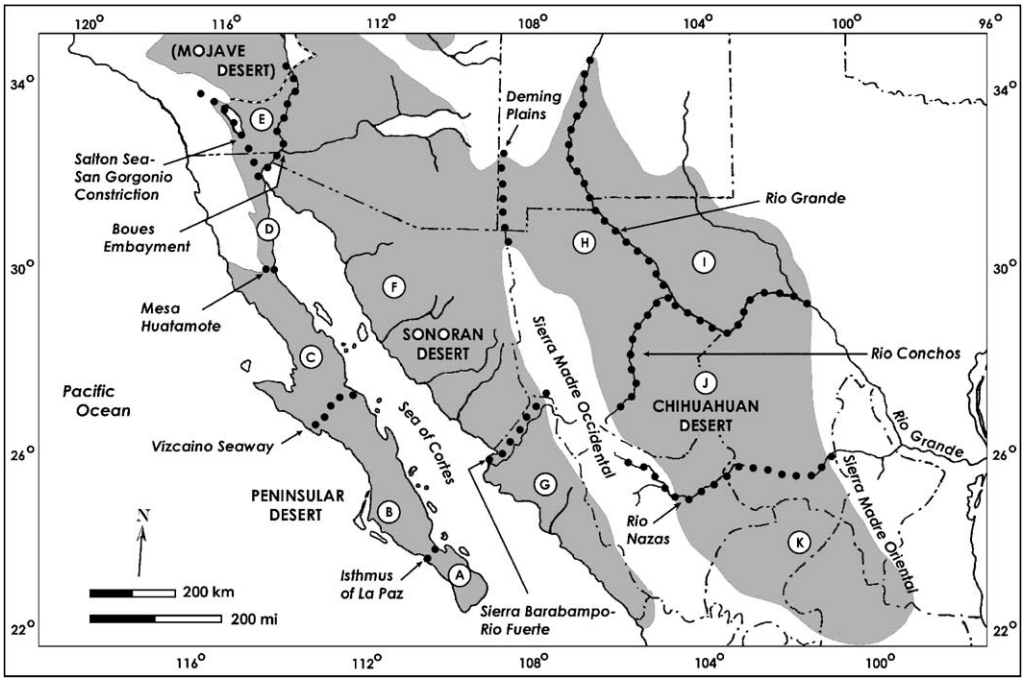

Fig. 1. Shaded areas are regional warm deserts, generally as delineated by Shreve (1942), but with recently suggested updates (the Peninsular Desert separate from the Sonoran [Hafner and Riddle, 1997]; addition of Sinaloan thornscrub unit, G [Hafner and Riddle, 2005]). Letters A–K designate distributional areas separated by either supported or postulated historical distributional barriers.

deserts might share common ancestry at one of at least two broadly construed ages, each defined by a qualitatively different set of potential isolating processes: late Miocene to Pliocene age along with tectonic events that underlay the early development of regional deserts (e.g. mountain and plateau uplifting, rifting along major fault systems); or Pleistocene age in association with climatic oscillations, having been isolated in separate desert refugia during pluvial periods. Widespread phylogroups occupying two or more regional deserts may have come to occupy a currently widespread distribution through post-Pleistocene range expansion from a latest pluvial desert refugium—a scenario that has been repeatedly invoked (e.g. Orr, 1960; Savage, 1960; Findley, 1969; Hubbard, 1973; Tanner and Banta, 1977; Schmidly et al., 1993).

1.1.2. Models of biotic history in the North American deserts

Hubbard (1973) developed a late Pleistocene vicariance model for the evolution of an aridlands bird fauna by imagining a widespread and continuously distributed southwestern aridlands biota during interglacials, followed by fragmentation into two or three isolated refugial populations, which subsequently became differentiated from one another during glacial periods. Findley (1969) and Morafka (1977) invoked Pleistocene isolation and divergence between the Chihuahuan and Sonoran deserts for mammalian and herpetological taxa, respectively.

Murphy (1983), Grismer (1994), Upton and Murphy (1997), and Murphy and Aguirre-Léon (2002) expanded the temporal scope of biogeographic history in the westernmost deserts to include postulated vicariance events during the latest Miocene and Pliocene in the assembly of the Baja California Peninsula herpetofauna. Specific events discussed by one or more of these authors included: late Miocene or early Pliocene opening of the Sea of Cortez (= Gulf of California) due to rifting and volcanic activity along the North American and Pacific plate boundary; Pliocene inundation of the Isthmus of La Paz between the Cape Region and remainder of the peninsula; Pliocene or early Pleistocene northward transgression of marine waters at the head of the Gulf into lowland deserts north to Lake Mojave (Bouse Embayment) and northwest to the San Gorgonio Constriction; and mid-Pleistocene creation of the Vizcaíno Seaway across a central portion of the peninsula. Morafka (1977) and Riddle (1995) considered evidence for vicariance events ranging from the Late Neogene to Late Pleistocene separating herpetofauna and rodents (respectively) of the western (Sonoran, Sinaloan, and Mojavean) and eastern (Chihuahuan) continental deserts across the Sierra Madre Occidental, with isolation events initially associated with geomorphological uplifting of the Sierra Madre Occidental and Mexican Plateau (Ortega-Gutiérrez and Guerrero-Garcia, 1982) and later with Pleistocene and Holocene climatic shifts closing and reopening contact between western and eastern deserts across the Deming Plains in southwestern New Mexico.

A growing number of phylogeographic studies of warm desert vertebrate taxa have demonstrated replicated patterns and depths of phylogroup disjunction that appear to be consistent with postulated Miocene to early Pleistocene vicariant events, rather than with the latest Pleistocene models previously considered (e.g. Findley, 1969; Hubbard, 1973; Tanner and Banta, 1977; Schmidly et al., 1993). Moreover, these same studies often have revealed previously unidentified (cryptic) patterns of divergence embedded within taxa and areas. For example, multiple co-distributed reptilian (Upton and Murphy, 1997), avian (Zink et al., 2001), and mammalian (Riddle et al., 2000a) taxa exhibit a pronounced phylogeographic break in the central Baja California Peninsula, suggesting presence of a previously cryptic vicariant event such as a seaway bisecting the peninsula in the Vizcaíno region. Another replicated pattern indicates separate phylogroups occupying peninsular and continental deserts, consistent with a postulated Pliocene or early Pleistocene barrier formed by northward transgression of marine waters (the "northern Pliocene vicariant complex" of Grismer, 1994). Collectively, these two patterns support an earlier contention (Hafner and Riddle, 1997) that Shreve's (1942) emphasis on floristic uniformity within the Sonoran Desert obscured one of the more distinct regional deserts, the Peninsular Desert of Baja California (discussed more recently in Hafner and Riddle, 2005). A third highly replicated pattern indicates separate phylogroups occupying western and eastern continental deserts (western lowlands and Mexican Plateau), consistent with a Late Neogene isolation initiated through uplifting of the Sierra Madre Occidental or more recent isolation associated with Pleistocene climatic cycles.

