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ADVANCES IN ARID LANDS PALEOBIOGEOGRAPHY: THE RODENT MIDDEN RECORD IN THE AMERICAS

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Introduction

Much of what we know about the late Quaternary vegetation history of the American deserts originated with the advent of rodent midden analysis in the 1960's for North America and the late 1990's for South America. The worldwide holdup in desert paleobotany has several explanations. Unlike humid regions, deserts harbor few permanent bodies of water suitable for continuous pollen deposition, and the typical alkalinity of desert sediments is bad for pollen preservation. Just as critical, warm desert floras have large proportions of insect or animal-pollinated plants, including the most prevalent species. Entomophilous and zoophilous species tend to produce less pollen than wind-pollinated ones, and what little is produced is immediately consumed. Imagine the broad expanses of creosote bush (*Larrea*: ZYGOPHYLLACEAE) that now characterize the Chihuahuan, Sonoran and Mojave Deserts of North America and the Monte Desert of South America. Even if its pollen were well preserved in desert sediment, there would be very little way of inferring *Larrea* dominance from the pollen stratigraphy of monotonous stands in any of these deserts.

It is no wonder that in his classic synthesis of Pleistocene biogeography of North America, Deevey (1949) reported no definitive Pleistocene fossil plant records in the deserts. He relied instead on relict fish distribution in Great Basin drainages, and chromosome inversions in fluit flies, to compliment shoreline evidence for large pluvial lakes that filled desert basins during the last ice age. By the late 1950's, radiocarbon dating confirmed that pluvial lake highstands were contemporaneous with glacial advances in nearby mountains. Flint and Gale (1958) showed it for Searles Lake and the Sierra Nevada in California, and Broecker and Orr (1958) for Lake Lahontan and the

Wasatch Range in Utah. At Searles Lake, Roosma (1958) found that desert playa sediments actually do preserve pollen. Lake mud dated between 27 and 11.5 cal kyr B.P. (calendar kiloyears before present; all radiocarbon ages in this chapter have been converted to calendar ages) contained pollen assemblages with closest analogs in pinyon-juniper woodlands on the Panamint Mountains, some 1200 m higher than the surface of the lake (Martin, 1964). Pollen evidence suggested that the same changes that produced glacial advances and pluvial lakes must have lowered vegetation zones 1000 m or more (Martin and Mehringer, 1965). It would be left to fossil woodrat (*Neotoma*) middens to confirm and fill in the precise biogeographic details.

The paleoecological worth of woodrat or packrat (*Neotoma*) middens was first discovered in 1961 at the Nevada Test Site near Las Vegas. The initial find was made by Phil Wells and Clive Jorgensen, two young biologists on a team contracted by the Atomic Energy Commission to study the biological effects of fission-type nuclear detonations. The revelation occurred happenstance on a hike to determine if the summit of a small, desert mountain was wet enough to support oaks and junipers. There were no trees on the summit, but underneath a limestone overhang they did find a dark, urine-cemented mass full of juniper twigs and woodrat fecal pellets. A few months later, W. F. Libby's Radiocarbon Laboratory at UCLA produced a date of 10,590 ± 400 cal yrs B.P. In their seminal paper, which reported on ten other nearby middens dated between 40 and 8.7 kyr B.P., Wells and Jorgensen (1964, p. 1172) prophesied that woodrat middens "may have unique value as a check of the palynological approach to Pleistocene ecology in the arid Southwest."

With the advent of woodrat midden analysis in the 1960s, there has been no shortage of late Quaternary fossil plant and animal records in the North American deserts. Quite the contrary, in the last 40 years fossil rodent middens in the Americas have developed into one of the more versatile and informative paleorecords worldwide. The body of knowledge generated from fossil rodent middens has been summarized elsewhere (Van Devender and Spaulding, 1979; Spaulding *et al*., 1983; Van Devender *et al.*, 1987; Betancourt *et al.*, 1990; Thompson *et al*., 1993; Grayson, 1993; Thompson and Anderson, 2000; Rhode 2000; Pearson and Betancourt, 2002; Betancourt and Saavedra, 2002). I will use this chapter to update and reflect on the significance of this knowledge

for contemporary issues in biogeography, and to feature extension of the method to the South American continent. I will conclude by pointing out the more promising frontiers for rodent midden analysis and late Quaternary biogeography in the American deserts.

Fossil rodent middens: Strengths and weaknesses

Fossil rodent middens represent rich amalgamations of plant fragments, pollen, fecal pellets, bones, and insects imbedded in crystallized rat urine and preserved in rock shelters, crevices and caves for tens of millennia. Since 1961, about 2500 woodrat middens have been dated and analyzed in arid and semi-arid regions of North America, from northern Mexico to southern Canada (Betancourt *et al*., 1990; Pearson and Betancourt, 2002). More recently, a parallel effort in arid and semi-arid South America has relied on analogous deposits made by leaf-eared mice (*Phyllotis*, MURIDAE), vizcachas (*Lagidium*, CHINCHILLIDAE), chinchilla rats (*Abrocoma*, ABROCOMIDAE) and chozchori or brushy-tailed rats (*Octodontomys*, OCTODONTIDAE). About 500 middens have been dated and analyzed from Argentina, Bolivia, Chile and Peru, mostly in the last decade (Pearson and Christie, 1993; Markgraf *et al*., 1997; Betancourt *et al.*, 2000; Holmgren *et al*., 2001; Betancourt and Saavedra, 2002; Latorre *et al*., 2002, 2003; Kuch *et al*., 2002; Hofreiter *et al*., 2003; Betancourt *et al*., 2003).

Advantages of rodent midden analyses include the high taxonomic resolution (often to species and potentially to genotype), the restricted origin of plant and animal material (generally within 100 m of the midden), the abundance of plant and fecal material for radiocarbon and other morphological, geochemical and genetic analyses, and the easy replicability within and across areas. Although best known for their rich plant macrofossil assemblages, rodent middens have also contributed critical information about the past distributions of vertebrates and arthropods (e.g., Van Devender *et al*., 1987; Van Devender and Hall, 1994; Elias *et al*., 1995).

