

The molecular phylogeographic bridge between deep and shallow history in continental biotas

Brett R. Riddle

In 1988, Cracraft¹ argued that new approaches would be required to unravel the complex history of evolving continental biotas. The pattern he perceived was one of 'cycles of vicariance of widespread species, followed by narrow endemism, followed by population dispersion of descendant species to produce more widespread forms, followed by new cycles of vicariance'. Thus, an area of endemism could include an array of taxa, each one reflecting a different episode of isolation and divergence. In fact, geotectonic and paleoclimatic records reveal a series of episodic landscape transformations throughout the past tens of millions of years coincident with changes in taxic and ecological diversity² (Fig. 1). Layered onto these deep events are the much more recent Pleistocene glacial–interglacial cycles, beginning about 2.5 million years ago, and switching from a dominant 41 000-year frequency to a 100 000-year frequency about 700 000 years ago⁹ (Fig. 1).

Efforts to understand the historical development of current patterns of distribution and diversity in continental biotas have placed great emphasis on events within the most recent glacial (85 000–10 000 years ago) to the interglacial period (10 000 years ago to present). For example, paleoecologists have recognized large changes in species distributions and associations owing to range shifting caused by changes in habitat distributions^{10–14}. Additionally, a number of scenarios have envisioned glacial–interglacial cycles as a mechanism driving population differentiation^{10,11} or speciation^{15–20} via geographical isolation of populations. For example, Haffer's classic Pleistocene Forest Refuge Model¹⁶ proposed a causal relationship between glacial-age forest refugia and speciation in the Neotropics.

However, the generality of Haffer's model of latest-Pleistocene speciation has come into question because levels of molecular divergence in several widespread neotropical bird and frog superspecies indicate that phylogenetic diversification preceded the latest Pleistocene by millions of years^{20,21}. Indeed, Miocene marine incursions into the Amazon Basin provide evidence of a dynamic earth history in Amazonia during the late Tertiary²². Molecular studies have also revealed surprisingly strong patterns of divergence and biogeographic structure in organisms from temperate regions on different continents^{8,23–26}. Generally, these studies have provided reason to be cautious about the acceptance of hypotheses of latest Pleistocene biotic diversification without critical examination of alternative, tem-

Recent studies have provided evidence that species diversity and distributions in continental biotas reflect a long history of responses (e.g. range shifts, speciation or adaptation) to habitat changes produced by geological activity over the past several million years (deep time) as well as glacial–interglacial cycles over the most recent hundreds of thousands of years (shallow time). Molecular sequences in extant taxa can be used to infer speciation and biogeographic history in deep time, as well as changes in population distributions produced by range shifts in shallow time, and thus provide a basis for constructing bridges between historical biogeographic, paleoecological and ecological biogeographic perspectives.

Brett Riddle is at the Dept of Biological Sciences, University of Nevada Las Vegas, 4505 Maryland Pk, Las Vegas, NV 89154-4004, USA.

porally deeper, models. It would be interesting to be able to partition biotic responses underlying current patterns of diversity and distribution into those associated with glacial–interglacial forcing events versus much older geotectonic events. However, progress in this direction will require development of new bridges between several traditionally independent fields of study.

Different perspectives on biotic history

The fields that investigate biotic responses to earth history are historical biogeography, paleoecology and ecological biogeography. Historical biogeography uses phylogenetic hypotheses 'to reconstruct the sequences of origin, dispersal and extinction of taxa and explain how geological events... and Pleistocene glaciations have shaped present day biotic distribution patterns'²⁷; thus, taxa are entities in a genealogical hierarchy²⁸. Alternatively, 'paleoecology is...the study of individuals, populations and communities of plants and animals that lived in the past and their interactions with and dynamic responses to changing environments'²⁹, thereby representing the historical dimension of community and evolutionary ecology. Ecological biogeography²⁷ differs from paleoecology in its emphasis on extant rather than fossil organisms and on biotic responses within more recent and shorter time frames (e.g. extinction/colonization equilibria), but both fields treat taxa as entities within an ecological hierarchy²⁸.

In short, historical biogeography, paleoecology and ecological biogeography contrast in terms of data (extant versus fossil organisms), the role of taxa (genealogical versus ecological entities) and conceptual foundations (phylogenetic systematics versus community and evolutionary ecology). These differences could represent considerable barriers to building more synthetic perspectives that consider the contributions of both deep and shallow histories on the development of continental biotic diversity, distributions and associations.