1.2. Objectives

The spatial scale of interest in this study includes the southwestern quarter of North America (Fig. 1), and the temporal scale is from the Late Neogene through the middle to late Pleistocene. Empirical evidence strongly indicates that phylogeographic-scale units of analysis (phylogroups) are critical for elucidating geographic structure associated with the

Late Neogene through Pleistocene assembly of this biota (e.g. Riddle and Hafner, 1999), and 22 taxon cladograms that meet this criterion have been either generated in our lab or gleaned from the literature (Table 1; Fig. 2). To date, only two studies have examined three or more co-distributed clades of principally warm desert taxa within a formal historical biogeographic framework (Zink et al., 2000a; Brooks and McLennan, 2001). Our study represents an extension of, and includes data sets from, the previously analysed avian portion of this biota, but differs from those previous efforts in several ways. First, we use a more inclusive set of co-distributed phylogroups, drawn from mammalian, avian, reptilian, amphibian, and cactus groups. Second, in accord with arguments for applying step-wise procedures in a historical biogeographic analysis, and in recognition that each step might require a different analytical method (Morrone and Crisci, 1995; Andersson, 1996), we present a step-wise procedure (Fig. 3) that incorporates a sequential set of analyses, proceeding from phylogeographic to phylogenetic biogeographic and back to phylogeographic arenas. Third, rather than relying on earlier (e.g. Hubbard, 1973) references to delineate areas of endemism, we begin our analyses with a parsimony analysis of endemicity (PAE) procedure used to evaluate distributional patterns of phylogroups utilized in this study across a prior set of areas of distribution (Fig. 1). This procedure

Table 1
Summary of taxon cladograms, cladogram codings (examined in previous studies of Zink et al. (2000a) and Brooks and McLennan (2001) if followed by an asterisk), and data sources

Taxon cladogram	Cladogram code	Original references
Ammospermophilus	a	8; 24
Chaetodipus baileyi species-group	b	9
Chaetodipus penicillatus species-group	c	1; 9
Chaetodipus arenarius	d	8
Chaetodipus nelsoni species-group	e	9; 24
Dipodomys merriami species-group	f	8; 24
Peromyscus eremicus species-group	g	10
Onychomys	h	7; 11
Neotoma lepida species-group	i	5
Pipilo fuscus species-group	j*	19; 20; 23
Callipepla squamata species-group	k*	16; 19
Polioptila melanura species-group	l*	14; 15; 19; 22
Toxostoma lecontei species-group	m*	18; 19
Toxostoma curvirostre species-group	n*	17; 19; 21
Auriparus flaviceps	o	22
Campylorhynchus brunneicappilus	p	22
Kinosternon flavescens species-group	q	12
Sauromalus	r	4
Cnemidophorus tigris	s	2; 6
Uta stansburiana	t	13
Bufo punctatus	u	8; 24
Lophocereus schottii	v	3

1—Lee et al. (1996); 2—Murphy and Aguirre-Léon (2002); 3—Nason et al. (2002); 4—Petren and Case (2002); 5—Planz (1992); 6—Radtkey et al. (1997); 7—Riddle (1995); 8—Riddle et al. (2000a); 9—Riddle et al. (2000b); 10—Riddle et al. (2000c); 11—Riddle and Honeycutt (1990); 12—Serb et al. (2001); 13—Upton and Murphy (1997); 14—Zink et al. (2000a); 15—Zink and Blackwell (1998a); 16—Zink and Blackwell (1998b); 17—Zink and Blackwell-Rago (2000); 18—Zink et al. (1997); 19—Zink et al. (2001); 20—Zink and Dittman (1991); 21—Zink et al. (1999); 22—Zink et al. (2000b); 23—Zink et al. (1998); 24—Jaeger et al. (2005).

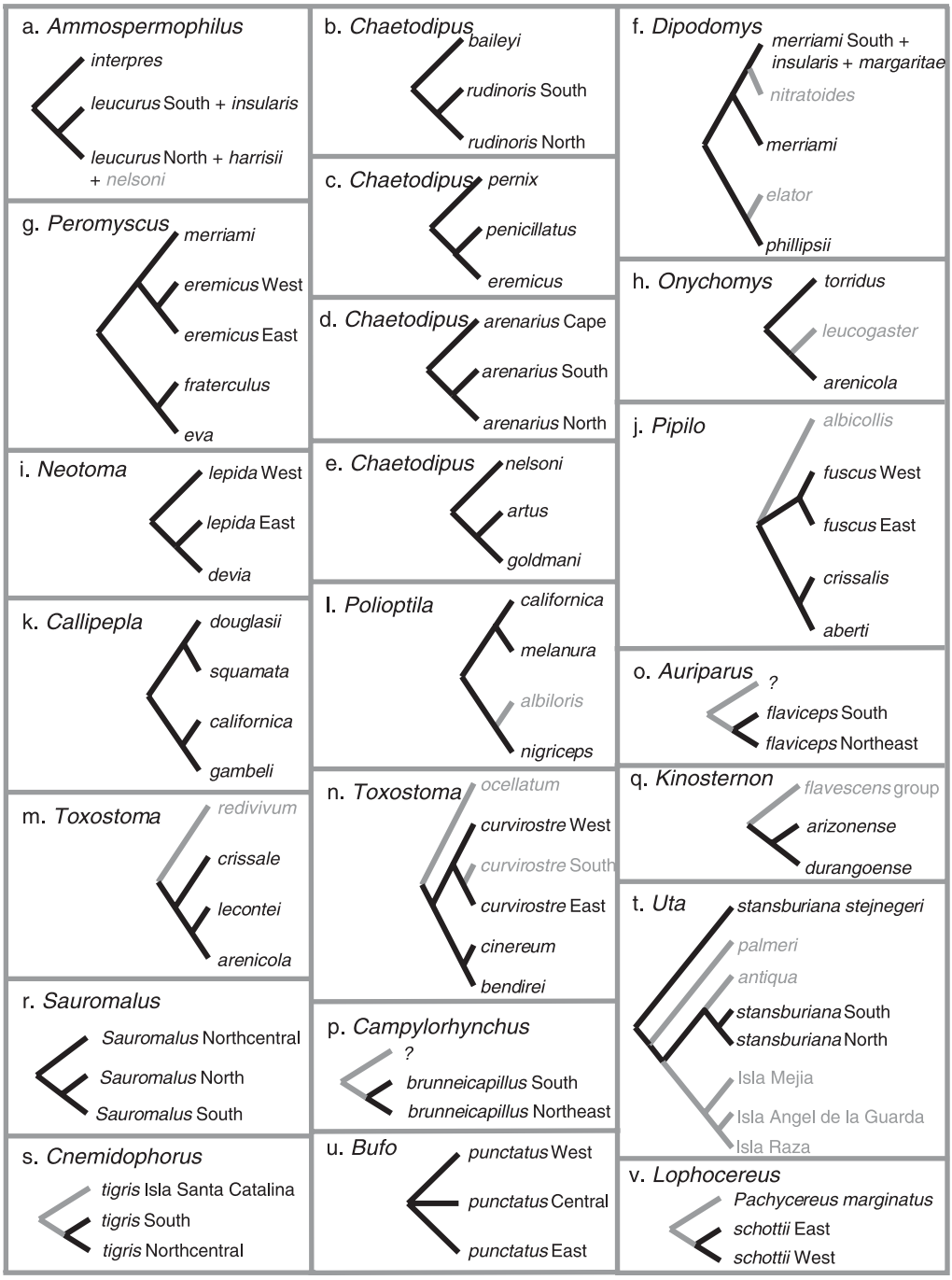

Fig. 2. Taxonomic cladograms used in this study (source literature in Table 1). Gray-shaded lineages—and so their biogeographic distributions—were trimmed prior to BPA analyses (see text for discussion). Question marks on cladograms o and p indicate uncertainty about sister-group relationships beyond the sister-taxa depicted. Original sources given in legend of Table 1.