The taxonomic and spatial accuracy associated with rodent middens can provide unprecedented resolution. For example, a late glacial hybrid zone between two species of pinyon pine can be pinpointed to particular hillslopes (Lanner and Van Devender, 1998); a specific founder event and its genetic consequences can be identified and tested for a

pinyon pine isolate (Betancourt *et al*., 1991); and the age of a clonal stand of starleaf Mexican-orange (*Choisya dumosa*: RUTACEAE) can be inferred from its continuous presence throughout a 20,000-year midden series, pending confirmation by ancient DNA analysis that it is the same individual (Betancourt *et al.*, 2000).

Disadvantages of rodent middens include dietary selectivity of different rodents, a clear bias for vegetation in bedrock escarpments and against more open terrain, occasional temporal mixing of midden assemblages and the episodic and discontinuous nature of midden deposition. Although woodrats are considered generalists, dietary bias has been identified among some of the species that produce middens (Dial and Czaplewski, 1990). This is apt to be more problematic in South America, where dietary preferences for midden agents cut across four families of rodents (Betancourt and Saavedra, 2002).

In most cases, individual middens represent discrete and isolated depositional episodes rather than continuous stratigraphic accumulation. Temporal averaging can be caused by contamination from older and younger material (Kidwell and Flessa, 1996), though at least some mixed assemblages can be detected by Accelerator Mass Spectrometer (AMS) dating of individual plant fragments (Van Devender *et a*l., 1985). The duration of the depositional episode is presumed to be bracketed by the standard deviation of a ^{14}C date (say, ± 100 years), but there are currently few ways to distinguish between episodes that lasted a few months, a few decades, and in some cases a few centuries. Among other pitfalls, uncertainty about the duration of the depositional episode is why midden inferences rely mostly on presence-absence, and put less stock on taxonomic abundance or diversity within single middens. This should serve as a note of caution for unscrupulous mining of the midden database (http://climchange.cr.usgs.gov/data/midden/) in support of macroecological studies.

In effect, rodent middens represent individual snapshots of vegetation that have to be collated into series or chronologies for any particular site or area (Betancourt *et al*., 1990). In my own graduate student days in the early 1980s, midden sampling involved two or three individuals collecting one or two dozen middens to develop a single chronology, both steered and limited by available funding for radiocarbon dates. Although the success of these midden surveys still relies on personal skill and field

experience, GIS-based approaches such as Weights of Evidence are now being used as a first approximation of suitable areas for midden preservation (Mensing *et al*., 2000). We now deploy larger field crews to comb extensive outcrops and generate series of 50 to 100 middens from a single area (Latorre *et al*., 2002), or multiple chronologies from many sites along a presumed pathway of plant migration (Lyford *et al*., 2003b). Ready access to vacuum gas lines for pretreatment of plant macrofossils to gas-CO_2 and graphite targets, and the associated discounts for AMS dating, now make these synoptic approaches economically feasible.

Although there was some debate early on about the methods and assumptions of midden analysis (Wells, 1976 vs. Van Devender, 1976), most authors tend to follow accepted methods for processing and analysis (Spaulding *et al*., 1990) with hardly a wrinkle. There have been few efforts to calibrate plant macrofossil assemblages in rodent middens with modern vegetation on par with the much more extensive and necessary empirical validation of pollen percentages in lake sediments (see discussion by Jackson in this volume). Two notable exceptions are Nowak et al.'s (2000) computation of probabilities that a taxon absent from a woodrat midden is necessarily absent from the paleolandscape (within 100 m radius of the midden), and a comparable analysis by Lyford *et al*. (2003b) to evaluate the significance of Utah juniper (*Juniperus osteosperma*) presence and absence in midden series to support its migrational history (Lyford *et al*., 2003a). For researchers like myself, both of these studies had comforting outcomes, but they still need to be repeated for South American middens. Less comforting have been calibration efforts to interpret paleoclimatic signals in stable isotopic (δD, $\delta^{18}O$, and $\delta^{13}C$) values from fossil leaf cellulose in middens. There is too much random scatter in stable isotopes between individual plants in the same stands and across populations along well-defined environmental gradients (Pendall *et al*., 1999; Van de Water *et al*., 2002; Terwilliger *et al*., 2002; Pedicino *et al*., 2002). This not only compromises paleoclimatic applications, but also suggests that stable isotopes in leaves are a very imperfect substitute for actual ecophysiological measurements.

Late Quaternary biogeography of the North American deserts: Highlights

In North America, the midden record spans a large area from the southernmost sites in Durango, Mexico to British Columbia in Canada. The majority of the work, though, has been done in the core deserts: the warm deserts (Chihuahuan, Sonoran, Mojave Deserts) and the floristic Great Basin (the Colorado Plateau, the physiographic Great Basin, and the Wyoming Basins extending into southern Montana). Winter precipitation in the warm deserts is highly variable from year to year, but well synchronized across the three deserts and closely teleconnected to the tropical Pacific (wet during El Niño and positive Pacific Decadal Oscillation (PDO); dry during La Niña and negative PDO)(Sheppard et al. 2002). The warm deserts are all characterized by a very arid foresummer (April-June). Summer, monsoonal precipitation (July-September) starts abruptly, is less variable from year to year but patchier than winter, and decreases in importance from the Chihuahuan to the Mojave Desert. Most of the summer air masses in July originate in the Gulf of Mexico, while those in August tend to come from the Pacific and Gulf of California. The floristic Great Basin is in the transition between Southwest-like (more precipitation) and Pacific Northwest-like (less precipitation) responses to El Niño.

The North American midden record has matured to the point of requiring constant updates. During the last glacial, desert vegetation was restricted to a few areas below 300 m in Death Valley and around the Gulf of California. Pinyon-juniper-oak woodlands covered large expanses of what is now classified as desertscrub between 300-1700 m. Mixed-conifer woodlands and forests in turn dominated rocky terrain above 1400 m in the Colorado Plateau and Great Basin, which now harbor ~20 million ha of pinyon-juniper woodlands. Now restricted spruce-fir forests covered extensive areas above 2000 m in the central and southern Rockies, the Mogollon Rim, the High Plateaus of Utah, and the Sierra Nevada and adjoining mountain ranges of the Great Basin. Forest and woodland expansions, glacial advances and pluvial lake highstands have all been attributed to a 5-10ºC decrease in summer temperatures and significant increases in winter precipitation (and probably reduced variance) with a 10º southward displacement in the average, winter position of the upper-air westerlies and the winter storm track (Van Devender *et al.*, 1987; Betancourt *et al.*, 1990; Thompson *et al.*, 1993; Bartlein *et al.*,

1998; Thompson *et al.*, 1998; Thompson and Anderson, 2000). Summer precipitation was much reduced over the western U.S., but remained a significant portion (~45%) of the annual precipitation in the northern Chihuahuan Desert (Connin *et al*., 1998; Pendall et. al., 1999; Holmgren *et al*., 2003). The July-September greenup, when areas to the north were experiencing seasonal drought and fire, may explain the rich assortment of megafaunal and Paleoindian sites in the northern Chihuahuan Desert.

