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Source: Journal of Mammalogy, 95(6):1107-1127.

Published By: American Society of Mammalogists

DOI: <http://dx.doi.org/10.1644/14-MAMM-S-064>

URL: <http://www.bioone.org/doi/full/10.1644/14-MAMM-S-064>

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Assembling the modern Great Basin mammal biota: insights from molecular biogeography and the fossil record

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Reconstructing the assembly of local ecological communities requires insight from a wide range of disciplines including biogeography, paleontology, ecology, and evolutionary biology. Community assembly depends on the availability of species in a regional species pool (a “biota”), which itself is assembled through a history of diversification, geographic range shifting, and adaptive responses to environmental change. The Great Basin contains a diverse mammal biota sorted into communities along elevational, latitudinal, and structural habitat gradients. Molecular genetic approaches have clarified the timing of diversification events in response to dynamic Neogene landscapes in several iconic Great Basin mammals, although the role of Great Basin landscape evolution on species diversification remains largely unexplored. Divergence continued into the Quaternary, as widespread species formed genetically unique lineages in and around the Great Basin. In response to Quaternary climatic oscillation, some mammalian species maintained their ranges whereas others exhibited dramatic range contractions or expansions, impacting the composition of regional species pools available for local community assembly. Advances will come from elucidating phylogenetic and phylogeographic structure in more taxa, but also from emerging genomic and modeling approaches to address how ecological traits, niche shifts, and adaptive evolution have influenced specific responses to dynamic landscapes and climates resulting in the species assemblages that characterize the Great Basin.

Key words: climate change, cryptic lineage, cryptic species, geomorphology, intermontane region, North American Land Mammal Age (NALMA), phylogeography, range expansion, range shifting, refuge

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DOI: 10.1644/14-MAMM-S-064

Mammals are abundant in Nevada, even in the most sandy areas which, because they appear to be barren, have but slight if any appeal to the casual visitor. (Hall 1946:1)

Nevada is made up of parallel, north-to-south mountain ranges and narrow and flat-floored valleys ... The trough along the eastern base of the Sierra Nevada has had much greater effect on the distribution and speciation of mammals than has the Humboldt River Valley. (Hall 1946:29)

The Great Basin (Fig. 1) became a landmark region in North American mammalogy early in the 20th century when Annie M. Alexander of the Museum of Vertebrate Zoology at the University of California, Berkeley, encouraged and financed the collecting trips of E. Raymond Hall as he travelled across the heart of the region documenting the distributions and natural history of mammals throughout the state of Nevada. Hall’s collections from the Great Basin augmented those from

prior trips organized and conducted by Alexander herself, along with Louise Kellogg (e.g., Taylor 1911), others encouraged by Joseph Grinnell (Linsdale 1938) or Grinnell and Hall (Borell and Ellis 1934), and earlier collections made under faunal survey employees of the United States Biological Survey (e.g., Vernon Bailey and Harry C. Oberholser). Together, these collections provided the core data for the *Mammals of Nevada* (Hall 1946), which became “the standard against which other state surveys of mammals have been measured” (Lawlor 1995:xiii).

Hall emphasized the “desert character of the mammalian fauna” (Hall 1946:67), using his *Introduction* to describe the workings of kangaroo rats, pocket mice, and kangaroo mice around sand dunes. He touched on historical biogeography and



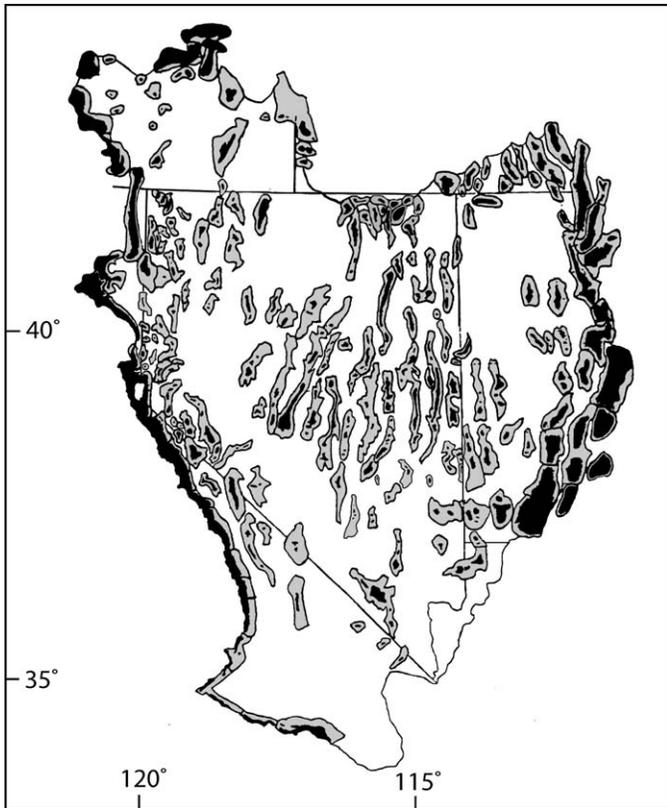


FIG. 1.—Illustration of the island-like distribution of mountain islands (light shading), including montane and subalpine habitats (dark shading), as defined by Charlet (2007) to include at least 1 montane conifer species, in the modern Great Basin. Intervening nonshaded areas comprise a mosaic of primarily shrub-steppe and pinyon-juniper woodland habitats. Note that the Great Basin is bordered to the west and east by much more continuous montane and subalpine habitats. Redrawn from Charlet (2007).

evolution with a detailed account of the influences of Quaternary Lake Lahontan (Fig. 2B) on distributional changes of sand-dwelling species and production of subspecies. Curiously, after detailing mammal distribution patterns according to floral belts, Merriam's life zones, and faunal areas, Hall did not emphasize the isolating influence (Fig. 1) of the many "parallel, north-to-south mountain ranges" on the distributions of nondesert mammals, which subsequently became iconic case studies in ecology, biogeography, and conservation biology (e.g., Brown 1971, 1978; McDonald and Brown 1992; Lawlor 1998; Beever et al. 2003; Galbreath et al. 2009, 2010).

In his species accounts, Hall (1946) would explore patterns of diversity, natural history, biogeography, and speciation of Great Basin mammals with a keen eye for detail. For example, his accounts of the 2 species of kangaroo mice in the genus *Microdipodops* describe ecological differences at sympatric localities, and the possibility of localized interbreeding based on several morphologically intermediate specimens in Penoyer Valley (Fig. 2B). He coupled these observations and inferences with speculation on ecological and distributional changes

through time to derive alternative scenarios of speciation that would in more modern terms be recognized as components of ecological speciation, ring species, and peripheral isolate speciation. Accounts such as these were of considerable value to mammalogists, not only because they formed the basis for hypothesis testing, but because of the care Hall used in recording locality information (a cornerstone of the "Grinnellian method" that originated with the 1st director of the Museum of Vertebrate Zoology, Joseph Grinnell). For example, Hafner et al. (1979) were able to test Hall's hypothesized local hybridization between the 2 species of kangaroo mice by returning to the exact localities that he had described in his field notes; they found no evidence to support the hybridization hypothesis.

Yet, even as recently as the 1970s, mammalogists approaching biogeographic and evolutionary questions in the Great Basin were operating without the tools of molecular-based approaches to historical biogeography (Riddle et al. 2008), including phylogeography (Avice et al. 1987). Phylogeography uses molecular genetic data and a combination of phylogenetic and population genetic analyses to reconstruct biogeographic history and regional population history within and between closely related species (Avice 2000; Riddle and Hafner 2006; Hickerson et al. 2009). Empirically, this approach has expanded the tractable time frame for reconstructing biogeographic histories into the Quaternary, with some studies extending into the Neogene (Riddle and Hafner 2006). More generally, historical biogeography has been revitalized by the infusion of molecular genetics and sophisticated analytical methods (Riddle et al. 2008; Lomolino et al. 2010).

The Great Basin has emerged as a physiographically distinct region within the past 30 million years (Badgley et al. 2014). This region incorporates an exceedingly complex topography that underlays a complex mosaic of shifting distributions of species across space and over time. Those multiple "parallel, north-to-south mountain ranges" Hall described have produced replicated elevational gradients, and motivated mammalogists to explore the ecological and evolutionary consequences of isolation in both mountains and intervening valleys. Several million years of climates oscillating between glacial and interglacial periods (as well as a multitude of shorter-duration "flickers" in climate nested within the larger cycles) have led to frequent changes in availability and location of habitats for mammals. Generally, montane habitats and species have undergone repeated episodes of both downslope and southern expansion, followed by upslope and northern retreat (summarized by Grayson 2011), while warmer and drier desert habitats have expanded and contracted along low-elevation corridors. The hydrography of this internally drained region dictated that many and sometimes enormous lakes (e.g., Lahontan and Bonneville [Fig. 2B]) developed in valleys during glacial periods, and desiccated during interglacial periods, leaving corridors for range expansion (e.g., the Lahontan Trough [Reveal 1979] along the western edge and Bonneville Basin to the east).