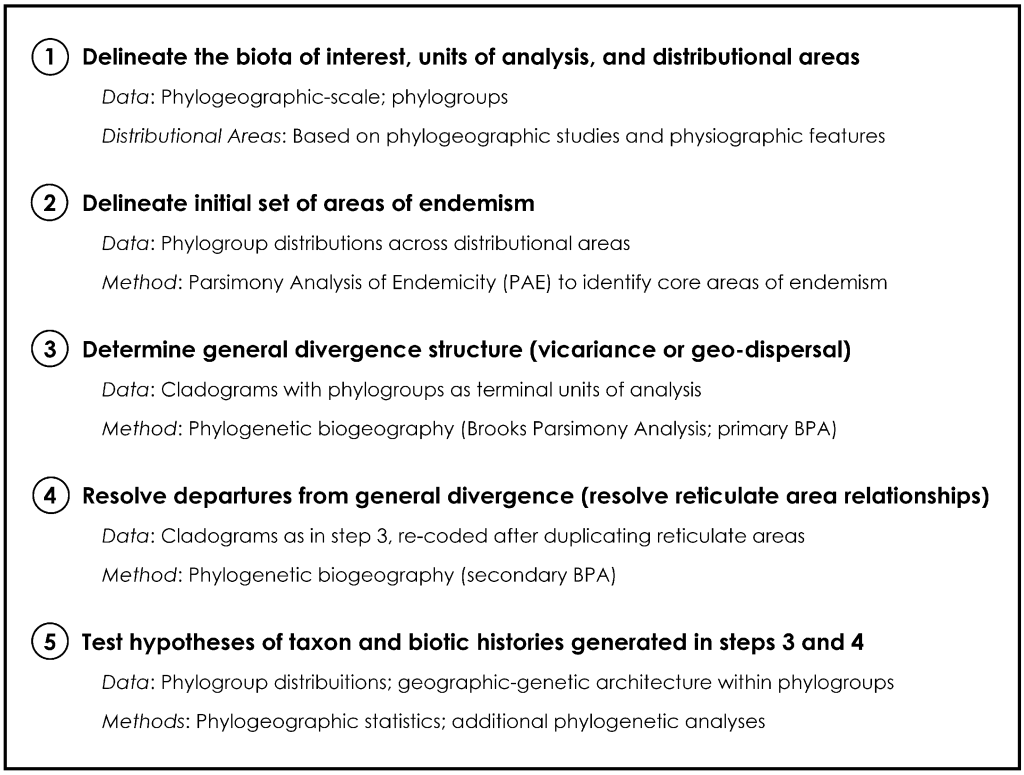

Fig. 3. Outline of five-step procedure illustrated in text, with data types and general methods employed in this study.

identifies an initial set of areas of endemism more objectively than has been done in previous studies of this system. In our concluding remarks, we use our results as a basis for delineating what we perceive to be several distinct advantages that come from performing comparative phylogeographic analyses within a phylogenetic biogeographic framework.

2. Methods

2.1. Units of analysis

We used a subset of the North American warm deserts biota (Table 1; Fig. 2; Appendix A) for which phylogenies and distributional data were considered adequate to support a robust inference of presence or absence of discrete phylogroups across areas of distribution (Fig. 1). Most of the phylogenies were generated with molecular sequence data (in most cases, mitochondrial DNA protein coding genes) although the *Lophocereus* data set is based on protein allozymes. Cladograms j, k, l, m, and n (Fig. 2) were used in previous studies of avian biogeographic history (Zink et al., 2001; Brooks and McLennan, 2002).

2.2. Identification of areas of endemism

The objective delineation of areas of endemism is a difficult but necessary aspect in historical biogeography (Crisci et al., 2003). Analytical problems can occur when a defined area of endemism incorporates overlapping taxa with varying phylogenetic affinities to other areas (reticulate areas), but use of primary and secondary BPA alleviates our concern about this complication because it is designed specifically to deal with reticulate areas (Brooks, 2004). The key remaining issue is to identify areas of endemism that reflect an informative scale of historical biogeographic pattern and process given the degree of phylogenetic resolution available in a set of data. Although we identify areas of endemism for analysis, our perception of what constitutes an area does not require perfect or even substantial overlap among taxa (Harold and Mooi, 1994). Instead, endemic taxa must show broadly coincident breaks at an area boundary, such as might have resulted from one or more historical vicariance events (Hovenkamp, 1997).

Parsimony analysis of endemicity (PAE; Rosen, 1988) has been used by a number of investigators to infer historical area relationships, but has been criticized when used in that context because it does not use taxon phylogeny information and therefore is not considered a historical method (Humphries and Parenti, 1999). Nevertheless, in a more restrictive context, PAE can be an effective tool for identifying provisional areas of endemism based on taxon presence–absence data among a set of distributional areas (Morrone, 1994; Morrone and Crisci, 1995) that can, if needed, be subsequently modified pending more detailed phylogenetic investigations (Harold and Mooi, 1994). In this study, we initially identified 11 core warm-desert distributional areas, delineated based on the possibility that various physiographic features could have served as barriers or filter barriers in the past (Fig. 1). An additional five areas (L–P, Table 2)—steppe, chaparral, subtropical forest, or grassland areas peripheral to the warm deserts—were included in some analyses in order to explore their contribution to patterns of endemism given the several warm-desert taxa whose distributions extend into these surrounding areas.

The initial data matrix included 74 taxa (31 mammalian, 27 avian, 11 reptilian, 3 amphibian, 2 plant; Appendix A) coded as either present (1), absent (0) or unknown (?) across distributional areas. Following standard procedure in PAE, a hypothetical ancestral area with all zeros was included for rooting purposes. We followed the recommendation of Enghoff (2000) to use irreversible characters so as to avoid the possibility of providing false support for an area of endemism based on reversals (extinction). Trees were constructed under maximum parsimony using the branch-and-bound algorithm in PAUP* 4.0b8 (Swofford, 2001) with options: characters weighted equally; type = irrev.up; and DELTRAN optimization of character transformation. Branch support was estimated using non-parametric branch-and-bound bootstrapping.

2.3. Analysis of area relationships and biogeographic history

The real-world expectation that biogeographic histories will often be more complex than assumed under the null model of simple vicariance forms the strongest argument for employing a phylogenetic biogeographic method such as Brooks Parsimony Analysis (BPA: Wiley, 1988; Brooks et al., 2001). This method was criticized originally for its potential to generate area-relationships other than those supported by the original distribution patterns (Humphries and Parenti, 1999), but this problem was eliminated

Table 2
Presence/absence distribution matrix for PAE analysis of 74 taxa (Appendix A) across 11 "core" warm deserts distributional areas (A–K; Fig. 1), and five peripheral areas (L–P)

Area code	Area name	Distribution matrix
	Ancestor	00000000000000000000000000000000000000000000000000000000000000000000000000000000
A	San Lucan	10010000000100010000010000000011000010001000000010000010100001001010010010
B	Magdalenan	10010000010000010000110000000011000010001000010010000010100001001010010010
C	Cirios	01001000001000001000100000000011000010001000100010000001110000100101010010
D	San Felipe	01001010001000001000100000011000000001000100100000000001110000?01010??010
E	Coloradan	01000110000000001000000100011000100001000100100001000001010000010101001000
F	Sonoran	01000110100010001000001100101001100010101101010010010010100100101010010001
G	Sinaloan	00000100100001000000000110000000000001010010000000000000000000000000000001
H	Chihuahuan	00000001000000001000000100100000?00110010000100000100101000000000??00100
I	Trans Pecos	00100001000000101000001000100000001000100100001000100001010000000000100100
J	Coahuilan	00100001000000101000001000100000001000100100001000100001010100000000100100
K	Zacatecan	00100001000000101001001000100000001000100100001000100001010100000000100?00
L	Altiplano South	00000000000000000001000000000000001000100001001000110000000000000000000000
M	Mexico South	00000000000000000000000000000000001000000100000001010000000000000000000000
N	Intermountain	01000000000000001100000001011000000000000000000000000000000000010001000100
O	Plains East	00000000000000000010000001000000000001000000000000000000010000000000000100
P	Californian	00000000000000000000000000100110000100010000010000000001000000000010000

through implementation of primary and secondary BPA (Brooks et al., 2001; Van Veller and Brooks, 2001). Briefly, a *primary BPA* parsimony analysis is performed in order to recover a general pattern of area relationships, which normally will exhibit some level of incongruence, or homoplasy, in the trees. Homoplasy is eliminated through a *secondary BPA* analysis, which involves the duplication of areas with homoplasies "…until assumption 0 is no longer violated" (Van Veller and Brooks, 2001, p. 4), i.e. until all homoplasy is removed. Inferences are then made regarding two kinds of area relationships depicted on a fully resolved secondary BPA tree: those that are depicted on the primary BPA trees as well (i.e. those representing an underlying backbone of generalized divergence); and those that are unique to the secondary BPA tree. Thus, the range of possible biogeographic and evolutionary events that might be inferred from a secondary BPA tree are more inclusive than those on a primary BPA tree, including vicariance, geodispersal, speciation of peripheral isolates, post-speciation dispersal, sympatric (or embedded allopatric) speciation, or lack of detectable divergence between areas (Brooks et al., 2001).