A molecular perspective

Thus far, the workhorse molecules for analysis of phylogenetic and population history have been the 'single-locus' genomes [mitochondrial DNA (mtDNA) in animals and chloroplast DNA (cpDNA) in plants], but investigators are beginning to incorporate data from a variety of nuclear loci because of limitations associated with single-locus data

sets^{23,30}. Several attributes of molecular evolution provide the rationale for using molecular sequence divergence to infer associations between biotic history (diversification and distributional change) and earth history^{23,30,31}.

First, rates of evolution vary across different coding and non-coding regions of a molecule, among different genomes within an organism, and among different kinds of organisms. By selecting a molecular data set that is likely to provide a high degree of resolution within a particular historical time frame (see Box 4.2 in Ref. 23), evolutionary divergence can be assessed at an array of different hierarchical levels

(e.g. genes, conspecific populations, species and higher taxa).

Second, levels of molecular difference are expected to increase with time since population isolation and divergence, providing the basis for using phylogenetic approaches to infer biotic histories. Within shallower time frames, statistical methods allow one to partition genetic variation into hierarchical nongeographic and geographic components^{23,32}. Although estimates of divergence time are often measured with large and unknown sources of error²³, recent investigations have provided evidence of correlations between

rates of molecular evolution in animal mtDNA with biological attributes including body size, thermal environment and generation time³¹. If the fossil record accurately reflects divergence times of extant lineages, and if relative rate tests provide evidence of equivalent rates of evolution across lineages in a phylogenetic tree, then the opportunity arises to calibrate rates of divergence within a specified group of organisms³¹.

These attributes are incorporated within the conceptual framework of molecular phylogeography²³, which is summarized in Box 1 by discrete phylogeographic hypotheses that are roughly along the lines that, traditionally, separate historical biogeographic perspectives from Quaternary paleoecological and ecological biogeographic perspectives. While this treatment risks oversimplifying a more continuous process of molecular and population divergence²³, it provides a framework for examining the relationship of molecular phylogeography to more traditional perspectives.

Deep patterns: the molecular phylogeographic bridge between historical biogeography and paleoecology

A fundamental unit of analysis in historical biogeography, the area of endemism, is recognized by 'distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence'³³. Areas of endemism are considered to be the products of a history of vicariant isolation and divergence. A molecular phylogeographic perspective would emphasize patterns of