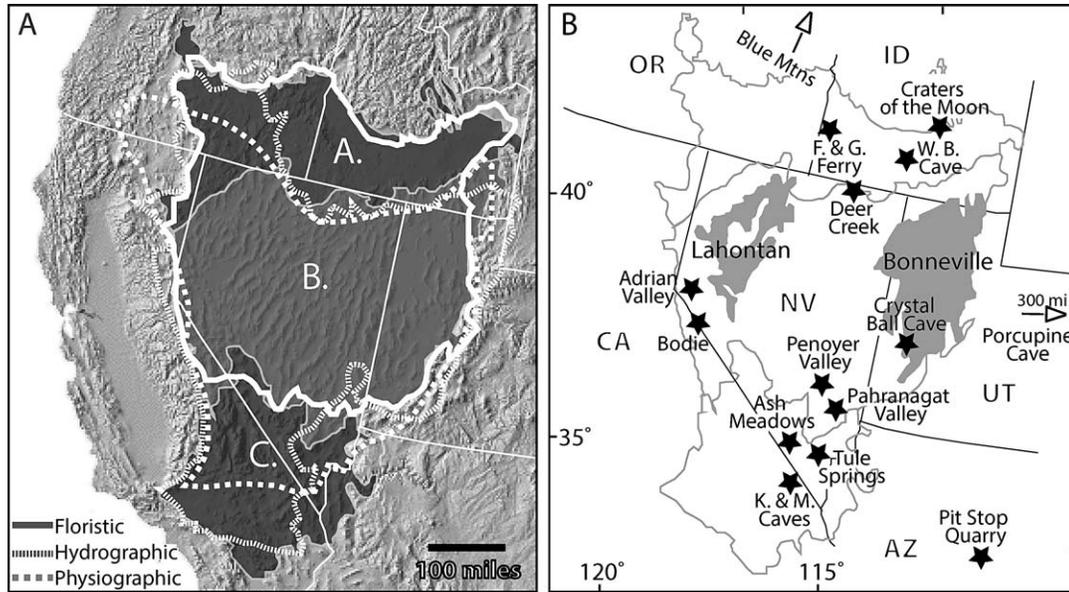


FIG. 2.—A) Three definitions of the Great Basin (see Grayson 2011) based on either dominant shrub and woodland plant assemblages (floristic), internal drainage (hydrographic), or northernmost portion of the Basin and Range Province (physiographic); and 3 shaded ecoregions (from Ricketts et al. [1999], includes: A. Snake River–Columbia Plateau shrub-steppe; B. Great Basin shrub-steppe; C. Mojave Desert) that collectively circumscribe the sum of all 3 of those concepts of the Great Basin (discussed further in text). B) Outline of the 2 massive glacial-age lakes of the Great Basin (Bonneville and Lahontan, the latter filling much of a low-elevation separation of the Sierra Nevada mountains from those of the Great Basin and has been called the Lahontan Trough); several sites discussed in text, including fossil sites, also are plotted as stars (abbreviations: F. & G. Ferry = Froman and Glens Ferry; K. & M. Caves = Kokoweef and Mesca Caves; W. B. Cave = Wilson Butte Cave).

Given this long history of geological and climatic change, we might expect multiple opportunities for divergence and range dynamics to have shaped the composition of the Great Basin mammal biota. Changes in diversity, originations, and extinctions at 1 million year (my) intervals were analyzed from the fossil record by Badgley et al. (2014). Here, our focus is on the extant mammals of the Great Basin. We also utilize the fossil record, but primarily in combination with evidence from molecular biogeography and phylogeography, to address several historical diversification and range dynamics themes that are likely to be of importance toward an eventual reconstruction of processes associated with the assembly of the modern Great Basin mammal biota. We begin with a discussion of the landscape that we delineate operationally as the Great Basin.

WHICH GREAT BASIN?

Hall (1946) listed 111 mammal species in Nevada, a number that has grown, through taxonomic revision, new range records, and introductions, to 131 species (120 naturally occurring and 11 introduced—Mantooth and Riddle 2005). Although Nevada is embedded within any of the several definitions of Great Basin boundaries—hydrographic, physiographic, floristic (Fig. 2A), or ethnographic (Grayson 2011)—the total diversity of a Great Basin mammal biota depends on which criterion one uses. The floristically defined Great Basin—reflecting distributions of dominant plant assemblages,

including saltbush and sagebrush in the valleys and pinyon–juniper woodlands on the mountain flanks—corresponds most closely to the “biotic” Great Basin based on the original delineation of 4 North American deserts by Forest Shreve (1942), whereas the physiographic to some degree, and the hydrographic even more so, incorporate large portions of the Mojave warm desert as well (Fig. 2A).

Many ecologists and conservation biologists rely on the concept of “ecoregions,” which have risen in popularity because of their attempt to incorporate a range of landscape, environmental, and biological features into regions that share a geographic (and possible evolutionary) coherence relative to surrounding regions. Although not exact, ecoregion boundaries, using the framework of Ricketts et al. (1999; Fig. 2A), approximate other definitions of the Great Basin as follows: combined Great Basin shrub-steppe and Snake River–Columbia Plateau shrub-steppe ecoregions, minus that portion of the latter north of the Blue Mountains of Oregon, approximate the floristic Great Basin; whereas the hydrographic Great Basin captures most of the Mojave Desert ecoregion to the south.

Given the several possible configurations of a Great Basin that could be used, we asked whether mammal distributional patterns could provide insight into the best operational delineation of a modern Great Basin mammal biota. We used the Smithsonian National Museum of Natural History North American Mammals online database (<http://www.mnh.si.edu/mna/>), which maps species to the ecoregions of Ricketts et al. (1999), to summarize mammal species distributions across 13

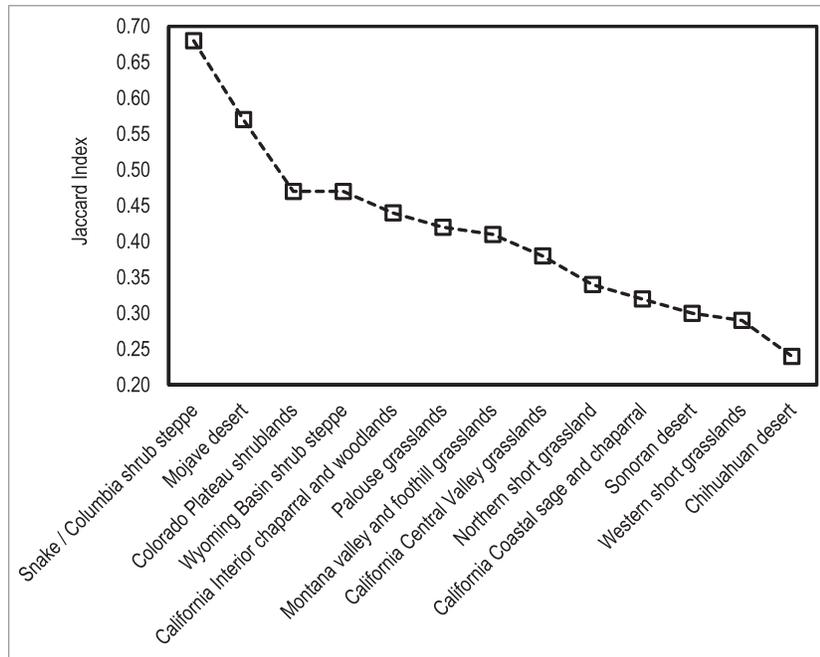


FIG. 3.—Plot of Jaccard similarity index values between the Great Basin shrub-steppe and 13 other primarily (but not exclusively—isolated or portions of mountain ranges could be embedded as well) arid or semiarid ecoregions in western North America. Species lists for each included small, nonvolant insectivores, lagomorphs, and rodents and originated from the Smithsonian National Museum of Natural History North American Mammals online database (available from the authors upon request).

western ecoregions composed primarily of arid and semiarid biomes (e.g., desert, shrub-steppe, grassland, chaparral, and woodland). We then calculated a Jaccard similarity index (Cheatham and Hazel 1969)—a commonly used index for biogeographic studies (Hagmeier and Stults 1964; Flessa 1981)—between the Great Basin shrub-steppe and each other ecoregion using only smaller-bodied, nonvolant species (insectivores, lagomorphs, and rodents; checklist used for each region available from the authors upon request), reasoning that the signature of ecoregion identity should be magnified after excluding the volant species, and large-bodied herbivores and carnivores with larger home ranges or seasonal migration, or both. Evident (Fig. 3) is the relatively high similarity between the Great Basin shrub-steppe and the Snake River–Columbia Plateau shrub-steppe ecoregion to the north (0.68), followed by an appreciable decline to the Mojave Desert ecoregion to the south (0.57), and then a more or less monotonic decrease ending with the Chihuahuan Desert ecoregion (0.24). We can further restrict our estimate of similarity between that portion of the Great Basin shrub-steppe and the Snake River–Columbia Plateau shrub-steppe ecoregions that is more equivalent to the traditionally defined floristic Great Basin (Fig. 2A) by excluding species that are either distributed only in the more northern Columbia Plateau portion of the latter ecoregion (2 species), or are very peripherally distributed (or included simply because of mapping errors) in either ecoregion (40 species). After doing so, the similarity index between the 2 ecoregions rises to 0.81, and all of these species occurring in the latter ecoregion also occur in the Great Basin ecoregion.