We used primary and secondary BPA to examine biogeographic structure across areas of endemism inferred from PAE. The same taxa (phylogroups and species) used in the final round of PAE (Appendix A) were used in BPA, but recoded in order to capture cladistic structure by incorporating interior nodes into the matrix (Van Veller and Brooks, 2001). The resulting data set (Appendix A) includes 107 characters distributed across 9 mammalian, 7 avian, 4 reptilian 1 amphibian and 1 plant cladograms. Trees were constructed under maximum parsimony using the branch-and-bound algorithm in PAUP* 4.0b8 (Swofford, 2001) with options: characters weighted equally; type = unordered; and DELTRAN optimization of character transformation.

3. Results

3.1. Areas of endemism

Two most parsimonious PAE trees were produced (Fig. 4a; one tree shown, length = 114, CI = 0.60, RI = 0.73) from the PAE matrix of 74 taxa across 16 areas (Table 2). These trees differed only in placement of the Altiplano South area. Relatively high endemism is evident for one area (Sonoran) and several groups of areas, whereas 5 areas (San Felipe, Chihuahuan, Altiplano South, Trans-Pecos, Zacatecan) contain no uniquely endemic taxa. We ran a second PAE analysis after removing the first three of those areas, producing one tree (Fig. 4b; length = 100, CI = 0.74, RI = 0.76), which increased endemic support for areas lying adjacent to the removed areas. The second tree contains four areas that are geographically and ecologically peripheral to the core warm desert areas (Sinaloan thornscrub, Californian chaparral, Intermountain cold deserts, Plains East grasslands) and do not contain many endemic taxa within what we have defined here as primarily warm-desert clades. We therefore ran a third PAE analysis after removing those four areas, producing one tree (Fig. 4c; length = 77, CI = 0.88; RI = 0.89), and except for the Sonoran (10 endemic taxa) area, none of the remaining original warm desert distributional areas alone contained more than two endemic taxa, but groups of two or more areas received strong support ($\geqslant$7 endemic taxa). Therefore, in our final PAE analysis, we simplified the matrix further by combining Trans-Pecos, Coahuilan, and Zacatecan into a *Continental East* area; Sonoran and Coloradan into *Continental West*; Magdalenan and San Lucan into *Peninsular South*; and renamed Cirios as *Peninsular North*. In order to simplify subsequent analyses and focus on area relationships among the warm deserts, we also removed Mexico South from further consideration because the four endemic taxa that define it are all either basal in their respective cladograms (*Papilo albicollis*, *Polioptila albiloris*, *Toxostoma occelatum*), or only weakly resolved as a separate phylogroup (*Toxostoma curvirostre* South). The resulting tree (Fig. 5; length = 71, CI = 0.73; RI = 0.68) demonstrates very strong support for three core

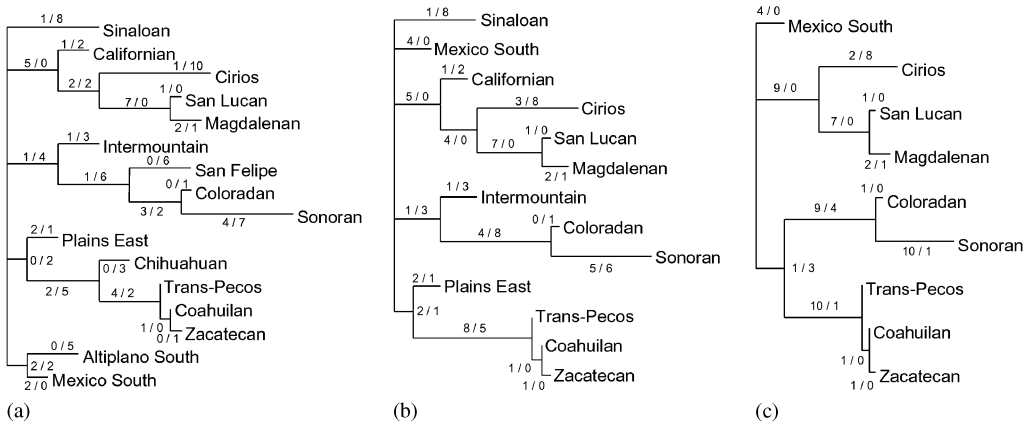

Fig. 4. Three PAE parsimony trees based on (a) 74 taxa and 16 areas (Table 2) and sequentially reduced data matrices (74 taxa, 13 areas), (b) 68 taxa, 9 areas, (c) matrices available upon request). Numbers indicate endemic/widespread taxa.

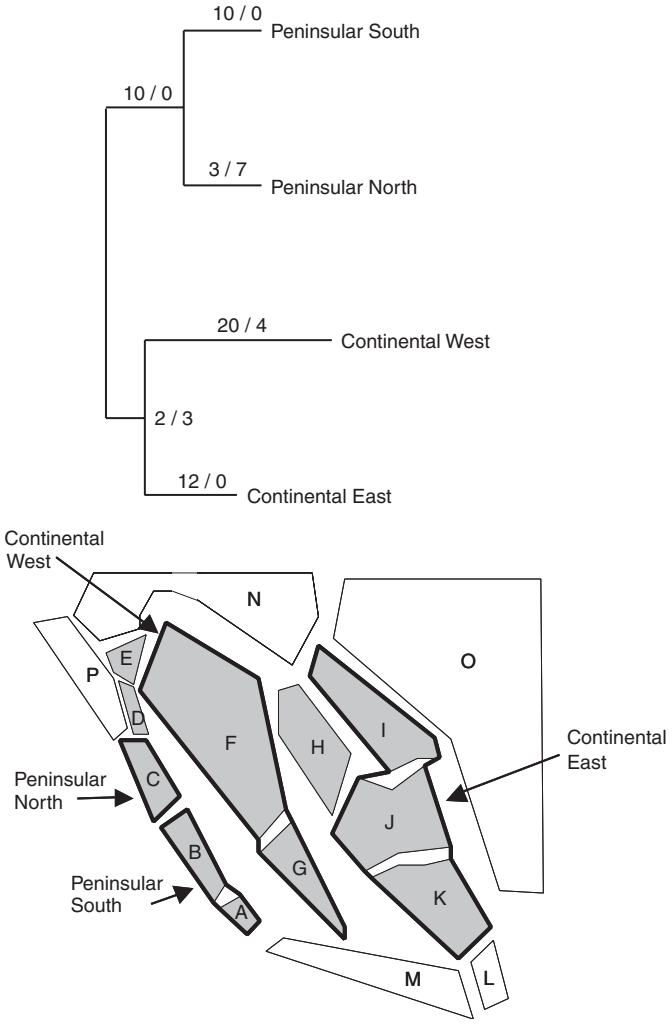

Fig. 5. Final PAE parsimony tree (top) and postulated areas of endemism comprised of one or more distributional areas (bottom). Numbers indicate endemic/widespread taxa.

warm-desert areas. The Peninsular North area receives less support (3 endemic and 7 widespread taxa), but has played an interesting role in the biogeographic history of this biota (see beyond) and therefore is maintained here as a separate area. Further resolution of existing phylogeographic structure within these four areas may be possible in some clades (e.g. *Dipodomys merriami*; Alexander, 2004), providing future opportunities to examine biogeographic history at spatially smaller and temporally more recent scales. Given the level of phylogenetic and phylogeographic resolution currently available across a broad array of taxa, these four areas depict a spatial scale of endemism among a set of core warm-desert areas that is analytically tractable. Moreover, this scale is likely to capture historical biogeographic patterns and processes that are associated with events in

earth history that are crucial to understanding the historical assembly of the core warm-deserts biota. (Intermediate presence–absence tables for each step of the PAE analysis are available on request.)

3.2. Area relationships and biogeographic history

One most parsimonious primary BPA tree was produced (Fig. 6; length = 120 CI = 0.70; RI = 0.58; character matrix available on request). On this tree, Continental West forms a clade with Continental East—supported by 12 homologous characters. The clade of Peninsular South and Peninsular North is supported by 14 homologous characters. The basal separation is between the combined continental vs. peninsular areas. The relatively high number of homologous characters along each branch suggests support for a history of general divergence between areas. However, the number of homoplasies is also high, with a large number distributed between the Continental West area and Peninsular North (five homoplasies) or between Continental West and Peninsular North + Peninsular South (five homoplasies). The additional three Peninsular North homoplasies occur also on the Continental West + Continental East branch. Thus, the pattern of homoplasy shows that Continental West and Peninsular North are both highly reticulate at the level of four areas of endemism.