Pluvial lake and ground-water levels dropped dramatically at 14 kyr BP, but vegetation held steady until ~13 kyr B.P. around the time of the major megafaunal extinction. Holocene deserts replaced Pleistocene woodlands, and in return Holocene woodlands replaced Pleistocene forests. If the Pleistocene ended with a "Clovis" megadrought ~13 kyr B.P. (Haynes, 1991), vegetation change at the Pleistocene-Holocene transition must have entailed massive tree dieoffs, widespread insect outbreaks, and catastrophic wildfires in forests above 2000 m. These disturbances cleared the way for forests of ponderosa pine, probably produced enigmatic and temporary fluctuations in ground-water levels, and must have translated large pulses of sediment from the mountains to the lowlands. Ponderosa pine, the dominant forest type across the southern and central Rockies, was surprisingly restricted to south of 35ºN (south of Albuquerque, New Mexico and Flagstaff, Arizona) during the last glacial. Paradoxically, its postglacial expansion produced considerable genetic diversity evident across much of its modern range (Rehfeldt, 1999).

The late Quaternary history of North American pinyon-juniper woodlands is better known than for any other vegetation type worldwide (see summary in Lanner and Van Devender, 1999). Most of the pinyon and juniper species are indistinguishable in pollen, but can be identified to species and even subspecies in macrofossils. The high taxonomic resolution afforded in middens has permitted a species-specific history of past distributions for pinyon and juniper species, including zones of past and present hybridization. During the last glacial, what are now desert lowlands (below ~1500m) supported *Pinus remota* and *P. edulis* in the Chihuahuan Desert, *P. fallax* in the Sonoran Desert, *P. monophylla* in the Mojave Desert, and *P. juarensis* in central Baja California. Hybrids of *P. juarensis* x *californiarum* var. *fallax* occurred in Joshua Tree National Monument, southeastern California. The northern limits of *P. edulis*, the dominant

species today in the southern Rockies and Colorado Plateau, were along the Little Colorado River Valley. Possible hybrids of *P. edulis* x *monophylla* occurred in the Lower Grand Canyon, and of *P. edulis* x *califoniarum* var. *fallax* on the south slope of the Santa Catalina Mountains near Tucson.

For junipers in the Chihuahuan Desert, some of the highlights include *J. ashei*, *J. pinchotii* and *J. coahuilensis* in the lowlands, *J. scopulorum* down to ~1500 m, and the absence of *J. deppeana*, which must have been displaced south of the U.S.-Mexican border. *J. scopulorum* was the dominant juniper in the foothills of the southern and central Rockies, the Colorado Plateau and the mid-elevations of the Great Basin. *J. scopulorum* was found as low as 975 m in the Ajo Mountains in Organ Pipe Cactus National Monument, 270 km from the nearest populations today. A similar displacement for *J. occidentalis* is recorded at Cataviña (~30°S) in central Baja California ~450 km south of its southernmost stands today in the San Bernadino Mountains. In the lowest elevations of the Southwest, dominant junipers included *J. californica* in the Lower Colorado River Valley and along the Arizona-Sonora border, and *J. osteosperma* in what are now the Sonoran Desert uplands, the Mojave Desert, and the southern Great Basin.

The Holocene record of these pinyons and junipers is complex. At desert elevations, pinyons were extirpated from desert elevations by ~12.5 kyr B.P. *Pinus remota* retreated upslope to a few mountain refugia in west Texas and Coahuila, and *P. californiarum* var. *fallax* wedged itself between 1250-1800 m and below *P. edulis* at the base of the Mogollon Rim. Some junipers persisted at desert elevations until ~9 kyr B.P. The Holocene migrational histories of pinyon and juniper species are dynamical, modulated by dispersal, climate and physiography. For example, after 12.5 kyr B.P. regional warming (and drying) lifted upper limits 500-800 m and pinyon (*P. edulis, P. monophylla*) and juniper *(J. osteosperma, J. monosperma*) species quickly spread northward into low elevation (1500-2200 m), rocky habitats of the southern Rockies, the Colorado Plateau and the Great Basin. *J. deppeana* also spread north from the Sierra Madre into the mountains of west Texas, southern Arizona and southern New Mexico.

The climate space for these pinyon and junipers species narrows considerably to the north, so that secondary climatic changes during the Holocene have either retarded or accelerated northward migration. At their northernmost sites, pinyons and junipers have

been spreading into progressively narrower elevational wedges constrained by relatively high base levels at the bottom and cooler summers and competitive exclusion by higher elevation conifers at the top. These wedges become available for invasion only during brief warm and dry episodes. For example, *J. osteosperma* abutted against the Rockies in northeastern Utah/southwestern Wyoming by 10 kyr B.P., jumped over them to reach its northernmost sites in southern Montana by ~6 kyr B.P., occupied only a fraction of its present range in Wyoming/southern Montana during the wet Neoglacial (~4-2.5 kyr B.P.), and then exploded across the Wyoming Basins in the last 2000 years (Lyford et al. 2003). Founder events in the last 1000 years explain northern disjuncts of *P. monophylla* in the northwestern Nevada (Nowak et al., 1994) and *P. edulis* in northeastern Utah (Jackson, Betancourt, Lyford and Gray, in preparation) and northern Colorado (Betancourt et al., 1991). In the northern peripheries of pinyon and juniper distributions, population expansion and infilling associated with ongoing, natural invasion could account for some of the increasing stem density and encroachment of grassland attributed to post-settlement grazing and fire suppression. Large-scale changes in climate are responsible for this suite of late Holocene northward migrations, and they should also be evident in the migrational histories for other woodland and desert species throughout North America.

Holocene migration of desert species has also been time-transgressive. For example, much of the saguaro's (*Carnegiea gigantea*) range was established quickly through migration northward from unidentified late Pleistocene refugia in coastal Sonora, northwestern Mexico. It established its northernmost limits of its present range by 12.3 kyr B.P. (McAuliffe and Van Devender, 1998). Such rapid migration may be due to long-distance dispersal of its small seeds by frugivorous birds, such as white-winged doves (*Zenaida asiatica*). By contrast, creosote bush (*Larrea divaricata* var. *tridentata*) was relatively slow in expanding to its northern limits in the Chihuahuan, Sonoran and Mojave Deserts (Hunter et al., 2001).