Therefore, for purposes of delineating a mammal biota that is most likely to uniquely define a Great Basin biota, we include Great Basin shrub-steppe and that portion of the Snake River–Columbia Plateau shrub-steppe south of the Blue Mountains in our concept of an operational Great Basin for addressing mammalian biotic assembly. In other words, we find that the mammalian biota that is delineated by the floristic Great Basin has a recognizable signature, and its assembly can be considered within the context of ecological and evolutionary processes both within its boundaries and between it and surrounding regions. After trimming species that are marginally distributed within these boundaries (many of these may actually have been listed within an ecoregion in the Smithsonian database in error as a consequence of coarse mapping procedure) as described in the above analysis, and excluding introduced species and those occurring only in that portion of the Snake River–Columbia Plateau shrub-steppe north of the Blue Mountains, our core Great Basin mammal species list includes 94 species (Appendix I).

ASSEMBLING THE MODERN GREAT BASIN MAMMAL BIOTA

The modern Great Basin mammal biota has been assembled over at least 10 North American Land Mammal Ages (NALMAs; Fig. 4) on a geologically dynamic and complex landscape (Badgley et al. 2014). Layered onto this history of geomorphological evolution is a turbulent climatic history, encompassing a general cooling trend since the mid-Miocene climatic optimum (17–14 million years ago [mya]—Zachos et

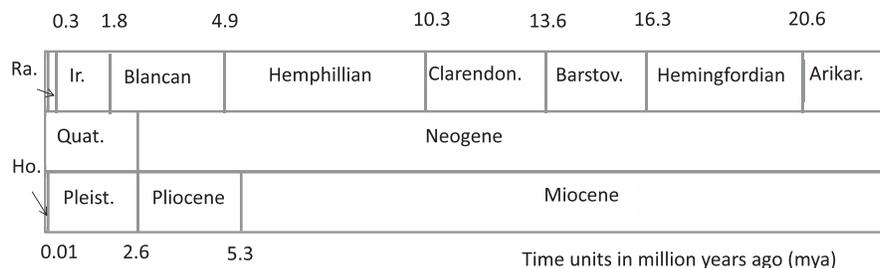


FIG. 4.—Comparison of 3 chronological systems used by North American paleontologists and geologists for the later portions of the Cenozoic Era (0–23 mya). Top: North American Land Mammal Ages (NALMAs; time intervals based on Alroy [2000]) system, used frequently throughout this paper. Middle: periods. Bottom: epochs. Arikar. = Arikareean; Barstov. = Barstovian; Ho. = Holocene; Ir. = Irvingtonian; Pleist. = Pleistocene; Quat. = Quaternary; Ra. = Rancholabrean.

al. 2001), and since the Pliocene, dominated by multiple glacial and interglacial oscillations that increased in magnitude during the last 1 my (Zachos et al. 2001).

The composition of the regional biota from which a local community is assembled (Graves and Rahbek 2005; Lessard et al. 2012) changes as species are added and subtracted by fundamental biogeographic and evolutionary processes such as speciation, adaptation, and range dynamics, which include cycles of range shifting, expansion, and contraction (extinction being an extreme product of range contraction). Insights into these processes can come from the fossil record (Badgley et al. 2014) and from reconstructing the geography of relationships between extant species and populations, most frequently using genetic data (Riddle et al. 2008; Marske et al. 2013).

Molecular data have allowed reconstruction of phylogenetic and regional population history, providing new insights into historical assembly of the Great Basin mammal biota in several ways. First, a number of cryptic lineages and species have been revealed (e.g., Hafner et al. 2008; Hafner and Upham 2011; Hornsby and Matocq 2012; Riddle et al. 2014), for example, in the heteromyid rodents (Alexander and Riddle 2005; Hafner et al. 2007), representing divergence events that had not been predicted based on morphology or older molecular approaches (e.g., allozymes and karyology). Cryptic lineages will not represent increases in the numbers of recognized species in the Great Basin unless formally recognized as separate species. However, regardless of taxonomy, they represent critical data for purposes of reconstructing biogeographic patterns and processes across Neogene and Quaternary time frames, including insight into the timing and geography of lineage divergence and speciation (e.g., high-resolution phylogenetic reconstructions). Second, divergence times can be estimated from molecular phylogenies. Although fossils can be used for general calibration of molecular phylogenies (e.g., Hafner et al. 2007; Riddle et al. 2014), we also can use molecular phylogenies to independently test the veracity of the fossil record's information about distributional and divergence histories. Third, detailed phylogeographic patterns have provided a basis for reconstructing range dynamics associated with Quaternary climatic oscillations.

In Appendix II, we summarize current molecular biogeographic knowledge for nonvolant small mammals into 4 categories. These include 3 categories of diversification: within the Great Basin; between the Great Basin and an adjacent region; and somewhere within the intermontane region if the role of the Great Basin cannot be inferred. The 4th category summarizes evidence of range dynamics (for the most part, but not exclusively, at an intraspecific scale) as range expansion, range contraction, range shift (a combination of expansion and contraction where overall range size has remained relatively constant, but has shifted location on the landscape), or simply range change if one of those categories cannot be inferred. In all cases, we place an event in the most likely NALMA, and directionality of sister lineage distribution or range change as north, south, east, or west if inferences can be drawn from the fossil record or molecular biogeographic reconstructions, or both.

Inspection of Appendix II reveals that molecular biogeographic information is far from complete for this assemblage. Nevertheless, what is available provides an opportunity to highlight patterns of diversification and range dynamics into several themes, largely within the context of 2 broadly defined habitat categories—the shrub-steppe and desert habitats that occupy the lower-elevation valleys, and the montane habitats of the higher-elevation mountain ranges. We recognize these delineations to be coarse and somewhat artificial, given that individual taxa might not adhere to them. Furthermore, the elevational distribution and discreteness of these habitat categories is true in a modern context only, because several mammals of broader glacial-age distributions are known to have extended into lower elevations (e.g., *Microtus montanus* [Mantooth and Riddle 2005]; *Ochotona princeps* [Grayson 2005]; and *Marmota flaviventris*, *Neotoma cinerea*, and *Thomomys talpoides* [Grayson 2011]). Nonetheless, we maintain this coarse habitat distinction to help organize the following discussion, which represents our current interpretation of some of the major processes (themes) that have influenced mammalian diversification and range dynamics in the Great Basin. Within each thematic area, we limit ourselves to discussion of only a handful of illustrative examples, and thus leave out much of the rich detail that is contained in the

studies included in Appendix II. We fully anticipate that ongoing and future work will lead to conceptual broadening of these themes as well as more thorough integration of the nascent ideas we present.

Theme 1: the role of the origins and early history of the Great Basin in diversification of extant mammal lineages.—Three rodent families—Muridae, Sciuridae, and Heteromyidae—have high diversity in the modern Great Basin (Appendix I), and all 3 families probably have occupied it continuously since at least 17 mya, along with several rodent families now either extinct or having lost most of their diversity (Badgley et al. 2014, see their figure 6). However, crown clades within Muridae that have high diversity within the modern Great Basin are not as old; neotomine–peromyscines, Hemphillian (Engel et al. 1998); and microtines, arrival in the Nearctic via Beringia in the Irvingtonian (Repenning 2001). Within the Sciuridae, the endemic lineage *Urocitellus mollis* + *U. canus* is Blancan (Harrison et al. 2003), and *U. elegans* is Irvingtonian (Harrison et al. 2003; Bell et al. 2010).

Conversely, the Heteromyidae has crown clades that originated during the geologically turbulent early Great Basin. The family Heteromyidae dates to at least the Orellan over 30 mya (Wahlert 1993), and contributes 11 named species in 4 genera to the modern Great Basin mammal biota. A molecular phylogenetic estimate (Hafner et al. 2007) places the common ancestor of the extant heteromyid lineages in the late Arikareean, whereas the common ancestor of extant species in each of the 2 modern subfamilies and 4 genera that are represented in the Great Basin today had early origins (Hafner et al. 2007): Perognathinae, Hemingfordian (including common ancestor of extant *Perognathus*, Hemingfordian; and *Chaetodipus*, Barstovian); and Dipodominae, Barstovian (including common ancestor of extant *Dipodomys*, Clarendonian; and *Microdipodops*, Hemphillian). Within *Perognathus*, the *P. parvus* species group and the *P. longimembris* species group currently occupy the Great Basin, and both probably originated within the Barstovian. Only 1 species within the genus *Chaetodipus*, the ecologically and morphologically unique *C. formosus*, is distributed widely within the modern Great Basin, and the origin of the lineage leading to this species is placed within a Clarendonian or Barstovian time frame (Hafner et al. 2007). The fossil record is silent on the geography and timing of divergence between *Chaetodipus* versus *Perognathus* because fossils of these genera have not been differentiated from one another (Wahlert 1993).

Thus, although the early development of the Great Basin could have played a role in the diversification history of one or more extant heteromyid subfamilies, genera, and species groups, its direct role in their origins is elusive because the oldest fossils generally lie on the perimeter or outside its borders, or are otherwise uninformative. Hemingfordian fossils attributed to *Perognathus* occur in central Wyoming and southern California (Carrasco et al. 2005), whereas putative earliest *Dipodomys* date to the Barstovian of southern California (Reeder 1956). The lineage leading to *Micro-*

dipodops is estimated from a molecular phylogeny to have diverged from a common ancestor with *Dipodomys* during the Barstovian (Hafner et al. 2007). However, with the oldest putative *Microdipodops* fossil being from Blancan-age deposits in far southern California (Carrasco et al. 2005; Jefferson and Lindsay 2006), the fossil record currently is not informative for reconstructing the geography of divergence of this genus.