Secondary BPA analysis of the primary BPA tree resulted in a tree with three area duplications (Fig. 7; character matrices available on request). Character-state changes for the 22 taxa on the secondary BPA tree (Fig. 7) include: 40 allopatric divergence events at the scale of areas delineated here; 19 widespread taxa (post-speciation dispersal or ancestrally widespread); and 2 cases of sympatric or embedded allopatric divergence events. Among postulated historical events associated with the secondary BPA tree (Fig. 8), allopatric divergence—with plausible vicariance explanations—is indicated at only three out of five possible nodes.

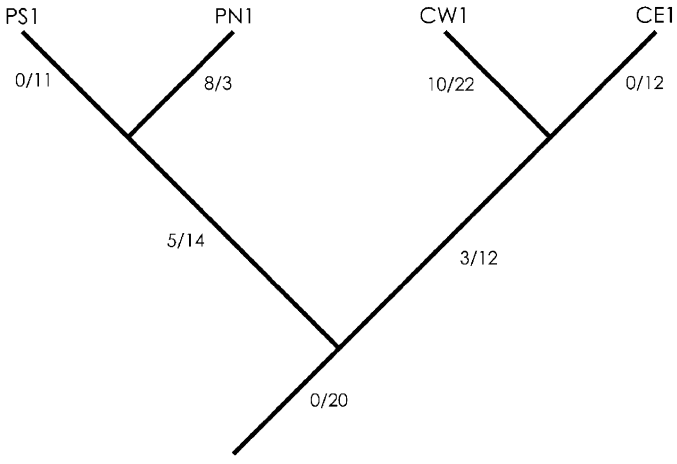

Fig. 6. Most parsimonious primary BPA tree using four original areas of endemism (character matrix and allocation of characters along tree available upon request). Homoplasious/non-homoplasious characters are indicated. PS1 = Peninsular South 1; PN1 = Peninsular North 1; CW1 = Continental West 1; CE1 = Continental East 1.

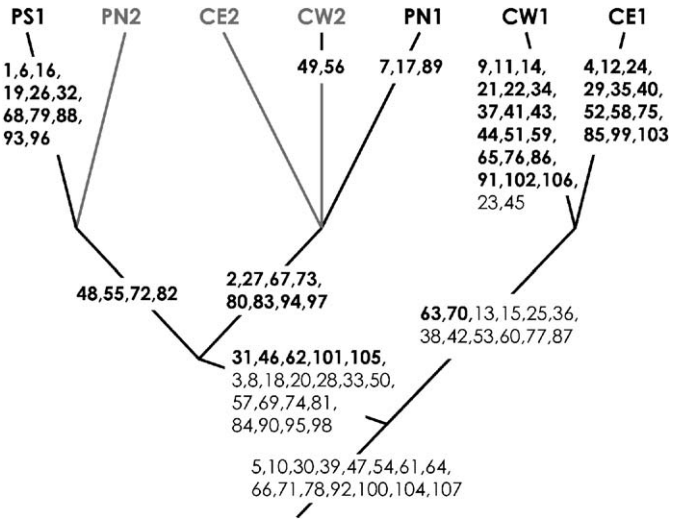

Fig. 7. Secondary BPA tree generated through area duplications of the primary BPA tree (Fig. 6; character matrix available upon request). Boldface areas and branches trace the primary BPA tree. Boldface numbers along branches represent terminal taxa (phylogroups or species); other numbers refer to internal nodes on cladograms (see Appendix A).

4. Discussion

Historical biogeography is rich in concepts and methods (Crisci et al., 2003), yet continues to be fragmented into factions with differing views: e.g. whether phylogeography is a valid approach; or whether dispersal can be explored rigorously within a cladistic framework. We consider phylogeography to be a legitimate approach to historical biogeography, but agree (Riddle and Hafner, 2004) that resulting patterns often have been interpreted in a rather ad hoc fashion. We suggest that a step-wise approach (Fig. 3) combining the strengths of phylogeography and phylogenetic biogeography provides a more rigorous framework for comparative phylogeography and enhanced hypothesis-testing power within the arena of phylogenetic biogeography.

4.1. What have we learned about the core warm deserts biota using the step-wise approach?

4.1.1. Step 1: Delineate biota of interest, units of analysis, and distributional areas

One of the often overlooked aspects of historical biogeography is the explicit consideration of the appropriate timeframe within which applicable events in earth history can be causally associated with the assembly of specified biotas, units of analysis, and areas of endemism (Donoghue and Moore, 2003). Various recent phylogeographic-scale studies of the core North American warm deserts biota (references in Table 1) have regularly posited that diversification and dispersal events precede late Pleistocene timeframes, often postulating events within Pliocene or Miocene times. These studies commonly reveal deep, geographically structured phylogenetic splits between phylogroups embedded within widespread taxonomic species, suggesting that the level of resolution provided is necessary to address diversification and assembly of this biota. More generally,

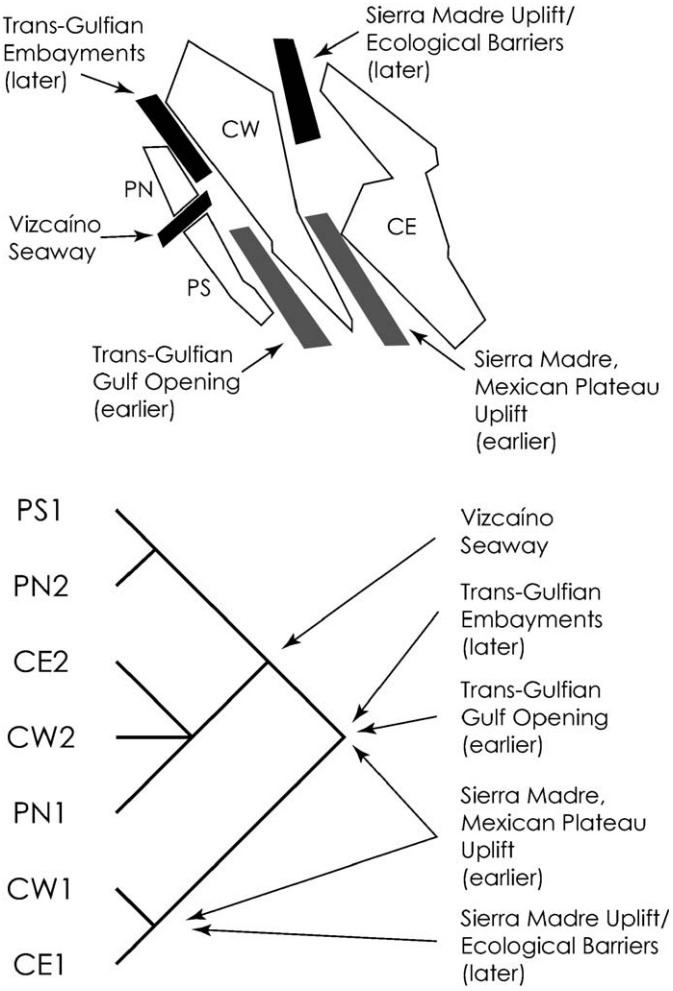

Fig. 8. Depiction of postulated vicariant events (top) among four areas of endemism, and a model of historical vicariance as the events are associated with the secondary BPA tree (Fig. 7).

to the extent that sampling has adequately delineated the geographic distributions of phylogroups, they can replace the more traditional species as OTUs in phylogenetic or cladistic biogeography without conceptual difficulties.

Given the generally indicated timeframes for phylogroup divergence, we must consider tectonic events in earth history, in addition to the more traditionally posited Quaternary climatic oscillations, as potential drivers of diversification in this biota. In fact, we have deliberately delineated a target biota of interest because of our a priori interest in the evolution of deserts and their biotas, and we suggest that any investigation of biotic assembly would benefit by taking a similar, explicitly ecological approach. One benefit of doing so is that it simplifies the difficult, but necessary, problem of delineating areas of endemism. As has been argued cogently (Brown, 1995), geographic barriers to dispersal are ecological features, and by delineating a biota of interest as an ecologically defined

assemblage, the delineation of postulated historical barriers becomes an exercise in interpreting attributes of a landscape within the context of the ecological attributes of the biota of interest.