Identification of teeth from middens also indicates dramatic shifts in the distribution of some *Neotoma* species during the last glacial-interglacial cycle. For example, with postglacial warming, *N. cinerea* contracted much of its southern glacial range in what is now Chihuahuan Desert, while other species (*N. albigula, N. lepida,* and

N. mexicana) expanded to the north (Harris, 1984). In northern Utah, *N. cinerea* abandoned its lowest elevations to *N. lepida* at ~9.2 kyr B.P. only to return just prior to 1 kyr B.P. (Grayson, 2000; Grayson and Madsen, 2000). Just to the north, *N. lepida* overshot its northern limits, becoming sympatric with *N. cinerea* in southern Idaho during the latter part of the middle Holocene (Smith and Betancourt, 2003). *N. mexicana* may still be expanding north in Colorado.

Late Quaternary biogeography of the South American deserts: Update on first results

The Atacama Desert

The hyperarid Atacama Desert extends along the Pacific Andean slope from the southern border of Peru (18°S) to Copiapó, Chile (27° S). The region's hyperaridity is due to the extreme rainshadow of the high Andes, which blocks the advection of tropical/subtropical moisture from the east; the blocking influence of the semi-permanent South Pacific Anticyclone, which limits the influence of winter storm tracks from the south; and the generation of a temperature inversion at ~1000 m by the cold and north-flowing Humboldt Current, which constrains inland (upslope) penetration of Pacific moisture. The South Pacific Anticyclone has been anchored against the westward bend in the South American continent throughout the Neogene, the Andean orogeny doubled the average elevation of the central Andes during the past 10 million years, and the Humboldt Current reached its present intensity by early Pliocene. Seasonal and annual precipitation totals in the region are determined by the number of precipitation days, and associated circulation anomalies during those days. Precipitation variability in both summer and winter is modulated primarily by Pacific sea surface temperature (SST) gradients and associated upper-air circulation anomalies. These anomalies promote either greater spillover of summer moisture from the Amazon Basin and the Gran Chaco to the east, or conversely, greater penetration of winter storm track from the southwest. Throughout the Quaternary, the most pervasive climatic influence has been millennial-scale changes in the frequency and seasonality of the scant rainfall, and associated shifts in plant and animal distributions with elevation.

During the past five years (1998-2003), a group from the University of Chile, University of Arizona, and USGS have mapped modern vegetation gradients and developed a number of paleoenvironmental records, including vegetation histories from fossil rodent middens, along an 1100-km transect (16-26°S) in the Atacama Desert (Betancourt *et al*., 2000; Holmgren *et al*., 2001, Latorre *et al*., 2002, 2003, Maldonado *et al*., 2003). This paleoclimate transect is being used to reconstruct the histories of the South American tropical and extratropical rainfall belts, precisely at those elevations where average annual rainfall wanes to zero. The seasonality of precipitation along the transect changes from 90% winter at 22º to 90% summer at 26ºS, over a distance of only 450 km. The midden focus has been on this latitudinal transition, specifically in the boundary from sparse, prepuna vegetation into absolute desert, an expansive waterless terrain that extends from just above the coastal fog zone (800 m) to more than 3000 m in the most arid sectors. The most compelling midden evidence for past changes involves elevational displacements of indicator plants and large-scale invasions of vegetation across what is now the edge of the absolute desert.

Midden results for the central Atacama (~22-24ºS) indicate maximum summer precipitation and 500-900 m lowering of plant distributions between 14 and 10.5 kyr B.P. (Betancourt *et al*., 2000; Latorre *et al*., 2002, 2003), contrasting with pluvial lake highstands on the adjacent Bolivian Altiplano from 26 and 15 kyr B.P. according to one group (Baker *et al.,* 2001) or 19-14 kyr B.P. according to another (Fornari *et al*., 2001). The disparity may have to do in part with different sources and mechanisms of summer precipitation across the central Andes. At stake in the timing is the extent to which pluvial events are driven by summer insolation maxima over the Bolivian Altiplano (i.e., intensifying the Bolivian High and increasing convection) or by changing tropical Pacific SST gradients (intensifying the easterlies and enhancing large-scale advection of moist air mases). For those of you not following the most recent development in paleoclimatology, there is now compelling evidence that SST's in the so-called "warm" pool of the western Pacific has fluctuated by ~4ºC, in synchrony with global atmospheric CO_2 variations but leading Northern Hemisphere deglaciation by 2000-3000 years. If insolation variations drive the ice ages and other climatic variations, they would surely have to involve the tropical Pacific and its complex interaction with the extratropics.

In the driest sector of the southern Atacama (25.5ºS), where the scant precipitation occurs mostly in winter, midden series were developed from two elevational belts (2650-2850m and 3450-3500 m)(Maldonado, 2003; Betancourt et al., in preparation). The lower site registers only the most extreme wet events, evident in full-glacial (23-18 kyr B.P.) expansion of steppe grasses and other high-elevation shrubs >800 m downslope into absolute desert. The higher site registers another, perhaps lesser, pluvial event between 17-10 kyr B.P. evident in an elevational displacement of steppe grasses by at least 100 m. The full glacial pluvial (perhaps due to a northward expansion of the westerlies and increased winter precipitation) recorded at the lower site did not produce wholesale expansion of steppe grasses in the central Atacama. Conversely, the late glacial/early Holocene summer pluvial, which yielded up to 1000 m expansion of steppe grasses in Salar de Atacama/Calama Basins, produced a lesser expansion recorded only at the higher site in the southern Atacama.

The so-called "Arid Diagonal" of South America (Abraham *et* al., 2000), which defines the transition between winter and summer precipitation regimes in the Atacama, shifted back and forth only slightly between 24 and 26ºS, north during the full glacial and south during the late glacial-early Holocene. The imprint of these shifts on modern floras and faunas of the Atacama remains fertile ground for biogeographic studies. Northern extension of the westerlies, for example, could explain Quaternary dispersal of southern taxa into northern Chile, including *Junellia, Mulinum, Chuquiraga, Azorella* and *Tetraglochin* (Villagran, 1995). A similar case has been made for expansion of now extinct megafauna into northern Chile (Moreno *et al*., 1994). By the same token, southward extension of summer rainfall could have produced peripheral isolates of rodents in the central and southern Atacama, which in turn have could have led to allopatric speciation (Kuch *et al*. 2001).