Although molecular estimates are consistent with a role for the origins and early history of the Great Basin in diversification of several modern subfamilies, genera, and species groups, clearly, there is much room for paleontology to better inform the geography of diversification within this deeper time frame if and when new fossils are discovered from the Great Basin. A more complete synthesis here would seek to establish temporal, spatial, and paleoecological connections between the decline and extinction of formerly diverse rodent taxa (Badgley et al. 2014) and the origins of modern taxa within the context of geologically transforming landscapes.

Theme 2: assembling the modern Great Basin shrub-steppe and desert biota through in situ diversification and biome connections beyond its borders.—From the middle Neogene through the Pleistocene, connections with adjacent regions have provided 2 major sources of unique species or cryptic lineages to the shrub-steppe and desert biota of the Great Basin: origination of new species or lineages within the Great Basin, and persistence of others that once had a broader geographic distribution.

Pleistocene shrub-steppe connections beyond the Great Basin have been of considerable importance in both of these situations, resulting in several of the “iconic” Great Basin mammals. Among these, Great Basin fossils of the pygmy rabbit (genus *Brachylagus*), are not recorded in the FAUN-MAP database (Graham and Lundelius 2010) prior to the late Pleistocene, but Irvingtonian records are available from Porcupine Cave (Fig. 2B) deposits on the front range of the Colorado Rocky Mountains (Graham and Lundelius 2010) and Pit Stop Quarry (Fig. 2B) in east-central Arizona (Murray et al. 2005). Fossils document Rancholabrean presence to the south of its current distribution at the Tule Springs (Fig. 2B) site in the Las Vegas Valley of southern Nevada, and distributions beyond the Great Basin at the Kennewick Roadcut on the Columbia Plateau in Washington (a disjunct population of pygmy rabbits has remained until modern times north of this locality), and Isleta Cave in central New Mexico.

We can add to these records of a broader Pleistocene distribution the observation that the sagebrush vole (*Lemmyscus curtatus*) also had a distribution during the Rancholabrean beyond its current range, extending to the southeast in southern New Mexico (Big Manhole, Dry, Dark Canyon, and U-Bar caves), east to the Colorado–Kansas border (Jones-Miller assemblage), and south into southern California (Antelope and Kokoweef caves). Furthermore, the genus *Lemmyscus*, with at least 2 recognized species in the fossil record, shared with *Brachylagus* an Irvingtonian distribution in Porcupine Cave, and also occurred at San Antonio Mountain Cave on the New Mexico–Colorado border. Merriam’s shrew (*Sorex merriami*)

had a former distribution in southernmost New Mexico similar to that of *L. curtatus* (Big Manhole, Dry, Anthony, U-Bar, and NW Musko caves).

The fossil record for *Brachylagus*, *Lemmiscus*, and *S. merriami* allows us to postulate an expansive mosaic of shrub-steppe habitats to the east and southeast of the Great Basin, at least intermittently, throughout the Pleistocene. However, although presence of these species within the Great Basin itself prior to the late Pleistocene cannot yet be inferred directly, other shrub-steppe species occupied the Great Basin early enough for historical disjunctions to have produced divergent western lineages in the Great Basin and adjacent regions. The Utah prairie dog (*Cynomys parvidens*) is one of these that has been regarded as a separate species and is a member of the subgenus *Leucocrossuromys* that includes *C. leucurus* and *C. gunnisoni*. Fossils of this subgenus are present in the late Blancan (Goodwin 1995), consistent with a mitochondrial DNA (mtDNA) cytochrome-*b* (Harrison et al. 2003) estimate of a late Blancan or early Irvingtonian divergence of *C. parvidens* from the other 2 species. Other unique shrub-steppe lineages in and around the Great Basin include the northern grasshopper mouse (*Onychomys leucogaster*)—Riddle and Honeycutt (1990) demonstrated matrilineal divergence (nuclear patterns currently unknown) that differentiated a Great Basin + Columbia Plateau mtDNA clade in *O. leucogaster*. Similar to *O. leucogaster*, *Dipodomys ordii* contains a unique “Western” clade (J. E. Wilkinson, Oklahoma State University, pers. comm.), although in this case certain Colorado Plateau populations show affinity with the Great Basin and Columbia Plateau. Neither study provided robust estimates of times of divergence, but given provisional estimates of sequence divergence for *Onychomys* in Riddle (1995) and sequence divergence estimates among *D. ordii* clades provided by J. E. Wilkinson, Oklahoma State University (pers. comm.), isolating events appear to greatly predate the last glacial maximum (LGM). In light of evidence for divergence of unique western lineages in these widespread shrub-steppe species, we suggest that it would be interesting to examine the pervasiveness of this pattern with phylogeographic studies of other codistributed taxa including *S. merriami*, *Lepus townsendii*, *L. curtatus*, *Tamias minimus*, and *Urocitellus elegans*.

The distributions of a number of extant Great Basin shrub-steppe taxa extend northward onto the Columbia Plateau in Washington (that portion of the Snake River–Columbia Plateau shrub-steppe ecoregion north of the Blue Mountains in Oregon), and connections between these regions have occurred on several vastly different time frames. Some taxa have Rancholabrean fossil records on the northern Columbia Plateau (*Brachylagus idahoensis*, *L. curtatus*, *O. leucogaster*, *P. parvus*, *D. ordii*, and *Spermophilus* cf. *mollis* [given current distribution, formerly included in *S. townsendii*, the taxon used in MIOMAP and FAUNMAP]—Graham and Lundelius 2010). At least 2 of these taxa, *O. leucogaster* and *D. ordii*, do not appear to have diverged appreciably from Great Basin populations to the south (Riddle and Honeycutt 1990; J. E.

Wilkinson, Oklahoma State University, pers. comm.), from which we can infer a late Quaternary connection between populations north and south. In stark contrast, mtDNA and nuclear DNA (nuDNA) show a striking subdivision within the *P. parvus* species group (Riddle et al. 2014). Examination of these data shows a northern species distributed across the Columbia Plateau north of the Blue Mountains (but also extending into southwestern Idaho) with several deep and perhaps geographically structured mtDNA and nuDNA lineages embedded within it, suggesting a long history of persistence and widespread distribution on the Columbia Plateau. The southern species occurs throughout the Great Basin (and is undifferentiated from the white-eared pocket mouse [*Perognathus alticolus*] in southern California). Molecular divergence estimates place the split between the northern and southern species within the Hemphillian (Riddle et al. 2014).

Pleistocene connectivity with the southwestern warm deserts is evidenced in a number of taxa, but tends to not have produced a large number of unique Great Basin lineages, with a few notable exceptions. First, gene trees (Patton and Smith 1994; Smith 1998; Álvarez-Castañeda 2010) demonstrate that a central and northern Great Basin pocket gopher, *Thomomys townsendii*, renders *T. bottae* (a species more broadly distributed throughout the lower elevations of the Great Basin to the west, east, and south, and then throughout the warm deserts to the south) as paraphyletic, and along with evidence of localized hybridization, suggests a relatively recent history of divergence, perhaps near the Blancan–Irvingtonian boundary (Smith 1998).

Second, the 2 species of *Microdipodops* that inhabit the Great Basin diverged during the Hemphillian (Hafner et al. 2007, 2008; Hafner and Upham 2011). However, Hafner and Upham (2011) posit that kangaroo mice would have been unlikely to occupy the Great Basin prior to development of sand sheets and sand dunes in association with Pleistocene lakes. Alternatively, sand could have been accumulating in the Great Basin throughout the Neogene via mountain erosion and downslope transfer of sediments, providing an alternative model of landscape history that would accommodate an earlier occupation of the Great Basin by sand-obligate species. In either case, we note that a sand-obligate kangaroo rat, *Dipodomys deserti*, represents a deep, Clarendonian divergence event, and indeed the most basal divergence event within the radiation of extant species in that genus (Alexander and Riddle 2005; Hafner et al. 2007). In combination with *Microdipodops*, the predilection of *D. deserti* for sand suggests that it was among the ancestral habitats of the Dipodomysinae. Phylogeographic reconstructions of genetic diversity in *D. deserti* (see below) suggest long-term occupancy of deserts south of the Great Basin, but not subsequent divergence similar to that of *Microdipodops* within the Great Basin. Thus, from either the late Neogene or early Pleistocene (e.g., *Microdipodops*) into the later Pleistocene (as is indicated in current phylogeography of *D. deserti*, see below), there appears to have been a connectivity between sand habitats spanning from the southern

hot deserts into the Great Basin. One could postulate origins of several of these taxa in association with development of a combination of shallow marine, riverine, and lake deposits in the Lower Colorado region at the head of the Gulf of California (Bell et al. 2010).

Regardless of the equivocal nature of the deeper biogeographic history of *Microdipodops*, the geography of divergence within each species has a strong Great Basin imprint, and shares several attributes. Each is composed of geographically structured cryptic lineages—2 cryptic lineages in *M. pallidus*, and the 2 most inclusive cryptic lineages in *M. megacephalus* largely define western and eastern Great Basin distributions and are coincident with one another in estimated times of divergence (Blancan). Geographically structured cryptic lineages within each of the subclades in *M. megacephalus* suggest that Great Basin diversification continued into more recent times: the easternmost clade is further split into separate Central and Eastern subclades (Hafner et al. 2008; Hafner and Upham 2011; Light et al. 2013); whereas the westernmost clade is further divided into a widespread Western subclade and an apparently more geographically restricted subclade in southwestern Idaho.