4.1.2. Step 2: Delineating an initial set of areas of endemism

Two of the more comprehensive previous studies of the aridlands biota (Zink et al., 2000a; Brooks and McLennan, 2001) analysed five avian clades within the frameworks of cladistic and phylogenetic biogeography, but differed from this study in ways that prevent a straightforward comparison of results across the three studies. Most importantly, those studies did not address one of the most important general patterns in this biota: the high level of endemism and rich historical integrity of the Peninsular South area. By accepting a previous estimate of the areas of endemism postulated by Hubbard (1973) without critical analysis of their content and context, the other two studies were unable to recognize the important historical differences in the roles of Peninsular South and Peninsular North areas of the Baja California Peninsula. Separation of Peninsular South from Peninsular North areas of endemism is critical to understanding the nature of historical vicariance and dispersal between the peninsula as a whole and the continental deserts. Our approach to postulating areas of endemism delineated a set of areas of endemism that were justified robustly by the distributions of the phylogroups and allowed us to distinguish between core and peripheral distribution areas in an objective fashion. Conceptual differences between the two studies and ours forced us to recode distributions of several avian taxa, which affected patterns of area relationships. While Brooks and McLennan (2001) employed the same phylogenetic biogeographic methods as this study, they re-analysed the data set and areas of endemism used by Zink et al. (2000a), and so produced hypotheses of area relationships that are not strictly comparable to ours.

4.1.3. Steps 3 and 4: Determine general divergence structure (vicariance or geo-dispersal) and resolve departures from general divergence (resolve reticulate area relationships)

Beyond the two studies discussed above, few previous phylogeographic studies of the aridlands biota have provided more than post hoc explanations for geological or paleoclimatic events possibly involved in diversification and dispersal histories. We believe that analysing phylogeographic patterns within a phylogenetic biogeographic framework has allowed us to examine postulated causal associations between earth and biotic history more rigorously than is typically done in phylogeography. By providing a method for investigating highly reticulated area relationships analytically, phylogenetic biogeography provides an objective framework for sorting general events replicated across co-distributed taxa—as might result from vicariance or geo-dispersal—from taxon-specific events such as post-speciation dispersal and peripheral isolates speciation.

The BPA approach has provided insight into the sources of the highly reticulate nature of the Continental West and Peninsular North areas. An equivalent number of diversification events involve Continental West and either Continental East or one or both peninsular areas (Fig. 7). This explains largely why the primary BPA tree has a large number of homoplasies. Zink et al. (2000a) argued that their area B (Sonoran Desert) had a deep vicariant history with the Baja Peninsula and a much shallower history of dispersal and some divergence with the Chihuahuan Desert. Our results differ in depicting an equally deep, and perhaps deeper, history of vicariance between Continental West and Continental East as between Continental West and one or both peninsular areas (Fig. 8).

A reasonable hypothesis to account for this pattern is that Continental West has played a central role in diversification between two geographically separate but contemporaneous arenas of diversification: those involving the evolution of the Sea of Cortez to the west; and those involving the evolution of the Sierra Madre Occidental and Mexican Plateau to the east.

The current pattern of reticulation in Peninsular North is very different from that in Continental West, and likely involves a fundamentally different sort of history. Whereas Continental West has a high proportion of endemic taxa, indicating this to be an important area of diversification, Peninsular North has only a few endemic taxa, but shares a large number of widespread taxa with Peninsular South and Continental West

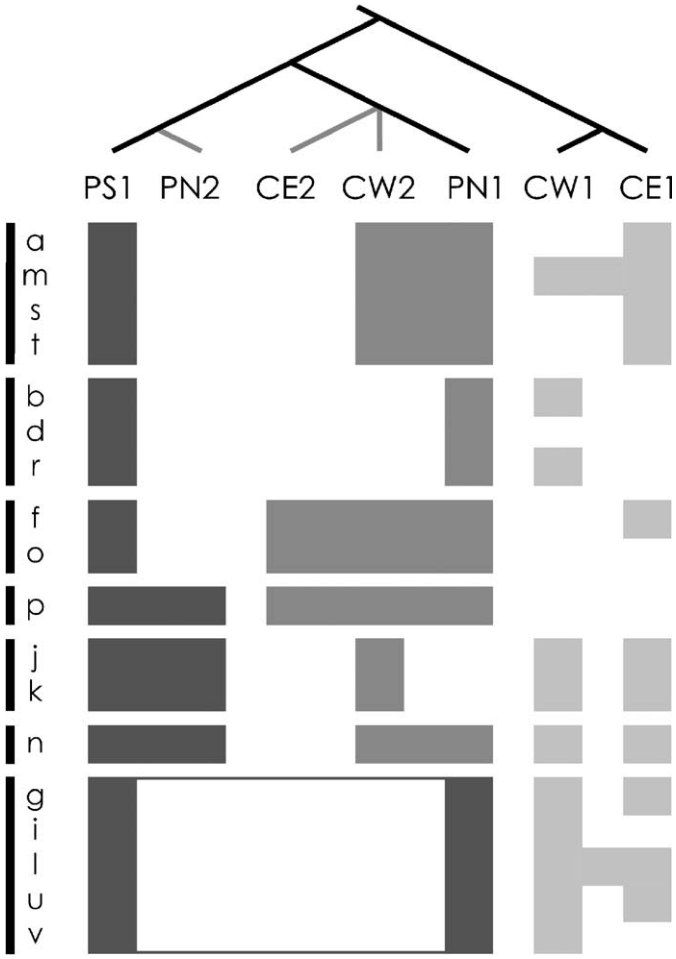

Fig. 9. Summary of taxon distributions mapped onto the secondary BPA tree (Fig. 7), including only those taxa with at least one representative in the Peninsular South area of endemism. Cladograms are grouped into sets of seven different patterns of taxon distributions between Peninsular South and two each of the Peninsular North and Continental West areas. More basal distributions in Continental West and Continental East areas are shown in light shading.

(extending, in three cases, to Continental East as well). The most striking pattern, however, is the complete separation between those taxa shared with Peninsular South vs. those shared with one or more Continental areas (Fig. 9).

We realize that if an area does not contain a taxon from a group that otherwise has a taxon in a sister area, it could represent extinction, but we prefer to not initially count absence as an extinction event because we believe that the primitive absence of a taxon from an area is an equally viable hypothesis. For example, four groups are part of the general divergence between Continental West and the peninsular areas, but do not have taxa in Continental East, probably because an ancestral taxon never occurred that far east prior to the postulated early vicariance separating the continental areas; four additional groups are part of the general divergence between Continental West and Continental East but do not have taxa in either of the peninsular areas, probably for the same reason.

The postulated association between the area cladogram and historical vicariance events (Fig. 8) attempts to incorporate some of the temporal complexity of earth history into a model of diversification and dispersal histories for the core warm deserts biota. In so doing, two nodes are each associated with two events—in each case an earlier and a later event. We believe that this depiction represents something of the progressive nature of geological, climatic, and hence ecological evolution over the course of time. Therefore, these nodes will most likely include mixtures of taxa that represent older to more recent times of vicariance, dispersal, and speciation.

Both Zink et al. (2000a) and Brooks and McLennan (2001) discuss problems involved in sorting true vicariance from pseudo-congruence within area trees derived from a subset of the clades we used here, and correctly suggest that molecular data might provide insight into cases of the latter when branch lengths differ greatly across different co-distributed clades and that difference can be attributed to different times of divergence. Recently, Donoghue and Moore (2003) have provided a nice summary of the value of utilizing molecular data to calibrate times of divergence when pseudo-congruence appears to be an issue. To some degree, however, we suggest that time alone might not necessarily cause us to resort to an explanation of pseudo-congruence. Pseudo-congruence should be used to describe overlapping and separate dispersal, isolation, and divergence events that artificially suggest a single event on an area cladogram. However, if ancestrally co-distributed taxa are becoming isolated and diverging at different times (e.g. the habitats of sandy substrate specialists might fragment more quickly than rocky substrate specialists during geological uplift), then perhaps we should continue to recognize a single vicariant event, but with older to more recent isolation times along the temporal continuum of that event.