The Monte Desert

Rodent middens are also being studied east of the Andes in the Monte Desert of Argentina. The Monte Desert covers ~40 million ha from 24-43ºS, and is surprisingly uniform in physiognomy and floristic composition. It is rich in endemic genera and species of plants and insects. The Monte is a xerophytic scrubland dominated by three

species of creosote bush or "jarilla" (*Larrea divaricata, L. cuneifolia,* and *L. nitida*) in association with a wide variety of mostly microphyllous, dry-deciduous, and aphyllous shrubs. There are relatively few herbaceous elements in the Monte flora, and annuals consists mostly of summer-flowering grasses. The Monte is a warm desert and more than 60% of the precipitation falls in the summer months. There are conspicuous floristic similarities between the Monte and Sonoran Desert, including 10% overlap in plant genera, most of which comprise the dominant vegetation in both deserts (e.g., *Larrea, Prosopis, Acacia, Celtis, Cercidium, Condalia, Ziziphus, Cereus*, and *Opuntia*). During the International Biological Program's Structure of Ecosystems Subprogram (IBP-SES) in 1968-1974, the likeness between the Sonoran and Monte Desert inspired studies of how communities in similar but geographically distant habitats converge in composition and function given same environmental pressures (Orians & Solbrig, 1977). One of the glaring differences, the dominance of seed-hoarding heteromyids in the Sonoran and the lack of granivorous rodents in the Monte (Mares and Rosensweig, 1976), has fueled a persistent dialog about worldwide differences in desert granivory (Lopez de Casenave *et al*., 1998; Marone *et al*, 2000; Saba and Toyos, 2003). The midden record from the Monte extends this dialog to further consider the hand of history.

Unlike the Atacama and North American deserts, midden chronologies from the Monte exhibit surprising stability. In the Monte, evidence is lacking for the kinds of latitudinal and elevational displacements documented for the other deserts. Despite evidence for significant glacial advances down major Andean valleys at 33-35˚S (Espizua, 1999), Andean floras were not displaced hundreds of meters downslope. Also, there apparently was no wholesale, northward expansion of forest elements (*Araucaria*, *Austrocedrus*, and *Nothofagus*) that today reach their northern limits at ~38-40ºS. Furthermore, dung deposits in Monte caves show that, prior to 12 kyr B.P., ground sloths browsed the same shrubs and herbs now growing at the site (Garcia and Lagiglia, 1999; Hofreiter *et al*. 2003). Holocene midden series from the Patagonian-Monte elevational transition, the southern equivalent to the desert-woodland ecotone, display none the sequential departures and arrivals typical of North American midden series (Betancourt et al. 2003).

While the modern Sonoran and other North American deserts were mostly wooded during Quaternary glaciations, the Monte stayed desert throughout the last glacial-interglacial cycle. Although the southern westerlies and winter storm tracks may have shifted far enough north to drive vegetation changes in the southern Atacama during the Last Glacial Maximum (LGM), the imposing rainshadow muted their impact on the leeward side of the Andes. The seasonality of precipitation in the Monte remained unchanged. During the glacial period, summer precipitation in the Monte Desert must have decreased with continental cooling, but the decrease was probably offset by cooler summers. Effective moisture thus remained more or less the same during glacial and interglacial stages.

So what does this have to do with desert granivory? First, I concur with Lopez de Casenave *et al.* (1998), who suggest that granivory in the Monte is not abnormally depressed compared to most deserts, but that it is exceptionally high in the Sonoran Desert due to some quirk of history. That quirk probably involved the evolutionary consequences of cyclical migration of the northern westerlies and winter storm tracks to lower latitudes. Today, annual plant species comprise 50% of local floras in the Sonoran Desert, and of these about 60 to 80% are winter annuals (Venable & Pake, 1999). This is in spite of the fact that summer rainfall generally exceeds 50% of the annual average, and is much more predictable from year to year than winter precipitation. After abundant winter rains, mostly in the occasional El Niño year, spring-blooming annuals add millions of seeds to the soil seed bank, renewing the major food source for granivores. The blooms clearly stimulate spring reproduction in rodents and the highly-synchronized and broadscale masting occurs in the arid foresummer, when there is little else to eat. It is easy to imagine how climatic fluctuations during the Quaternary could have driven an impressive radiation of winter annuals and seed-hoarding heteromyids, which flourished in pinyon-juniper woodlands during the winter-wet glacial periods and persisted in desertscrub during dry interglacials. The only comparable climatic histories include smaller areas in the southern Atacama, southern Namibian, and the Israeli deserts. The other deserts of the world, like the Monte, were presumably stable throughout the Quaternary and exhibit average levels of granivory (Betancourt *et al*., 2003).

Paleobiogeography and surficial processes in deserts

In understanding landscape evolution and surficial processes, there are myriad applications for the kinds of explicit paleobiogeographic information yielded by middens. In the Atacama, for example, we can specify times and places when vegetation has invaded what is now Absolute Desert. This means that we can uniquely study the influence of vegetation on the physics, chemistry and biology of desert soils by comparing sites that have supported or now support vegetation with those that have never been occupied by vascular plants (Rech *et al*., 2003). While vegetation and its influence on desert soils has remained more or less constant in the Monte Desert of Argentina, this has not been the case in the North American deserts. It is clear that soil age and properties heavily influence the distribution of desert plants (McAuliffe, 1994), but it is just as clear that on older surfaces modern vegetation is in disequilibrium with slow-accumulating properties of the underlying soil. Many soil processes such as the more advanced stages of soil carbonate formation (e.g., K or petrocalcic horizons) take 10^4 to 10^5 yrs to develop. If pinyon-juniper woodland has alternated with desertscrub across every glacial-interglacial cycle, and glacial periods tend to be at least five times longer than interglacials, then the older soils in the warm deserts of North America must have developed primarily under pinyon-juniper woodlands and not desertscrub. These are not desert soils.