Finally, connections to the western chaparral and grasslands are demonstrated by 2 species of kangaroo rat. The chisel-toothed kangaroo rat (*Dipodomys microps*) has phylogenetic affinities within a geographically discrete western clade of kangaroo rats (Alexander and Riddle 2005; Hafner et al. 2007). The best current estimate (Hafner et al. 2007) is a Hemphillian origination for the *D. microps* clade. Thus, although its membership in a Great Basin mammal biota likely predates any of the other 4 kangaroo rats currently represented in this assemblage, it still is perhaps a more recent member of this assemblage than either the genus *Microdipodops* or the *P. parvus* species group. Habitat dissimilarity between the Great Basin versus the chaparral and grassland habitats occupied by other species of kangaroo rats in the western clade suggest that ancestors of *D. microps* experienced a significant niche shift after entering the Great Basin. Indeed, Kenagy (1973) argued that several morphological (chisel-shaped lower incisors) and physiological features in *D. microps* are unique adaptations that allow it to consume and process plants in the genus *Atriplex*, currently widespread throughout the Great Basin (Kenagy 1973; Csuti 1979). *Dipodomys panamintinus* shares with *D. microps* affinities with the western clade of kangaroo rats (Alexander and Riddle 2005; Hafner et al. 2007), but in contrast appears to have shared an ancestor with *D. heermanni* within the Rancholabrean (Hafner et al. 2007) and therefore is likely to be a relatively recent inhabitant of the Great Basin, perhaps associated with a niche shift toward more arid habitats.

Theme 3: late Quaternary range dynamics in Great Basin shrub-steppe and desert species.—The size and positioning of the Great Basin ensures that it captures a suite of climatic influences that are dynamic not only on decadal and millennial scales, but also shift dramatically at glacial–interglacial scales. Phylogeographic studies have suggested that many Great Basin desert species, including mammals, appear to have responded

to climate change at these larger time scales through southward depression of their ranges during glacial stages followed by northward range expansions during interglacial stages. The most recent episode of retraction and expansion can in some cases essentially “erase” genetic evidence of prior dynamics; nonetheless, use of molecular data has been particularly powerful in recovering patterns of expansion.

Two species within the “floristic” Great Basin that exhibit clear patterns of range expansion are *Dipodomys deserti* and *D. merriami*. Codistributed populations of both species ranging from the northern Mojave Desert into northern portions of the Great Basin exhibit genetic signals consistent with very recent northern range expansions (T. Jezkova, University of Nevada Las Vegas, pers. comm.). Concordantly, fossil evidence, although limited, suggests that neither species was present in the northern Mojave Desert or farther north until after the LGM, because there are no known fossil records from these regions before approximately 10,100 radiocarbon years before present (approximately 12,000 calendar years before present—Hockett 2000). Both species likely persisted within the warmer southern Mojave and Sonoran deserts during the cold glacial period and expanded northward only after the LGM, following the warming climate and desiccation of pluvial lakes (Thompson and Mead 1982; Thompson 1990). It is possible, however, that similar range expansions happened repeatedly during previous interglacial periods, but that no fossil evidence has been found and any genetic evidence may have been lost through the most recent episode of contraction and expansion.

A genetic signal of a recent range expansion northward has been documented in other warm desert (Mojave and Sonoran) mammals, such as *Neotoma lepida* (Patton et al. 2007) and *Ammospermophilus leucurus* (Mantooth et al. 2013), as well as lizards (Jezkova 2010), snakes (Mulcahy 2008), and scorpions (Graham et al. 2013). At least several intraspecific clades in both *Microdipodops* species demonstrate a pattern of south-to-north haplotype sharing suggestive of range expansion and contraction dynamics, perhaps coincident with Pleistocene climate cycles. In *M. megacephalus*, a complex network of southernmost haplotypes in the central clade implies a southern Great Basin glacial-age refugium. Light et al. (2013) use additional population genetic analyses for the mtDNA data to both further support these reconstructions, and suggest locations of several other glacial-age refugia in each species.

Replicated signatures of range expansion from more southern warm deserts, when added to the evidence of range expansion within the “floristic” Great Basin in several clades of *Microdipodops* (Hafner et al. 2008; Hafner and Upham 2011; Light et al. 2013), suggest a grand reshuffling of the biotic assemblage across the Great Basin shrub-steppes and deserts within the past few thousands of years. Further, this strong signal of congruent response in many taxa not only predicts a similar pattern in codistributed species that have not yet been investigated, but suggests that this is a system with much to offer for understanding the mechanics of a biotic-level response to past changes in global climates. In particular, the Great Basin gives researchers a unique opportunity to explore

how the genetic architecture of ecological and physiological adaptations in codistributed, expanding species has influenced their potential for adaptation and resistance to extinction.

In stark contrast to the phylogeographic evidence in multiple species of northward post-LGM range expansion from more stable (often more southerly) glacial-age refugia, the phylogeographic structure of *D. microps* reveals that much of its range has been relatively stable throughout the Great Basin during the climatic oscillations of the late Pleistocene (Jezkova et al. 2011). This is quite surprising because the low-elevation communities currently represented by the dominant shrub *Atriplex*, also prime forage for *D. microps*, were not established (or reestablished—the *Neotoma* middens that provide most late Pleistocene paleoecological records in the arid west are limited to the latest glacial–interglacial cycle and so any of these patterns could have been replicated through earlier cycles) throughout the Great Basin until the end of the Pleistocene or even the beginning of the Holocene (Spaulding 1990; Thompson 1990). Jezkova et al. (2011) speculated that *D. microps* likely was utilizing a habitat that differed from *Atriplex*-dominated communities during colder periods, raising the prospect of a niche shift from the LGM to the present that would have allowed for the in situ persistence of this species throughout the Great Basin across profound climatic changes.

Theme 4: connections to the north and across the Great Basin “sky islands.”—As in the desert and shrub-steppe species, the earliest known fossils from Great Basin montane species are from other regions. The oldest fossils of *N. cinerea* and *O. princeps* are from Irvingtonian deposits of Porcupine Cave in Colorado, and *N. cinerea* is additionally found in Irvingtonian deposits of the San Antonio Mountain Cave in New Mexico (Graham and Lundelius 2010). No specimens of *M. flaviventris* have been identified from Irvingtonian deposits; however, a lack of specimens in the paleorecord is poor evidence for absence. Particularly in the Great Basin, only 2 deposits date to the Irvingtonian (Froman Ferry and Glenss Ferry in southern Idaho, and Adrian Valley in western Nevada; Fig. 2B), leaving us few opportunities to identify when these species may have moved into this region. By the Rancholabrean, all 3 of these species are found frequently in deposits across the Great Basin, including Deer Creek Cave in northeastern Nevada, Crystal Ball Cave in western Utah, and Wilson Butte Cave in southern Idaho (Graham and Lundelius 2010; Fig. 2B). During the Rancholabrean, these species also are found in deposits such as Kokoweef Cave and Mescal Cave in what is now the Mojave Desert (Graham and Lundelius 2010). Such records are outside the current geographic and elevational ranges of these species, indicating that they have contracted their ranges northward and upward since the Irvingtonian and concurrent Pleistocene glacial epoch. In combination with the shrub-steppe and desert species, the record for montane species indicates that the mammalian biota found in the Great Basin today may have assembled by the late Pleistocene, although attributes such as species abundances and composition of local assemblages (e.g., communities) have

continued to fluctuate over time (e.g., Grayson 2006; Terry et al. 2011).

In contrast to the shrub-steppe and desert species, the montane species currently inhabit highly discontinuous “sky islands” across the Great Basin, surrounded by a matrix of uninhabitable shrub-steppe and desert habitats. Our understanding of the assembly of this mammalian community is largely a question of how the montane species came to occupy and persist on these isolated mountain ranges. Students of Great Basin history are familiar with Jim Brown’s (1971) attempt to explain the distribution of mammals on Great Basin ranges using dispersal-based island biogeographic theory. He ultimately rejected this explanation in favor of a vicariant-based hypothesis wherein downslope movement of montane habitats allowed dispersal during Pleistocene glacial intervals, whereas upslope retraction fragmented populations during interglacials and prompted local extirpations. Under this paradigm, population extirpation was considered the major process shaping composition of small montane mammal communities, in comparison to more volant groups such as birds and winged insects (Wilcox et al. 1986; Cutler 1991). This conclusion has been largely discounted because increased sampling has uncovered substantially different patterns (Grayson and Livingston 1993; Lawlor 1998; Rickart 2001; Grayson 2011), and because molecular evidence suggests that dispersal even through the Holocene has been an important process for species such as *N. cinerea* (Grayson and Madsen 2000) and *M. flaviventris* (Floyd et al. 2005). If Brown’s thesis holds for any of the Great Basin montane mammals, it is for the comparatively sedentary and temperature-sensitive *O. princeps*. This species likely colonized many of the Great Basin ranges during the most recent Wisconsin glaciation (Grayson 2011) and then experienced widespread local extirpations continuing through the Holocene (Beever et al. 2003; Grayson 2005). Demonstrating why it has become a species of concern, *O. princeps* remains a member of the mammalian fauna in a decreasing number of Great Basin montane ecosystems.