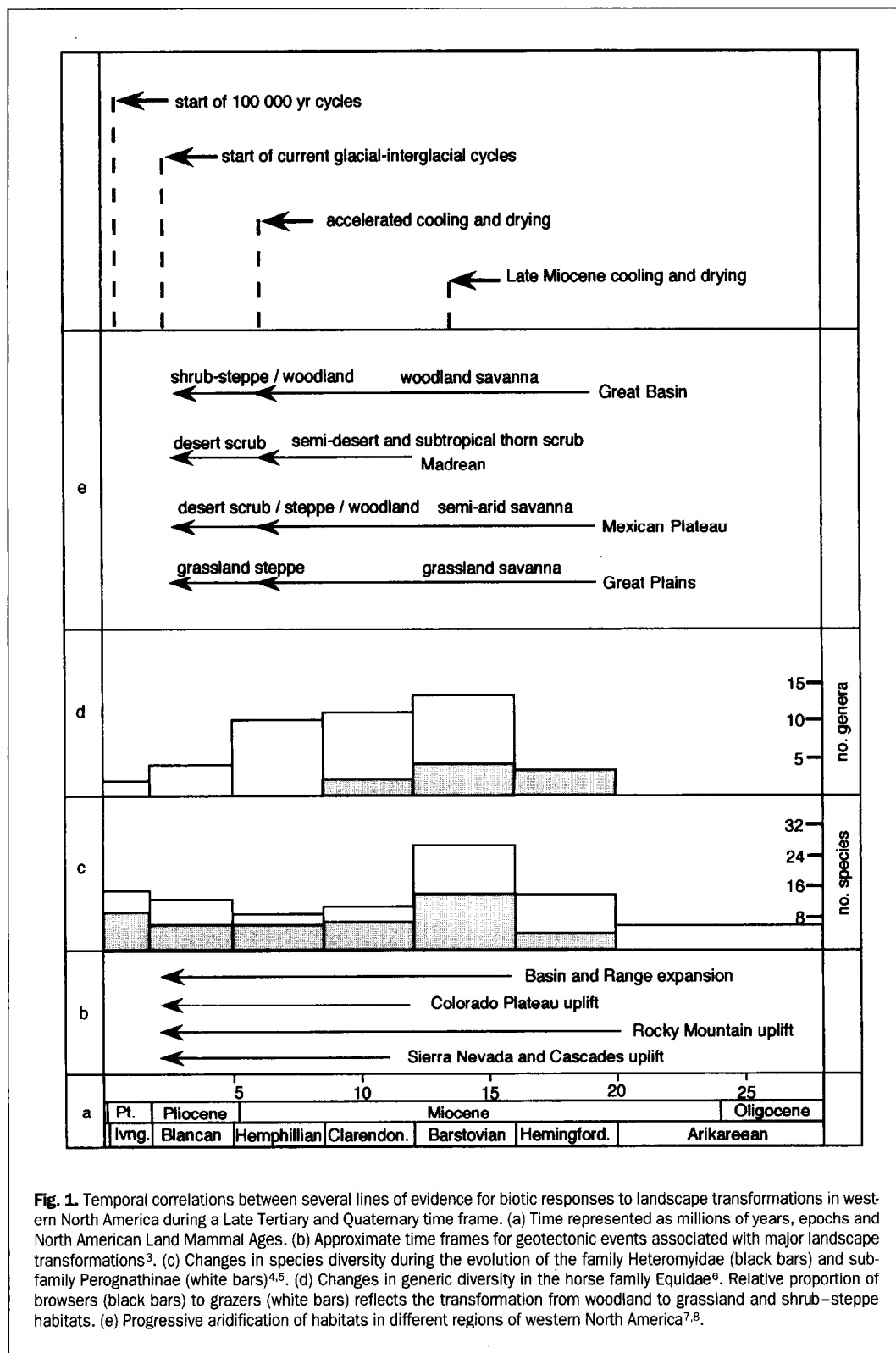


Fig. 1. Temporal correlations between several lines of evidence for biotic responses to landscape transformations in western North America during a Late Tertiary and Quaternary time frame. (a) Time represented as millions of years, epochs and North American Land Mammal Ages. (b) Approximate time frames for geotectonic events associated with major landscape transformations³. (c) Changes in species diversity during the evolution of the family Heteromyidae (black bars) and sub-family Perognathinae (white bars)^{4,5}. (d) Changes in generic diversity in the horse family Equidae⁹. Relative proportion of browsers (black bars) to grazers (white bars) reflects the transformation from woodland to grassland and shrub-steppe habitats. (e) Progressive aridification of habitats in different regions of western North America^{7,8}.

Box 1. Molecular phylogeography: definition and hypotheses

Molecular phylogeography: 'refers to the study of the principles and processes governing the geographic distributions of genealogical lineages, including those at the intraspecific level'²³.

Phylogeographic hypothesis I – 'deep' history: populations delineated by large phylogenetic gaps are usually associated with stable biogeographic barriers to gene flow. The following three corollaries are associated with this hypothesis:

- **Biotic/abiotic concordance:** the geographic position of phylogenetic gaps is likely to be associated with boundaries between traditionally-recognized biogeographic provinces.
- **Taxonomic concordance:** the geographic position of phylogenetic gaps may be concordant across different taxa.
- **Gene-tree concordance:** the probability of phylogeographic concordance across different gene genealogies increases with the time since isolation.

Phylogeographic hypothesis II – 'shallow' history: populations not clearly delimited by large phylogenetic gaps are genetically connected through ongoing or recent dispersal.

gene lineage rather than taxon divergence as evidence of endemism, and one of the corollaries of phylogeographic hypothesis I (taxonomic concordance; Box 1) is the molecular equivalent to a phylogenetically-based definition of areas of endemism. However, because some degree of phylogeographic structure can theoretically arise without absolute geographic isolation³⁴, biotic/abiotic, gene tree and fossil concordance provide important ancillary evidence of a history of vicariant isolation and divergence.