In the Mojave Desert, midden data have been crucial to understanding the distribution of desert pavements, a characteristic and somewhat enigmatic, geomorphic surface in arid environments worldwide. Desert pavements are conspicuous surfaces of closely-packed angular or rounded rock fragments, usually one or two fragments thick, overlying a stone-free layer of fine, eolian sediment. The exposed surfaces of the coarse fragments are commonly coated with a dark patina called desert varnish. There has been considerable discussion about what forms desert pavements and, given their inherent mechanical weakness, what contributes to their long-term stability (McFadden *et al*., 1987).

Quade (2001) has adapted what we know about paleozonation of vegetation with elevation to estimate the ages and rates of formation for desert pavements and associated rock varnish in the Mojave Desert. First, he examined the relationship between pavement

density and modern vegetation cover along elevational gradients to show that vegetation is the main agent of pavement disruption. Today, desert pavements do not occur above 1800 m, roughly the lower limit of pinyon-juniper woodland. As recounted earlier, these woodlands extended down to 400 m during the last glacial period until ~13 kyr B.P. Therefore, desert pavements have never formed above 1800 m in the Quaternary, all desert pavements above 400 m are of Holocene age and only those pavements below 400 m could possibly be of Pleistocene age. This work not only constrains the use of desert pavement as a way to date Quaternary surfaces, but also has implications for inferring paleoclimate from desert varnish (Broecker and Liu, 2001). In the course of his study, Quade (2001) determined that rock varnish preservation varies as a function of clast size. Hence, only pavements below 400 m can preserve multiple glacial-interglacial varnish-forming in clasts of different sizes.

Bioclimatic modeling with midden data

Various types of models are currently being used in the western U.S. to understand and predict large-scale vegetation responses to past and future climate change, including shifts in the distribution of biomes and individual species. At regional scales, deterministic biogeographic models can simulate the distribution of biomes, including deserts. Models such as BIOME (Haxeltine *et al.*, 1996), DOLY (Woodward *et al.*, 1995), and MAPPS (Neilson, 1995) are deterministic renditions of the climate-life zone correlations implied in the Holbridge (1967) classification. These models simulate the distribution of growth forms across spatial grids of 0.5° resolution for global vegetation and 10-km resolution for subcontinental scales. Because they are deterministic, these models can be verified by comparing simulated vs. actual biome distributions. Such physiognomic or biome models are difficult to use for predicting finer-scale changes within deserts, which usually encompass many functional types and dominant species.

In the absence of complete knowledge about physiological tolerances, species-based biogeographic models tend to be statistical, and entail constructing climatic envelopes around species distributions and abundances (see summaries in Franklin, 1995; Scott et al. 2002). These statistcal models are intended to describe "climate spaces" occupied by individual species. They are arguably circular, but nevertheless useful for

exploring the bioclimatology of modern species, and for generating climatic reconstructions from distributional shifts through time.

The most commonly-used statistical biogeographic model in the western U.S. (referred to herein as the USGS-OSU Model) envisions plant distributions as stochastic, spatial realizations of response surfaces-- functions that describe the way in which each species' expected distribution and abundance depends on the combined effects of several environmental variables (Bartlein *et al.*, 1998; Thompson *et al*., 1998, 2000a, b and c). Solutions of the climate space occupied by a particular species vary widely, but generally start with development of a climate database for the region of interest, interpolated into grid cells at the desired resolution. The USGS-OSU Model uses a least-squares estimation technique to develop regression equations for estimating the monthly and annual values for temperature and precipitation at each point in an equal-area 25-km grid as functions of location and elevation. A Digital Elevation Model (DEM) is used to calculate the mean elevation across each grid cell, and climatic variables for that elevation (grid point) are estimated from local relationships between elevation and climate. This should only be considered a first approximation. Mean climate at the mean elevation is hardly representative of the whole suite of elevations that can occur in a 25-km grid cell, roughly the same area as some desert mountain ranges . In such cases, the mean elevation may be 1500 m, but the grid cell can encompass desert (0-1400 m) to subalpine (>3000 m) elevations. Using digitized range maps, the USGS-OSU Model determines at which of the points on the 25-km grid a species is present to create a presence-absence matrix of plant distributions associated with modern climate data. Because the distributional data is gleaned from a flat range map, and is not point and elevation-specific, the same climatic value (the mean climate of the mean elevation of one grid cell) would be assigned to a saguaro (*Carnegiea gigantea*) as a corkbark fir (*Abies lasiocarpa* var. *arizonica*). I say this not to be disparaging-- the USGS-OSU Model is a good first approximation and lays out some of the necessary groundwork-- but rather to point out critical data needs in the future.

Response surfaces from the USGS-OSU Model can be mapped for times in the past using the output from general circulation models (GCM's) forced by changing boundary conditions such as insolation and CO_2 levels. This top-down modeling

approach can be used to determine the probability of species occurrence for simulated modern climate. For most western U.S. species, the modern range aligned with the 0.4 probability of occurrence in the simulated distribution for species in the western U.S. (Thompson et al. 2000 a,b and c). A related approach involves biomization, or the grouping of individual plant taxa in plant functional types (PFTs), specification of the set of PFTs that can occur in a biome, and then construction of climatic envelopes for each of the biomes (Thompson and Bartlein, 2000).

The USGS-OSU Model has been used to extract climatic information from individual species, as well as biome distributions (gleaned from both midden and lake pollen data), in western North America since the Last Glacial Maximum (Bartlein et al., 1998; Thompson and Anderson, 2000; Sharpe 2002). Interestingly, plant macrofossils from packrat middens and pollen spectra from lakes, when available from the same region, yielded identical biome reconstructions (Thompson and Anderson, 2000). This explains the long-recognized agreement between Late glacial vs. modern vegetation maps of the southwestern U.S. based on pollen in lakes (Martin and Mehringer 1965) and woodrat middens (Swetnam et al., 1999). Finally, other geostatistical approaches using point-specific plant distributional data are been used to develop climatic envelopes and reconstruct paleoclimates from Sonoran Desert middens (Craig et al. 2000, 2003; Arundel 2002).

Rewards of a rich archive: morphological, isotopic and genetic studies

A side benefit of the midden work has been the accumulation of a rich archive of plant and animal remains identified to species and spanning one of the most dramatic transitions in the geologic record. Between 15 and 12 kyr B.P., atmospheric CO_2 concentrations increased by 30%, land temperatures increased by 5-10ºC, seasonal precipitation regimes shifted, and there were broadscale changes in biotic distributions, at least in some deserts. Midden researchers are taking advantage of this rich archive by conducting a variety of morphological, geochemical and molecular analyses to develop unique insights about evolutionary and ecophysiological responses to global change.