Phylogenetic and population genetic patterns offer more evidence that the histories of montane species in the Great Basin have been dynamic. Genetic diversity in Great Basin *M. flaviventris* adheres to an isolation-by-distance model, suggesting that rather than evolving along independent trajectories on isolated mountain ranges, continued dispersal has maintained connectivity between populations throughout the region (Floyd et al. 2005). Likewise, *N. cinerea* shows low interpopulation genetic divergence across the Great Basin (Mewaldt and Jenkins 1986), and all Great Basin specimens belong to the same relatively shallow mtDNA clade, which diverged from other western *N. cinerea* clades by 0.8 mya (Hornsby and Matocq 2012). This Great Basin clade shows a strong signature of demographic expansion and may have largely replaced another clade that is now restricted to a disjunct distribution between the central Sierra Nevada and the northwest.

In contrast to *M. flaviventris* and *N. cinerea*, whose genetic homogeneity across the Great Basin suggests ongoing

population connectivity with recent demographic expansion, or both, *O. princeps* shows a deep genetic division across the region. This decreased connectivity may be a function of generally lower vagility, as well as increased isolation between the highest elevation habitats where *O. princeps* is found (Rickart 2001). Most *O. princeps* in the Great Basin belong to an mtDNA clade spanning across the Sierra Nevada, whereas northeast populations belong to a different clade spanning the northern Rocky Mountains (Galbreath et al. 2009). Because these clades coalesce individually by 0.2–0.9 mya (Galbreath 2009), they evidently diverged from each other by 1 mya or earlier during the Irvingtonian. Tests of demographic expansion show that both clades have undergone demographic contraction from the Pleistocene–Holocene transition through today (Galbreath et al. 2009). Data from allozymes (Hafner and Sullivan 1995) and nuDNA echo this split in mtDNA; however, although the northern Rocky Mountain clade has exchanged alleles with other clades—likely during glacial periods as Brown (1971) envisioned—the Sierra Nevada clade appears to have remained genetically isolated (Galbreath et al. 2010). This clade also lacks geographic structuring of nuDNA variation, suggesting that although alleles have not been exchanged with neighboring clades, the populations within the Sierra Nevada clade have intermixed broadly, at least until recently.

SYNTHESIS AND FUTURE DIRECTIONS

We have attempted to illustrate several of the emergent themes that underlie the historical assembly of the Great Basin mammal biota, highlighting information provided by a nascent molecular biogeographic framework (Appendix II), in combination with available evidence from paleontology. A grand emergent theme is that the Great Basin represents not only a region in which new mammal lineages originate (although not clear at this point just how many did so early in its inception), but perhaps more importantly, one that has been positioned at the crossroads of shifting species distributions and connections extending well beyond the Great Basin. A particularly interesting attribute of this region is the degree to which the waxing and waning of distributions are stratified across not only strong latitudinal but also elevational gradients such that, at least in a more recent (Rancholabrean to present) time frame, the region integrates an intriguing mix of species from biomes as extreme as northern montane forests and southern warm deserts. The long history of assembly of species includes taxa with long (Neogene through Pleistocene) histories of divergence in the vicinity of and perhaps within the Great Basin, but often without explicit evidence for their origins within its boundaries; accumulation of new and persistence of older taxa that appear to be associated with a geographically more expansive shrub-steppe biome to the east and south during portions of the Pleistocene; and extensive reshuffling of taxa, both old and recent, and across the suite of shrub-steppe, desert, and montane biomes, since the LGM that has relatively

abruptly redefined the assemblages that characterize the Great Basin.

More powerful molecular biogeographic reconstructions will become possible along several fronts. First, advances in molecular techniques are continually allowing more complex data sets and questions. Studies should aim to incorporate newer multigene and next-generation sequencing approaches for more complete genome sampling, which will benefit all downstream applications such as divergence dating and demographic modeling, and also can be useful to identify signatures of neutral and adaptive evolution. Likewise, the increasing sophistication of coalescent modeling (e.g., approximate Bayesian computation—Cilléry et al. 2010) and the explicit hypothesis-testing frameworks being developed will profoundly increase our capacity to compare and contrast historical scenarios in statistically rigorous ways (e.g., Leaché et al. 2007). Approaches such as Bayesian phylogeography (Lemey et al. 2009) may provide the opportunity to estimate not only divergence dates between taxa but also the geographic locations of common ancestors (internal nodes).

Second, advances in our understanding of geological history (Badgley et al. 2014) and paleoclimate (see excellent review in Grayson 2011) will allow for increasingly sophisticated inferences and analyses. On their own, these reconstructions help us better understand the basic environmental conditions associated with taxonomic divergence and geographical range dynamics. When coupled with species distribution models (also known as ecological niche models) and genetic patterns, we can estimate habitat suitability through time for groups at various taxonomic levels, as well as begin to test whether the abiotic niches of these groups differ significantly (Warren et al. 2010; Jezkova et al. 2011). Species distribution models and genetic patterns also can be analyzed in a landscape genetic framework, using spatially explicit models to investigate population structure, demography, and dispersal (e.g., Knowles and Alvarado-Serrano 2010; Brown and Knowles 2012).

Third, molecular data and species distribution models may be coupled, when possible, with the paleorecord in various ways. At its simplest, the paleorecord allows us to validate inferences of distributional shifts by comparing historically projected species distribution models to fossil and subfossil occurrence patterns from the same time periods (Waltari and Guralnick 2009; McGuire and Davis 2013). If the paleorecord is sufficiently complete, it also could be used to model abiotic niches at different points in time to determine if niche parameters have changed. Further, the frequency of taxa through time could show demographic trends, as could genetic data (ancient DNA) if it is available from different time periods for comparison. Lastly, other approaches such as stable isotope evidence of dietary shifts (Kimura et al. 2013) and analysis of phenotypic change (Barnosky and Bell 2003; Smith and Betancourt 2006; Blois et al. 2008) could complement and help increase the explanatory power of results from molecular- and species distribution models-based studies. Given these exciting potential avenues of research, it is worth remembering that the value of very basic paleobiological data cannot be overem-

phasized; new contributions to our knowledge of Great Basin history through the analysis of fossil and midden deposits, even in simple taxonomic identification and radiometric or stratigraphic dating, are fundamental if we ever hope to have direct evidence of the patterns and processes that we attempt to model by other means.

Finally, reconstructions from many Great Basin taxa need to be considered collectively in order to gain insight into the relative roles of biotic (ecological, physiological, etc.) and abiotic factors contributing to divergence and range dynamics. This will especially include determining the magnitudes and tempos of response to change, and whether these responses are idiosyncratic or occur in ways common to many mammalian taxa. More targeted questions regarding community-level species assembly might find novel insight from such comparative studies. For example, the genus *Dipodomys* currently is represented by 5 species in the Great Basin, and from synopses discussed above, and consistent with the available fossil record (Hockett 2000), this complete assemblage appears to have likely not been established until the early Holocene, because these species originated in different regions and invaded the Great Basin during different times.

One of the most pointed results of this review of Great Basin mammal biogeography is the recognition of how very much is still unknown, from our lack of basic phylogenies for many taxa through the complexities of understanding how and when groups have evolved, shifted, and interacted with other mammals and with the environment at large. In our view, the Great Basin has remarkable potential as a region in which many kinds of information can be integrated into questions regarding drivers of assembly and disassembly of a biota across space and through time. Addressing these kinds of questions will most certainly expand on the foundational insights of E. Raymond Hall, his students, and a large cadre of 20th century mammalogists.

ACKNOWLEDGMENTS

We thank the American Society of Mammalogists for supporting the symposium that led to this contribution. We also thank members of the Matocq and Feldman laboratories for their insightful comments on a previous draft.

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Special Feature Editor was Eric Rickart.

APPENDIX I

Checklist of 94 core Great Basin mammals, composed of species distributed throughout the Great Basin shrub-steppe and the southern (south of the Blue Mountains) portion of the Snake River–Columbia Plateau shrub-steppe ecoregions. Species from the original checklists (Smithsonian National Museum of Natural History North American Mammals online database: <http://www.mnh.si.edu/mna/>) that were considered peripherally distributed in these ecoregions or included erroneously because of the coarseness of the original mapping work were removed from this list. Species in boldface type were not considered in detail in searches for available molecular biogeographic or fossil evidence, or both, of diversification or range dynamics (Appendix II).