A number of molecular phylogeographic studies have revealed previously undetected patterns of endemism^{8,23–26,35}. Endemism that is hidden at the morphological level (i.e. 'cryptic' endemism), if common, could have important implications for paleoecological interpretations of the extent of provincialism within a continental biota³⁶. In North America, a large faunal turnover 5–10 million years ago resulted in the demise of the 'Clarendonian chronofauna', which included widespread extinction of woodland savanna mammals (Fig. 1)⁷. This extinction episode coincided with a proliferation of granivorous and omnivorous rodents in the developing western North American aridlands. In particular, the family Heteromyidae (including pocket mice, kangaroo rats and kangaroo mice) represents a highly successful radiation whose diversification coincided with the late Miocene and Pliocene aridification of western North American landscapes³⁷.

What does a molecular phylogeographic approach tell us about patterns of endemism in rodent lineages in arid lands, and of what value is this information to paleoecology? A recent study⁸ of mtDNA postulated widespread isolation and divergence of regional populations in the pocket mice genera *Chaetodipus* and *Perognathus* within a Miocene–Pliocene time frame. A high degree of phylogeographic structure appears to be embedded within taxa that have been considered previously to represent single, widespread species, based on morphology. Thus, 'cryptic' endemism could be common in these genera.

For example, continuous distribution of the Desert pocket mouse (*C. penicillatus*) across Chihuahuan and Sonoran–Mojavean deserts, with minimal morphological differentiation among populations, has been used as evidence supporting a model of latest-Pleistocene dispersal and gene flow between desert regions¹⁵. However, mtDNA differences between Sonoran–Mojavean and Chihuahuan populations are considerable, and are inferred to indicate divergence between regional populations before the end of the Pleistocene³⁸

(Fig. 2). This inference is supported by corollary evidence (Box 1). First, a large mtDNA difference allows inference of a phylogeographic gap that is associated with an elevated transition zone along the Continental Divide separating Chihuahuan and Sonoran deserts (i.e. biotic/abiotic concordance). Second, mtDNA geographic structure parallels isozyme and karyological assays of nuclear DNA variation (i.e. gene tree concordance)⁴². Third, the mtDNA phylogeographic gap between eastern and western populations of *C. penicillatus* is geographically congruent with a similarly pronounced demarcation between two species of grasshopper mice, *Onychomys torridus* and *O. arenicola* (i.e. taxonomic concordance)^{8,35}. In both genera, the degree of genetic difference between Chihuahuan and Sonoran–Mojavean populations is an order of magnitude greater than maximum difference within either region. Collectively, these data provide a basis for inferring that the Chihuahuan and Sonoran–Mojavean warm deserts represent separate areas of endemism for a suite of arid-adapted taxa.

As another example, Williams⁴¹ proposed that the Apache and Plains pocket mice (*Perognathus apache* and *P. flavescens*, respectively) (Fig. 2) actually represent a single widespread species based on morphological and karyological data. Furthermore, he developed a scenario of Holocene range expansion to the north and west from a single glacial-age refugium in the southern Great Plains to account for the alleged similarity among populations. However, although Southern Intermountain Basins and Great Plains populations have high levels of mtDNA genetic diversity, mtDNA differences between regional populations are large (D.C. Nickle, pers. commun.; Fig. 2) making Williams' hypothesis of Holocene range expansion from a single latest Pleistocene refuge unlikely. Likewise, although Columbia Plateau and Great