For example, two characteristics of plant gas exchange and water relations that are quantifiable by measurement in modern and ancient plant leaves are stomatal density

and stable isotope variations. These parameters are sensitive to changes in climate as well as atmospheric CO_2 levels, such as have occurred since industrialization (280 ppmv to 360 ppmv), and during the last deglaciation (200 to 280 ppmv). To evaluate ecophysiological responses to environmental variability, stomatal density and stable isotopes (δD, $\delta 0^{18}$, & $\delta^{13}C$) are being measured across individuals, across environmental gradients, and through time in modern populations, time series of herbarium specimens, and fossil leaves of species with different life histories and photosynthetic pathways (C_3, C_4 and CAM)(Van de Water *et a*l, 1994, Pendall *et al*. 1999, Pedicino *et al*. 2002, Van de Water *et al*. 2002, Telwilliger *et al*. 2002). There are many take-home messages from this body of work. For example, plants responded to CO_2 enrichment during deglaciation by reducing stomatal density and increasing water use efficiency (WUE) *(Van de Water et al*., 1994). These savings in WUE, however, were not enough to offset increasing aridity, so Holocene deserts quickly replaced Pleistocene woodlands. At some threshold in effective moisture, climate trumps direct CO_2 effects on vegetation dynamics.

Stomatal characters in fossil leaves from middens also have allowed detailed mapping of polyploidy races of creosote bush since the Last Glacial Maximum (Hunter et al. 2001). North American creosotebush (*Larrea divaricata* var. *tridentata*) generally exhibits a classic and much discussed gradient of diploidy in the Chihuahuan Desert, tetraploidy in the Sonoran and hexaploidy in the Mojave. Stomatal guard cells increase in size with increasing amounts of DNA and ploidy level, allowing ploidy levels to be inferred from fossil leaves. Using the extensive midden record for creosote bush, Hunter et al. (2001) showed that the higher ploidy races had not evolved with Holocene migration from Mexico into the southwestern U.S., as previously thought, but rather were already present during the last glacial and simply reorganized their distributions in the Holocene. A moral to this story is that populations, and not whole species, migrate. Modeling the response of creosote bush to climate change would produce quite different outcomes by simply changing the unit of analysis from the whole species to the individual ploidy race.

The midden record also provided a novel opportunity to gage the influence of climate on a key animal, the woodrat itself. Woodrats are particular sensitive to environmental temperature and, as predicted by Bergmann's Rule, a strong correlation

exists between mean adult body mass and ambient temperature across populations in the western U.S. It turns out that diameter of woodrat fecal pellets, which are abundant in individual middens, are highly correlated with body size. If that's the case, then how did body size change in particular species of woodrats with late Quaternary fluctuations in ambient temperature? At hand was the opportunity to secure quantitative measures of the magnitude and rates of genetic change (versus phenotypic plasticity) associated with the evolution of a basic determinant of physiology, ecology and behavior- that is, body size. In the first midden study, a 6ºC warming was inferred from body size changes in *Neotoma cinerea* during the last deglaciation, a temporal test of Bergmann's Rule (Smith et al 1995). There have been follow-up efforts to hone this apparent paleothermometer, apply it throughout the Holocene, and use fecal pellet diameter to delineate areas of past sympatry between different species of woodrats (Smith and Betancourt, 1998, 2003). Advances in ancient DNA could add a genetic dimension to these body size studies.

The advent of polymerase chain reaction (PCR) has not only enhanced molecular phylogeography, it has also made possible identification of ancient DNA sequences from bones and plant and animal tissue. There have been a few technological hurdles to overcome. PCR amplification of the DNA is apparently blocked by cross-links between reducing sugars and amino groups. These cross-links are generally the product of Maillard reactions, a series of condensation reactions that bind proteins and carbohydrates with long-term preservation of plant and animal tissue. Recently, it was discovered that such cross-links can be cleaved by the chemical reagent, N-phenacylthiazolium bromide (PTB)(Vasan *et al*., 1996), permitting routine amplification of both mitochondrial (mtDNA) and chloroplast DNA from a variety of depositional settings, including dry caves in the Americas (Poinar *et al.*, 1998; Hofreiter *et al*., 2000). Such dry caves had not yielded nuclear DNA, which until recently was thought to preserve only in permafrost. Nuclear DNA is typically longer and contains more information than mtDNA, which could allow resolution of phylogenies, determination of sex, and characterization of genes in phenotypic traits. A major breakthrough was made recently when Poinar *et al*. (2003) recovered single-copy nuclear DNA from the dung of Shasta ground sloth (*Nothrotheriops shastensis*) at Gypsum Cave, Nevada. In this particular instance, nuclear DNA resolved a previously intractable problem, mainly that

the extinct Shasta ground sloth and extant three-toed sloth (*Bradypus*) share a more recent ancestor than do the Shasta and extant two-toed sloth (*Choeloepus*).

It is only a matter of time before rodent middens, surely the richest sources of well-preserved and dated plant and animal tissue in the American deserts, become one of the more popular targets for such genetic studies. The first successful studies involved two South American middens, one from the southern Monte and the other from the central Atacama. The Monte midden was made by a vizcacha but also incorporated numerous fragments of larger herbivore dung dated at 17.3 and 16.2 kyr B.P. Phylogenetic analyses of the mitochondrial 12S rDNA show that the dung originated from a small ground sloth species not yet represented by skeletal material, and not closely related to any of the four previously sequenced (*Nothrotheriops* and *Mylodon*) extinct and extant sloth genera (*Choelopus* and *Bradypus*) (Hofreiter *et al*., 2003).

The second genetic study showed that *Phyllotis limatus*, a leaf-eared mouse, was the principal agent in accumulation of an 11.7 kyr B.P. midden from the Atacama Desert (Kuch et al. 2002). The modern and ancient sequences reported in this paper reinforce the proposal that *P. limatus* was derived very recently from a western lineage of *P. xanthopygus rupestris* (Steppan, 1998). The midden agent apparently was part of the ancestral *P. limatus* populations that extended at least 100 km further south than today. This expansion happened during the summer pluvial event that affected the northern and central Atacama between 14 and 10.5 kyr B.P.