Species	Species	Species	Species
<i>Sorex merriami</i>	<i>Brachylagus idahoensis</i>	<i>Perognathus longimembris</i>	<i>Lemmiscus curtatus</i>
<i>Sorex monticola</i>	<i>Sylvilagus audubonii</i>	<i>Perognathus parvus</i>	<i>Ondatra zibethicus</i>
<i>Sorex palustris</i>	<i>Sylvilagus nuttallii</i>	<i>Chaetodipus formosus</i>	<i>Zapus princeps</i>
<i>Sorex preblei</i>	<i>Lepus californicus</i>	<i>Microdipodops megacephalus</i>	<i>Erethizon dorsatum</i>
<i>Sorex tenellus</i>	<i>Lepus townsendii</i>	<i>Microdipodops pallidus</i>	<i>Canis latrans</i>
<i>Sorex vagrans</i>	<i>Tamias amoenus</i>	<i>Dipodomys deserti</i>	<i>Vulpes macrotis</i>
<i>Notiosorex crawfordi</i>	<i>Tamias dorsalis</i>	<i>Dipodomys merriami</i>	<i>Vulpes vulpes</i>
<i>Myotis californicus</i>	<i>Tamias minimus</i>	<i>Dipodomys microps</i>	<i>Urocyon cinereoargenteus</i>
<i>Myotis ciliolabrum</i>	<i>Tamias panamintinus</i>	<i>Dipodomys ordii</i>	<i>Ursus americanus</i>
<i>Myotis evotis</i>	<i>Tamias umbrinus</i>	<i>Dipodomys panamintinus</i>	<i>Bassariscus astutus</i>
<i>Myotis lucifugus</i>	<i>Marmota flaviventris</i>	<i>Castor canadensis</i>	<i>Procyon lotor</i>
<i>Myotis thysanodes</i>	<i>Ammospermophilus leucurus</i>	<i>Reithrodontomys megalotis</i>	<i>Mustela erminea</i>
<i>Myotis volans</i>	<i>Cynomys parvidens</i>	<i>Peromyscus boylii</i>	<i>Mustela frenata</i>
<i>Myotis yumanensis</i>	[<i>Uroditellus</i>] <i>Spermophilus beldingi</i>	<i>Peromyscus crinitus</i>	<i>Taxidea taxus</i>
<i>Lasiurus blossevillii</i>	[<i>Uroditellus</i>] <i>Spermophilus canus</i>	<i>Peromyscus eremicus</i>	<i>Lontra canadensis</i>
<i>Lasiurus cinereus</i>	[<i>Uroditellus</i>] <i>Spermophilus mollis</i>	<i>Peromyscus maniculatus</i>	<i>Spilogale gracilis</i>
<i>Lasionycteris noctivagans</i>	[<i>Uroditellus</i>] <i>Spermophilus elegans</i>	<i>Peromyscus truei</i>	<i>Mephitis mephitis</i>
<i>Pipistrellus hesperus</i>	[<i>Callospermophilus</i>] <i>Spermophilus lateralis</i>	<i>Onychomys leucogaster</i>	<i>Puma concolor</i>
<i>Eptesicus fuscus</i>	[<i>Otospermophilus</i>] <i>Spermophilus variegatus</i>	<i>Onychomys torridus</i>	<i>Lynx rufus</i>
<i>Corynorhinus townsendii</i>	<i>Thomomys bottae</i>	<i>Neotoma cinerea</i>	<i>Cervus elaphus [canadensis]</i>
<i>Antrozous pallidus</i>	<i>Thomomys talpoides</i>	<i>Neotoma lepida</i>	<i>Odocoileus hemionus</i>
<i>Euderma maculatum</i>	<i>Thomomys townsendii</i>	<i>Phenacomys intermedius</i>	<i>Antilocapra americana</i>
<i>Tadarida brasiliensis</i>		<i>Microtus longicaudus</i>	<i>Ovis canadensis</i>
<i>Nyctinomops macrotis</i>		<i>Microtus montanus</i>	
<i>Ochotona princeps</i>			

APPENDIX II

Summary of diversification and range dynamics events gleaned from the literature leading to the assembly of the modern Great Basin core small, nonvolant mammals (insectivores, lagomorphs, rodents, and 2 carnivores; see Appendix I for complete list). Searches concentrated on molecular biogeographic literature, but relevant, although not exhaustive, fossil information is included as well. When a time frame for an event has been estimated, it is reported here in a North American Land Mammal Age (NALMA) context (see Fig. 4). mtDNA = mitochondrial DNA; nuDNA = nuclear DNA.

Great Basin taxon	Diversification within Great Basin (NALMA specified if possible)	Intermontane diversification—specific role of Great Basin unknown (NALMA specified if possible)	Diversification between Great Basin and adjacent region (NALMA specified if possible)
<i>Notiosorex crawfordi</i>		Hemphillian. mtDNA and nuDNA divergence among southern deserts.	
<i>Sorex merriami</i>		mtDNA evidence of coastal–inland divergence.	
<i>Sorex monticolus</i>			
<i>Sorex palustris</i>			
<i>Sorex preblei</i>		1. Irvingtonian. Split between Sierra Nevada clade in south/west/north and Northern Rocky Mountain clade in the northeast of the Great Basin.	
<i>Sorex tenellus</i>			
<i>Sorex vagrans</i>			
<i>Ochotona princeps</i>			
<i>Brachylagus</i> versus <i>Sylvilagus</i>		Hemphillian. Possible sister relationship between <i>Brachylagus</i> and <i>Sylvilagus</i> .	
<i>Sylvilagus audubonii</i> versus <i>Sylvilagus nuttallii</i>		Irvingtonian/Blancan. Sister relationship between these 2 species.	
<i>Brachylagus idahoensis</i>			
<i>Sylvilagus audubonii</i>		Divergence south of Great Basin.	
<i>Sylvilagus nuttallii</i>			
<i>Lepus californicus</i>			
<i>Lepus townsendii</i>		1. Divergence north of Great Basin.	
<i>Tamias amoenus</i>		Intraspecific diversification into multiple geographically restricted clades, with 1 Great Basin clade in southeast Idaho–Raft River Mountains and north to Bighorn Mountains; timing unclear.	
<i>Tamias dorsalis</i>			
<i>Tamias minimus</i>			
<i>Tamias panamintinus</i>			
<i>Tamias umbrinus</i>			
<i>Marmota flaviventris</i>			
<i>Ammospermophilus leucurus</i>		Hemphillian/Blancan. Split of <i>Ammospermophilus leucurus</i> + <i>A. harrisii</i> lineage from <i>A. nelsoni</i> , distributed west of Great Basin.	
<i>Cynomys parvidens</i>			Irvingtonian. Split from <i>Cynomys gunnisoni</i> + <i>C. leucurus</i> , both distributed east of Great Basin.
<i>Urocyon beldingi</i>			Blancan. Split from <i>Urocyon armatus</i> , distributed east of Great Basin.

APPENDIX II.—Extended.

Range dynamics (range expansion, range contraction, range shift, or simply range change if not clear) within Great Basin or between Great Basin and adjacent region (E, W, S, N and NALMA of fossil occurrences specified if possible)	Additional explanation	Citation(s)
	Mojave/Great Basin samples not included in the study. First occurrence of <i>Notiosorex</i> in the fossil record (6–7 mya) coincides with the genetic data.	McAliley et al. 2007; Carraway 2010
Rancholabrean. Distributed to southeast of Great Basin. Demographic expansion in coastal and northern clades but not southern clade (including Great Basin).	Fossil data. Authors elected to not provide estimates of divergence times between major clades.	Graham and Lundelius 2010 Demboski and Cook 2001; Lessa et al. 2003
Rancholabrean. Fossil evidence of range shift to north and west.	mtDNA evidence of demographic expansion in Pacific Northwest clades but not Great Basin.	Himes and Kenagy 2010
	mtDNA shows no evidence of demographic expansion. Data not available	Hope et al. (2012)
	Data not available	
2. Rancholabrean. Demographic stability or contraction; nuDNA gene flow among geographically structured mtDNA lineages.	1. Evidence from mtDNA and nuDNA. 2. mtDNA and nuDNA indicate demographic stability and possibly contraction. Coalescent simulations used to address timing of gene flow.	Hafner and Sullivan 1995; Galbreath et al. 2009, 2010
	mtDNA and nuDNA evidence shows putative relationship, albeit weakly.	Halanych and Robinson 1997; Matthee et al. 2004; Robinson and Matthee 2005
	mtDNA and nuDNA evidence shows relationship.	Halanych and Robinson 1997; Matthee et al. 2004; Robinson and Matthee 2005
1. Irvingtonian. Distributed to east of Great Basin. 2. Rancholabrean. Decline in abundance and range contraction/fragmentation.	1. Fossils document occurrence at Porcupine Cave, Colorado, and Pit Stop Quarry, Arizona.	Graham and Lundelius 2010; Grayson 2006
	Data not available	
	Data not available	
	Split from <i>Lepus alleni</i> (mtDNA evidence); timing unspecified.	Halanych et al. 1999
2. Rancholabrean/Holocene. Range contraction at the end of Pleistocene.	1. Split from arctic hares (mtDNA evidence); timing unspecified. 2. Ecological niche models suggest more extensive distribution during the last glacial period	Halanych et al. 1999; Waltari and Guralnick 2009
Demographic expansion in Sierra Nevada and southern Cascades clade.	mtDNA evidence; possible coastal–inland divergence.	Demboski and Sullivan 2003
	Data not available	
2. Irvingtonian/Rancholabrean. Expansions into new areas during glacials (e.g., replacement of <i>Marmota monax</i> at Porcupine Cave). 3. Rancholabrean. Range contraction/fragmentation and decline in abundance after the last glacial maximum. 4. Rancholabrean/Holocene. Isolation-by-distance structure supports ongoing dispersal among Great Basin mountains.	1. Fossil and mtDNA data. 2. Fossil data. 3. Fossil data. 4. nuDNA data.	Steppan et al. 1999; Polly 2003; Floyd et al. 2005; Grayson 2006
Rancholabrean/Holocene. Likely range expansion from south to north after last glacial maximum.	mtDNA data show demographic expansion in northern clade, inferred as range expansion although with few Great Basin samples.	Whorley et al. 2004; Mantooth et al. 2013
	mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004
	mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004

APPENDIX II.—Continued.