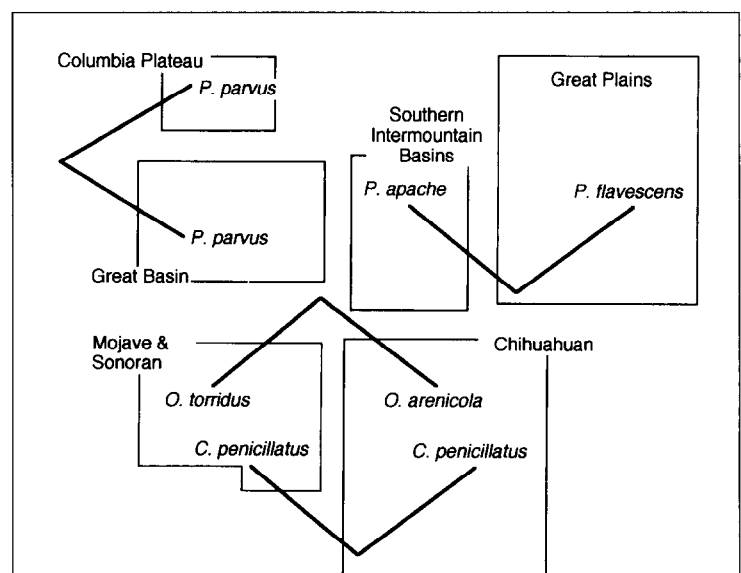


Fig. 2. Simplified illustration of 'cryptic' mtDNA phylogeographic structure in several arid-adapted rodents in western North America. In each case, although morphologically-based studies indicated single, widespread species without appreciable geographic structure, mtDNA and, in several cases, other genetic studies indicate that populations within a geographic region form monophyletic assemblages and are separated by distinct phylogenetic gaps from populations in the adjacent region. The species depicted are: *Chaetodipus penicillatus* (Desert pocket mouse)^{8,38}; *Onychomys torridus* and *O. arenicola* (Southern and Chihuahuan grasshopper mice)^{8,36}, previously considered to be a single species (*O. torridus*) before karyological and allozyme studies were carried out^{39,40}; *Perognathus apache* and *P. flavescens* (Apache and Plains pocket mice; D.C. Nickle, pers. commun.), considered to be a single species (*P. flavescens*) in the most recent taxonomic revision⁴¹; and *P. parvus* (Great Basin pocket mouse; C.S. Ferrell, pers. commun.).

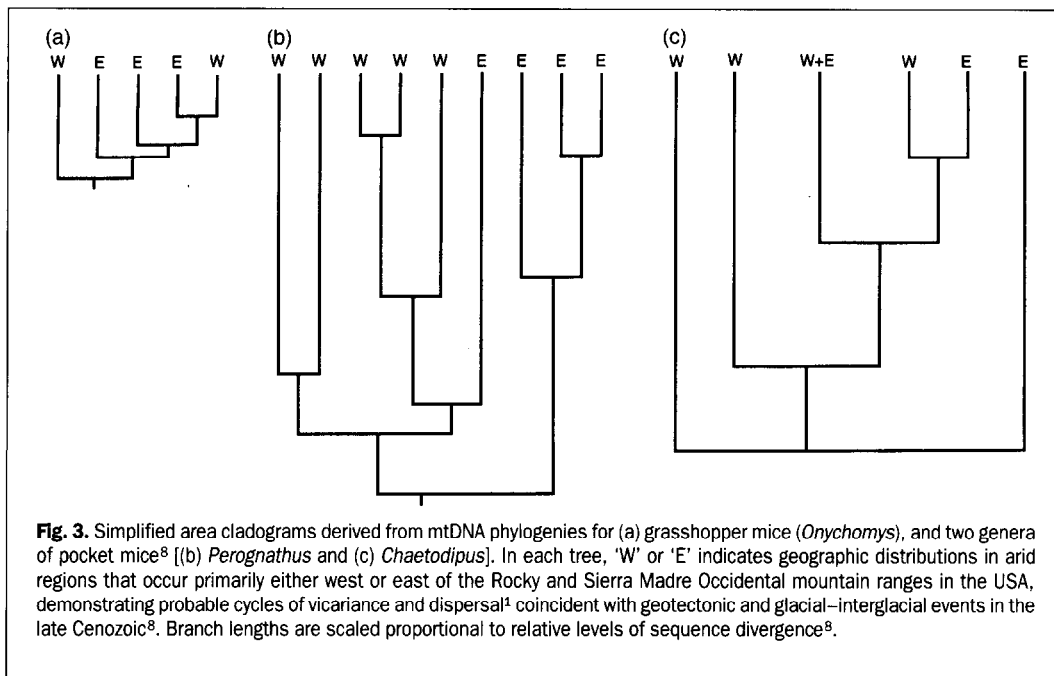


Fig. 3. Simplified area cladograms derived from mtDNA phylogenies for (a) grasshopper mice (*Onychomys*), and two genera of pocket mice⁸ [(b) *Perognathus* and (c) *Chaetodipus*]. In each tree, 'W' or 'E' indicates geographic distributions in arid regions that occur primarily either west or east of the Rocky and Sierra Madre Occidental mountain ranges in the USA, demonstrating probable cycles of vicariance and dispersal¹ coincident with geotectonic and glacial–interglacial events in the late Cenozoic⁸. Branch lengths are scaled proportional to relative levels of sequence divergence⁸.