4.2. What more can we learn about the core warm deserts biota?

4.2.1. Step 5: Testing hypotheses of taxon and biotic histories generated in steps 3 and 4

We intentionally left causal explanations for patterns summarized on the secondary BPA tree of a very general nature. Because we are using phylogeographic-scale and molecular data, we can more productively evaluate those patterns within either a phylogeographic framework or by comparing levels of molecular divergence across clades. Specifically, these population-level approaches may be employed to test sets of dispersal and vicariance hypotheses generated through secondary BPA (or in the near future, an

updated approach called PACT—Parsimony Analysis for Comparing Trees; Wojcicki and Brooks, 2004).

4.2.2. Dispersal

Do taxa that are widespread between two or more areas represent an ancestral distribution or dispersal from a smaller ancestral area following erosion of a barrier between areas? In cases where more than one taxon share the same widespread distribution pattern, does this represent a mosaic of unique dispersal events and ancestral distributions, or does it represent an example of synchronous dispersal of a biota from an ancestral area? For purposes of illustration, we focus attention on the distributional patterns of taxa widespread between some combination of Peninsular South, Peninsular North, and Continental West areas (Figs. 7–9). The pivotal area here is Peninsular North, which shares nine taxa with Peninsular South, and eight different taxa with Continental West, with three of those extending into Continental East as well (Fig. 9). Given the high level of endemism in Peninsular South, provisionally attributable primarily or entirely to the Vizcaíno Seaway vicariant event, a reasonable hypothesis would be that the taxa widespread between both peninsular areas result from a fairly recent (post-vicariance) range expansion, primarily in a south – north direction. (A clear exception is *Peromyscus fraterculus*, in clade g, which expanded north – south). Several phylogeographic predictions associated with a signature of range expansion include: a unimodal pair-wise mismatch distribution; significant isolation-by-distance structure; decreasing gene diversity along the expansion gradient; and a serially nested cladogram shape along the expansion gradient (reviewed in Althoff and Pellmyr, 2002; Knowles and Maddison, 2002; Zink, 2002). This hypothesis might be rejected in favor of the alternative—that taxa were distributed across these areas prior to the vicariant event and did not respond to it—by finding geographic genetic structure contrary to one or more of these predictions.

Two studies have supported the recent expansion from Peninsular South to Peninsular North: Zink et al. (2000b) found the predicted mismatch distribution, gene diversity, and cladogram shape signatures in *Polioptila californica*; and Nason et al. (2002) found predicted isolation-by-distance, gene diversity, and cladogram shape signatures in *Lophocereus schottii*. Should a large portion of remaining widespread taxa demonstrate similar structure, this would represent a phylogeographic-scale version of the process identified by Lieberman (2000, 2004) as the first stage of a geo-dispersal event, and represent a significant recent transformation of ecological assemblages in the Peninsular North area (also discussed by Zink, 2002).

The taxa widespread between Peninsular North and Continental West might be attributable to a similar history of recent range expansion. Given the relatively few endemic taxa in Peninsular North, it might be reasonable to hypothesize that the main direction of dispersal has been from continent to peninsula with expansion of desert habitats (at the expense of woodland and chaparral) at the close of the Pleistocene. However, another possibility is that some of the ancestral taxa expanded into the peninsula after the Trans-Gulfian barriers eroded but prior to the Vizcaíno Seaway event. In this case, the latter event would have led to the divergence of a Peninsular South taxon, but there may have been only ephemeral or no loss of connectivity between Peninsular North and Continental West populations. Again, these alternatives—earlier than mid-Pleistocene vs. end of Pleistocene—should offer sets of alternative and testable predictions of geographic population genetic architecture.

4.2.3. Vicariance

We have provided a model of history (Fig. 8) in which recovered biotic histories across 22 clades appear to be highly consistent with a general summary of earth history (discussed in the introduction) that predicts several vicariant events between the four areas examined in this study. This interpretation of earth history explicitly predicts that areas would have been involved in isolation and divergence of warm desert biotas across a continuum of timeframes—interpretable variously as a single, progressive vicariant event, or as pseudo-congruence representing multiple rounds of isolation and divergence. In reality, the opportunities for isolation and divergence between peninsular and continental areas, and between each of the continental areas, could have been even more frequent than depicted by dividing them into two earlier and two later events (see previous discussion).

Each of the vicariant events postulated on these trees are potentially refutable given contradicting evidence. For example (Fig. 8), events attributed to the Vizcaíno Seaway could also include several that actually involved a prior peninsular vs. continental subdivision (the Trans-Gulfian [later] event), followed by extinction of the peninsular clade in Peninsular North and subsequent dispersal of the Continental West clade into that region. The primary sources of data that could contribute to evaluating these alternatives would come from rigorous comparisons of molecular divergence levels, estimates of times of isolation, and population genetic architectures across all taxa suggested here as having been isolated by the Vizcaíno Seaway. The alternative Trans-Gulfian [later] event is postulated to have occurred somewhere between a million to several million years prior to the Vizcaíno event, and so is theoretically distinguishable in taxa for which rates of molecular evolution have been calibrated. Levels of divergence in at least nine of the clades with Peninsular South endemics (Riddle et al., 2000a; Zink et al., 2001) appear to be consistent with the Vizcaíno event hypothesis. Caution is warranted because precise estimates of divergence times are usually difficult to achieve, given the range of factors that reduce confidence in molecular-derived time estimates (e.g. lineage-specific rate heterogeneity, dependence of coalescence times on population size and structure, difficulties in discovering informative fossils to use in rate calibrations).

Heterogeneity in times of isolation and divergence at nodes with a possible mixture of older and more recent events (Fig. 8) also should be diagnosable in a very general sense with molecular divergence data given the large gaps in time between the earlier (Miocene and Pliocene) vs. more recent (late Pleistocene) events. Differentiating between earlier and later Trans-Gulfian events is likely to be more problematic, because the timeframes between events are smaller (late Miocene/early Pliocene vs. late Pliocene).

Finally, we can find preliminary evidence in this group of taxa for the possibility of additional historical isolation and divergence of populations—perhaps in the form of other vicariant events (see Fig. 1)—embedded within the areas of endemism assessed herein. For example, for the *Dipodomys merriami* Northeast phylogroup in clade f, which here is treated as a single widespread taxon, a nested clade analysis (Alexander, 2004) revealed statistically significant divergence between Peninsular North, Continental West, and Continental East populations, as well as between northern and southern groups of populations embedded within Continental East. The striking similarities in divergence and distributional patterns shared by *D. merriami*, *Auriparus flaviceps* (clade o), and *Campylorhynchus brunneicapillus* (clade p; Fig. 9) provides a motivation for testing for embedded patterns in the latter two species that parallel those in *D. merriami*—and if

congruence were discovered, would provide evidence for embedded, temporally shallow vicariant events within and among the four warm desert areas focused on in this study.

4.3. Concluding remarks

Our intent was to focus directly on the historical relationships across the core warm deserts, and so we trimmed "non-desert" taxa from cladograms prior to conducting phylogenetic biogeographic analyses. We recognize that in so doing we are restricting our analysis to an assessment of area relationships and speciation events between core desert areas, but do not think that it biases our interpretation of that history because taxa in peripheral areas of occurrence either join cladograms basal to subsequent diversification across the core warm deserts, or their speciation represents individualistic and unique events. Future analyses should include peripheral areas and events in order to address formally the manner (timing and geography) in which ancestral taxa have been incorporated into the evolving desert biota from surrounding habitats (e.g. subtropical thornscrub, chaparral, grassland).