Great Basin taxon	Diversification within Great Basin (NALMA specified if possible)	Intermontane diversification—specific role of Great Basin unknown (NALMA specified if possible)	Diversification between Great Basin and adjacent region (NALMA specified if possible)
<i>Urocitellus canus</i> <i>Urocitellus mollis</i>			Irvingtonian. Split from <i>Urocitellus townsendii</i> , distributed north of Great Basin.
<i>Urocitellus elegans</i>			Irvingtonian. Split from <i>Urocitellus richardsoni</i> and <i>U. parryi</i> , distributed east and north of Great Basin.
<i>Callospermophilus lateralis</i>			Blancan/Hemphillian. Split from <i>Callospermophilus saturatus</i> (to the north), then <i>C. madrensis</i> (to the south).
<i>Otospermophilus variegatus</i>			Blancan. Split from <i>Otospermophilus beecheyi</i> , distributed west of Great Basin.
<i>Thomomys bottae</i> + <i>Thomomys townsendii</i>	1. Blancan/Irvingtonian. Putative timing of split between separate populations of <i>Thomomys bottae</i> and adjacent ancestral populations of <i>T. townsendii</i> .	2. Great Basin occupied by widespread intermontane and western lineage.	
<i>Thomomys talpoides</i> <i>Perognathus longimembris</i>			1. Barstovian/Clarendonian. Split from the <i>Perognathus flavus</i> / <i>P. merriami</i> group, distributed east of Great Basin. 2. Hemphillian/Blancan. Diversification of the <i>P. longimembris</i> species group into <i>P. inornatus</i> (coastal), <i>P. longimembris</i> (west of Colorado river), and <i>P. amplus</i> (east of Colorado River).
<i>Perognathus parvus</i> species group		Barstovian/Hemingfordian. Some evidence of common ancestry with <i>Perognathus flavescens</i> species group but not well supported	
<i>Perognathus parvus</i> versus <i>Perognathus mollipilosus</i>			Hemphillian. Broadly, Great Basin–Columbia Plateau divergence, but precise geographic boundaries not yet known.
<i>Perognathus parvus</i> versus <i>Perognathus alticolus</i> <i>Chaetodipus formosus</i>		Barstovian/Clarendonian. Split from either <i>Chaetodipus hispidus</i> clade, distributed east of Great Basin, or <i>C. baileyi</i> clade, distributed south of Great Basin.	
<i>Microdipodops</i> versus <i>Dipodomys</i> <i>Microdipodops megacephalus</i> versus <i>Microdipodops pallidus</i>		Barstovian. Split from common ancestor with <i>Dipodomys</i> . Hemphillian.	
<i>Microdipodops megacephalus</i> lineages <i>Microdipodops pallidus</i> lineages	1. Blancan. Divergence of 4 clades in east, central, west, north Great Basin. 1. Blancan. Divergence of 2 clades in east versus west Great Basin.		
<i>Dipodomys deserti</i>		Clarendonian. Basal split from all other extant <i>Dipodomys</i> species.	

APPENDIX II.—Continued. Extended.

Range dynamics (range expansion, range contraction, range shift, or simply range change if not clear) within Great Basin or between Great Basin and adjacent region (E, W, S, N and NALMA of fossil occurrences specified if possible)	Additional explanation	Citation(s)
	Data not available mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004
	mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004
	mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004
	mtDNA evidence.	Harrison et al. 2003; Herron et al. 2004
	1. mtDNA and nuDNA evidence. 2. mtDNA evidence.	Patton and Smith 1994; Smith 1998; Álvarez-Castañeda 2010
	Data not available 1. mtDNA evidence. 2. mtDNA evidence.	Hafner et al. 2007; McKnight 2005
	mtDNA evidence.	Hafner et al. 2007
	mtDNA, nuDNA evidence.	Riddle et al. 2014
Rancholabrean. Data do not differentiate 1 of the 2 recently extant populations of <i>Perognathus alticolus</i> from <i>P. mollipilosus</i> .	mtDNA, nuDNA evidence.	Riddle et al. 2014
	mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007
	mtDNA evidence. Earliest <i>Microdipodops</i> fossil Blancan in S. California mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007 Hafner et al. 2007
2. Rancholabrean. Within Great Basin range contraction/expansion in at least 1 clade.	mtDNA evidence.	Hafner and Upham 2011; Light et al. 2013
2. Rancholabrean. Within Great Basin range contraction/expansion evident in each clade.	mtDNA evidence.	Hafner et al. 2008; Light et al. 2013
	mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007

APPENDIX II.—Continued.

Great Basin taxon	Diversification within Great Basin (NALMA specified if possible)	Intermontane diversification—specific role of Great Basin unknown (NALMA specified if possible)	Diversification between Great Basin and adjacent region (NALMA specified if possible)
<i>Dipodomys merriami</i>			1. Hemphillian/Blancan. Split from <i>Dipodomys phillipsi</i> , distributed south of Great Basin. 2. Blancan/Irvingtonian. Split from <i>D. nitratoides</i> , distributed west of Great Basin.
<i>Dipodomys microps</i>	2. Irvingtonian/Rancholabrean. Irvingtonian diversification within the Great Basin in the absence of significant range shifts.		1. Hemphillian. Split from the coastal (western) <i>Dipodomys</i> .
<i>Dipodomys ordii</i>		1. Hemphillian. Split from <i>Dipodomys compactus</i> , distributed east of Great Basin.	2. Irvingtonian/Rancholabrean. Intraspecific divergence of western versus eastern lineages.
<i>Dipodomys panamintinus</i>		Irvingtonian. Pleistocene split from <i>Dipodomys heermanni</i> .	
<i>Reithrodontomys megalotis</i>			
<i>Peromyscus boylii</i>			
<i>Peromyscus crinitus</i>			
<i>Peromyscus eremicus</i>			
<i>Peromyscus maniculatus</i>			
<i>Peromyscus truei</i>			
<i>Onychomys leucogaster</i>			1. Blancan/Irvingtonian. Divergence between intermontane and eastern populations.
<i>Onychomys torridus</i>			1. Irvingtonian. Split of intermountain lineage covering Great Basin by about 0.8 mya from lineages to north and east.
<i>Neotoma cinerea</i>			1. Hemphillian. Divergence of intermountain from lineage to south. Irvingtonian. Divergence of intermountain from lineage to east.
<i>Neotoma lepida</i>			
<i>Phenacomys intermedius</i>			
<i>Microtus longicaudus</i>			
<i>Microtus montanus</i>			
<i>Lemmiscus curtatus</i>			
<i>Ondatra zibethicus</i>			
<i>Zapus princeps</i>			Divergence of intermontane lineage from lineages in East and North, and deep divergence from lineages in West.
<i>Erethizon dorsatum</i>			
<i>Mustela erminea</i>			
<i>Mustela frenata</i>			Divergence between “deserts” lineage covering Great Basin and other deserts, and lineage spanning remainder of western North America.

APPENDIX II.—Continued. Extended.

Range dynamics (range expansion, range contraction, range shift, or simply range change if not clear) within Great Basin or between Great Basin and adjacent region (E, W, S, N and NALMA of fossil occurrences specified if possible)	Additional explanation	Citation(s)
	1. mtDNA evidence. 2. mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007
	1. mtDNA evidence. 2. mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007; Jezkova et al. 2011
	1. mtDNA evidence. 2. mtDNA, nuDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007
	mtDNA evidence.	Alexander and Riddle 2005; Hafner et al. 2007
	Data not available	
	Data not available	
	Data not available	
	Origin outside Great Basin; no Great Basin data available.	Riddle et al. 2000
Holocene. Postglacial expansion.	Origin outside Great Basin. Postglacial expansion within “Rocky Mountain clade” that occupies Great Basin.	Dragoo et al. 2006
	Data not available	
2. Rancholabrean. Shrub-steppe extension into eastern Mojave Desert.	1. mtDNA evidence, timing very provisional. 2. Fossil evidence.	Riddle and Honeycutt 1990; Riddle 1995; Graham and Lundelius 2010
	Data not available	
2. Demographic expansion in intermountain lineage.	1. mtDNA evidence. 2. mtDNA evidence.	Hornsby and Matocq 2012
2. Demographic expansion in intermountain lineage.	1. mtDNA evidence. 2. mtDNA evidence.	Patton et al. 2007
Rancholabrean/Holocene. Several fossil localities in Great Basin, but no longer extant there.	Fossil data.	Graham and Lundelius 2010
	All 3 major mtDNA clades (Northwest, Central, Southern Rockies) found in or near Great Basin, but Great Basin not sampled well.	Conroy and Cook 2000; Speath et al. 2009
	Data not available	
Irvingtonian/Rancholabrean. Distributed to east and southeast of Great Basin.	Fossil data.	Graham and Lundelius 2010
	Data not available	
	mtDNA evidence. Great Basin populations not well sampled.	Malaney et al. 2013
	Data not available	
	Data not available	
	mtDNA evidence.	Harding and Dragoo 2012