Basin populations of the Great Basin pocket mouse have high levels of mtDNA genetic diversity, large mtDNA differences between regional populations (C.S. Ferrell, pers. commun.; Fig. 2) suggest a deep historical isolation and divergence.

A molecular phylogeographic approach can also elucidate the layering effect that Cracraft predicted would result from multiple episodes of vicariance and dispersal¹, because the inferred phylogeny of genes provides access to the hierarchical structure of biotic history in evolving lineages. For example, area cladograms derived from mtDNA phylogenies in the pocket mice (*Chaetodipus* and *Perognathus*) and grasshopper mice (*Onychomys*) suggest a long history of cycles of vicariance and dispersal between arid regions bisected by the Rocky and Sierra Madre Occidental mountains⁸ (Fig. 3). More taxa need to be examined in order to clarify the vicariance components of patterns illustrated in Fig. 3, but one implication is that biotic responses to more recent glacial–interglacial events are not large enough to erase biogeographic structure produced by earlier episodes of isolation and divergence.

In each of the above examples, fossil data alone would not have allowed for a correct interpretation of biotic histories in pocket mice or grasshopper mice. Although perognathine fossils are common and represent a full Late Cenozoic time frame in western North America, their extreme morphological conservatism does not provide a means of tying fossils to their correct evolutionary lineages⁴³. For grasshopper mice, there is a similar lack of sufficient information at the morphological level⁴⁴ to assess patterns of historical isolation and divergence through fossil data alone. Although areas of endemism are fundamental units of analysis in historical biogeography, the concept of endemism also extends into a paleoecological realm (e.g. provinciality, biofacies, ecological evolutionary subunits). Thus, molecular phylogeography can provide a bridge between these disciplines through identification of areas of endemism and patterns of historical connectivity between areas.

Shallow patterns: a molecular phylogeographic framework for Quaternary paleoecology and ecological biogeography

Phylogeographic hypothesis II (see Box 1) suggests that molecular data can be employed to address basic questions

in Quaternary paleoecology and ecological biogeography including assessment of patterns of range shifting, population expansion and contraction, and alterations in community-level associations. The late Quaternary paleoecology of North America and Europe has revealed a series of southward range contractions during the latest glacial period followed by rapid northward range expansions following deglaciation^{14,45}. Hewitt¹⁷ has outlined expected patterns of geographic variation in genetic diversity given a model of rapid biological invasion into newly available habitats following glacial retreat. Repeated bottlenecks through cycles of long-distance colonization

by pioneers, most likely from populations proximal to the leading edge of expansion, leads to a predicted reduction in genetic variability in newly colonized regions.

Several molecular studies have supported the general hypothesis of latest Pleistocene southward depression, followed by postglacial northward expansion of ranges in Palearctic⁴⁶ and Nearctic⁴⁷ taxa. For example, the widespread Palearctic grasshopper species *Chorthippus parallelus*⁴⁶ is genetically subdivided into mtDNA lineages whose distributions and patterns of genetic diversity support models predicting the postulated localities of glacial-age refugia in southern Europe⁴⁵. In North America, isozyme studies of allelic diversity in populations of lodgepole pine (*Pinus contorta latifolia*) demonstrate a strong negative correlation with time since founding of a population following postglacial expansion from glacial-age refugia⁴⁷.

Alternatively, high levels of mtDNA genetic diversity associated with large phylogenetic differences between Columbia Plateau and Great Basin populations of the Great Basin pocket mouse (*Perognathus parvus*) (Fig. 2) would be difficult to explain under a model of latest Pleistocene depression of populations into southern refugia with subsequent Holocene expansion to the north. Even within widespread North American rodent species without large phylogeographic gaps, cycles of range contraction and expansion may have been less extensive than paleoecological models would predict^{34,48}. In short, a molecular phylogeographic perspective may give Quaternary paleoecology a way of critically examining the extent to which the fossil record provides a general framework for explaining biotic responses to events within a latest-Pleistocene and Holocene time frame.

Conclusions

DiMichele⁴⁹ argued for an hierarchical view of processes influencing the organization of biotic assemblages. To what degree is the assembly of modern biotas a product of responses to older geological events versus more recent glacial–interglacial cycles? Molecular phylogeography offers biogeographers and paleoecologists one approach to addressing this question, and should be of particular value in revealing 'cryptic' divergence and endemism embedded within widespread taxa, examining patterns of range shifting

and illuminating patterns of hierarchical historical structure in continental biotas.

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