By coalescing all distributional patterns into just four initial areas of endemism, we recognize that we will be missing important details of distributional and historical differences embedded within each of the areas. For example, within the Continental West area, distributions and relationships suggest that the traditionally recognized Sonoran Desert could be separated from the Sinaloan Thornscrub across the Sierra Barabampo-Rio Fuerte physiographic feature (Fig. 1). Examples of taxa that might be members of a separate Sinaloan area of endemism include *Chaetodipus pernix*, *C. artus*, *Peromyscus merriami*, *Polioptila nigriceps*, and *Callipepla douglasii*. The habitat preferences of each of these species appear to be more subtropical thornscrub than warm desert scrub. Yet, with the exception of *C. artus*, the ranges of each of these species currently extend northward into the heart of the Sonoran Desert, sometimes as far north as southern Arizona. While these distributions have characteristics that suggest a recent range expansion (as we discussed above for a number of peninsular species), we believe that additional phylogeographic-scale work that evaluates evidence for or against this hypothesis is warranted prior to justifying the recognition of a separate area of endemism. If warranted, such future analyses will be interesting in that they might separate the two postulated vicariant events across the Sierra Madre Occidental (early and late) into ecologically distinct episodes: an earlier event between Continental East and a Sinaloan thornscrub area separate from a later isolation between Continental East and a more northern Sonoran desertscrub area. This hypothesis would make sense if one imagines that, as the Sierra Madres and Mexican Plateau are uplifting in Miocene and early Pliocene time, the earliest isolation events might have occurred between thornscrub rather than later-evolved desert species. The same might be true relative to earlier vs. later events separating continental and peninsular lineages.

This study represents merely the first comprehensive approximation of historical biogeography and diversification within the North American aridlands biota, and future advances will come from addition of greater numbers and variety of taxa (excellent candidates include fruit flies, Hurtado et al., 2004; and scorpions, Gatenbein et al., 2001), more detailed analyses of phylogeographic structure across any of the taxa, and increasing attention to the contribution of biological attributes (e.g. host-plant mutualisms, plant vs. animal responses to climatic changes) to the geography of diversification.

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Appendix A. Clades and taxa (phylogroups and species) employed in this study. See Fig. 3 for taxon cladograms. PAE numbers reference positions in four matrices (the first column are the same taxon codes used in Table 2; whereas the second through fourth are codes used in matrices used to produce Figs. 4b, c, d, and 5, respectively).

Clade	Common name	Scientific name	PAE numbers	BPA number
a	White-tailed antelope squirrel	*Ammospermophilus leucurus* South + *A. insularis*	01 01 01 01	01
a	White-tailed and Harris' antelope squirrel	*A. leucurus* North + *A. harisii* + *A. nelsoni*	02 02 02 02	02
a	Texas antelope squirrel	*A. interpres*	03 03 03 03	04
b	Baja pocket mouse	*Chaetodipus rudinoris* South	04 04 04 04	06
b	Baja pocket mouse	*C. rudinoris* North	05 05 05 05	07
b	Bailey's pocket mouse	*C. baileyi*	06 06 06 06	09
c	Desert pocket mouse	*C. penicillatus*	07 07 07 07	11
c	Chihuahuan pocket mouse	*C. eremicus*	08 08 08 08	12
c	Sinaloan pocket mouse	*C. pernix*	09 09 09 09	14
d	Little desert pocket mouse	*C. arenarius* South	10 10 10 10	16
d	Little desert pocket mouse	*C. arenarius* North	11 11 11 11	17
d	Little desert pocket mouse	*C. arenarius* Cape	12 12 12 12	19
e	Goldman's pocket mouse	*C. goldmani*	13 13 13 13	21
e	Narrow-skulled pocket mouse	*C. artus*	14 14 xx xx	22
e	Nelson's pocket mouse	*C. nelsoni*	15 15 14 14	24
f	Merriam's kangaroo rat	*Dipodomys merriami* South	16 16 15 15	26
f	Merriam's kangaroo rat	*D. merriami* Northeast	17 17 16 16	27
f	Fresno kangaroo rat	*D. nitratoides*	18 18 xx xx	xx
f	Texas kangaroo rat	*D. elator*	19 19 xx xx	xx
f	Phillip's kangaroo rat	*D. phillipsii*	20 20 17 17	29
g	Baja cactus mouse	*Peromyscus fraterculus*	21 21 18 18	31
g	Eva's mouse	*P. eva*	22 22 19 19	32
g	Cactus mouse	*P. eremicus* West	23 23 20 20	34

g	Cactus mouse	*P. eremicus* East	24 24 21 21	35
g	Mesquite mouse	*P. merriami*	25 25 22 22	37
h	Northern grasshopper mouse	*Onychomys leucogaster*	26 26 xx xx	xx
h	Chihuahuan grasshopper mouse	*O. arenicola*	27 27 23 23	40
h	Southern grasshopper mouse	*O. torridus*	28 28 24 24	41
i	Desert woodrat	*Neotoma lepida* West	29 29 25 25	43
i	Desert woodrat	*N. devia*	30 30 26 26	44
i	Desert woodrat	*N. lepida* East	31 31 27 27	46
j	California towhee	*Pipilo crissalis*	32 32 28 28	48
j	Abert's towhee	*P. aberti*	33 33 29 29	49
j	Canyon towhee	*P. fuscus* West	34 34 30 30	51
j	Canyon towhee	*P. fuscus* East	35 35 31 31	52
j	White-throated towhee	*P. albicollis*	36 36 32 xx	xx
k	California quail	*Callipepla californica*	37 37 33 32	55
k	Gambel's quail	*C. gambelii*	38 38 34 33	56
k	Scaled quail	*C. squamata*	39 39 35 34	58
k	Elegant quail	*C. douglasii*	40 40 36 35	59
l	California gnatcatcher	*Polioptila californica*	41 41 37 36	62
l	Black-tailed gnatcatcher	*P. melanura*	42 42 38 37	63
l	Black-capped gnatcatcher	*P. nigriceps*	43 43 39 38	65
l	White-lored gnatcatcher	*P. albiloris*	44 44 40 xx	xx
m	Le Conte's thrasher	*Toxostoma lecontei*	45 45 41 39	67
m	Vizcaino thrasher	*T. arenicola*	46 46 42 40	68
m	Crissal thrasher	*T. crissale*	47 47 43 41	70
m	California thrasher	*T. redivivum*	48 48 xx xx	xx
n	Gray thrasher	*Toxostoma cinereum*	49 49 44 42	72
n	Bendire's thrasher	*T. bendirei*	50 50 45 43	73
n	Curve-billed thrasher	*T. curvirostre* East	51 51 46 44	75
n	Curve-billed thrasher	*T. curvirostre* South	52 52 47 xx	xx
n	Curve-billed thrasher	*T. curvirostre* West	53 53 48 45	76
n	Occelated thrasher	*T. occelatum*	54 54 49 xx	xx
o	Verdin	*Auriparus flaviceps* South	55 55 50 46	79
o	Verdin	*A. flaviceps* Northeast	56 56 51 47	80
p	Cactus wren	*Campylorhynchus brunneicapillus* South	57 57 52 48	82
p	Cactus wren	*C. brunneicapillus* Northeast	58 58 53 49	83
q	Yellow mud turtle	*Kinosternon flavescens* group	59 59 xx xx	xx
q	Yellow mud turtle	*K. durangoense*	60 60 54 50	85
q	Yellow mud turtle	*K. arizonense*	61 61 55 51	86
r	Chuckwalla	*Sauromalus* South	62 62 56 52	88
r	Chuckwalla	*Sauromalus* North	63 63 57 53	89
r	Chuckwalla	*Sauromalus* Northcentral	64 64 58 54	91
s	Western whiptail	*Cnemidophorus tigris* South	65 65 59 55	93
s	Western whiptail	*C. tigris* Northcentral	66 66 60 56	94
t	Common side-blotched lizard	*Uta stansburiana* South	67 67 61 57	96

t	Common side-blotched lizard	*U. stansburiana* North	68 68 62 58	97
t	Common side-blotched lizard	*U. stansburiana stejnegeri*	69 69 63 59	99
u	Red spotted toad	*Bufo punctatus* West	70 70 64 60	101
u	Red spotted toad	*B. punctatus* Central	71 71 65 61	102
u	Red spotted toad	*B. punctatus* East	72 72 66 62	103
v	Senita	*Lophocereus schottii* West	73 73 67 63	105
v	Senita	*L. schottii* East	74 74 68 64	106

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