Frontiers of rodent midden analysis and desert paleobiogeography

The growing midden database for North and South America has great potential for populating and testing a wide variety of biogeographic models to address key questions such as the role of history in community assembly, species coexistence and biodiversity. For now, applications of biogeographic models have been limited to estimating paleoclimates from past distributions and predicting future vegetation from global change. The bioclimatic models that already have been applied in the western U.S. are elegant, but leave much room for improvement. Probably the greatest limitation in deserts is the lack of point-specific georeferenced data for plant distributions, and reliance instead on digitized flat range maps. This will be less of a problem to remedy in

the Atacama and Sonoran Deserts, where there are at least some digitized atlases of plant distribution (e.g., Turner *et al*. 1995; Marticorena *et al*. 1998), though these compilations are incomplete and influenced by sampling bias (Burgess *et al*., 1995). Ongoing efforts such as the Gap Analysis Program (http://www.gap.uidaho.edu/) and SALVIA (Spatial Analysis of Local Vegetation Inventories Across Scales: http://www.salvias.net) deserve our full support.

In the South American deserts, there also is a lack of appropriately-gridded climatological data that can be extrapolated to all points of species occurrence across complex topographies. The western U.S., however, has a well-honed and accessible analytical tool (PRISM- Parameter-Elevation Regressions on Independent Slopes Model) that uses point data, a digital elevation model, and other spatial data sets to generate gridded estimates of monthly, yearly, and event-based climatic parameters, such as precipitation, temperature, snowfall, degree-days, and dew point (Daly et al. 1994). The low density of weather stations may thwart extension of PRISM to South America.

At present, few of the biogeographic models integrate physical parameters other than climate, even though soils and substrate, for example, can explain a large portion of both the local and regional variance in plant distributions across complex landscapes typical of some deserts (McAuliffe, 1998; Lyford *et al.*, 2003b). Bigeographic models also presently ignore that the distribution of a given species to some degree reflects interactions with other plant and animal species, such as competition and plant-herbivore interactions (Davis et al., 1998).

Existing biogeographic models are only static comparisons of past, present and future distributions, with little regard to how a species might actually shift from one distribution to the other. The real breakthroughs will come with the marriage of bioclimatic models with cell automaton and other spread models (e.g., Carey, 1996; Aassine and El Jaï, 2002) that incorporate both short and long-distance dispersal capabilities, population dynamics in the context of varying and not just changing climate, and the permeability of heterogeneous landscapes to invasion. Now that we know the migrational histories of many species in western North America, perhaps it is time to bring back and apply the chronosequence approach in ecological field studies. To what extent are population, community and ecosystem properties (e.g., genetic distance from

source populations, biodiversity, heterogeneity of soil resources, erosion potential, etc.) a function of time since arrival of the dominant plant species? Could integrated biogeographic models be developed and tested as formal platforms for exploring the spatial-temporal context of modern phylogeographic structure in populations of species with well-known migrational histories such as woodrats, creosote bush, Utah juniper, and pinyon pine?

Phylogeographers increasingly rely on the historical record to evaluate the plausibility of their interpretation (e.g., Mitton et al. 2000), still many biogeographic and evolutionary models based on modern phylogeography remain unverified. Rather than voicing general skepticism about phylogeographic methods, I think it is this lack of verification that prompted Brown (1995, p. 191) to lament that, "it would be difficult or impossible to reconstruct the spatial pattern of the history of lineage." In the American deserts, however, ancient DNA breakthroughs could provide an unprecedented opportunity to conduct phylogenetic analyses of both modern and ancient rodent populations at comparable spatial resolutions.

Recent analyses of ancient cytochrome *b* fragments from fecal pellets have proven reliable in identifying rodent agents of fossil middens (Kuch et al. 2002). This development could provide a springboard for what I term paleophylogeography, permitting phylogeographic structure to be defined directly in fossil populations. This time-lapse view of molecular diversification could provide both the dynamics of datable range shifts and the timing of origination of phylogeographic structure observed today. This comparative effort can also furnish a set of empirical tests for the analytical methodology of population genetics and coalescence theory.

The molecular phylogeographic structures of several western species of *Neotoma*, based on mtDNA cytochrome *b* gene sequences, have been studied well enough in modern populations to construct detailed phylogenetic trees and generate a battery of historical hypotheses (Planz *et al*. 1996; Edwards *et al*., 2001; Patton and Alvarez-Castañeda 2002; Matocq, 2002). Though fossil teeth already provide several genetic hypotheses, they are sporadically available, and preclude identification of subspecies or geographic clades. In the majority of dated middens, there are sufficient fecal pellets remaining in the archived material for mtDNA and with a bit of luck, nuclear DNA

analyses. More middens could be collected from key areas to supplement the existing archive or to focus in on geographic clade boundaries of special interest. We have already begun such an effort for *N. lepida* (Betancourt, Patton, Smith and Poinar, in progress) in the Great Basin, Mojave and Sonoran Deserts, and understand there is a similar study under way for *N. cinerea* in the northern Great Basin (Marjorie Matocq, pers. comm.). Of the three widespread midden agents in South America (*Abrocoma*, *Lagidium*, and *Phyllotis*), the molecular phylogeographic structure is only adequately known for *Phyllotis* (Steppan, 1998). We expect to extend the initial results of Kuch *et al*. (2002) to further characterize the phylogenic history of this *Phyllotis* in the Atacama Desert.

Even with the many advances in arid lands paleobiogeography, there remain a number of physical, conceptual and technological frontiers for rodent midden research. Despite 40 years of midden surveys, there is still plenty of unexplored terrain in North America. For example, there's been surprisingly little work in Baja California and the Mexican mainland, and the coverage for some states (Arizona, California, Colorado, Idaho, and Utah) is patchy at best. Also, much of the fieldwork was done before 1990, when resources were scarce and chronologies consisted of at most two dozen middens. Precise timing has become critical in our ability to sort out leading explanations of both regional and global climate change in the late Quaternary, justifying resampling of key midden sites. There is even more unexplored territory in South America ranging from Patagonia to northern Peru. As might be expected, mammals also produce middens in other parts of the world. Paleoecologists have long nibbled at the midden record from Africa and Australia with modest results (see discussion in Pearson and Betancourt, 2002), but midden potential exists even in the aridlands of central Asia and the Middle East. In the meantime, the rich midden archive keeps increasing its holdings, and our ability to make morphological, geochemical and genetic measurements continues to improve. As a final example that is particularly germane to contemporary biogeography, there are still unlimited opportunities to explore how scaling of plant anatomy might have behaved under dramatically different temperature and atmospheric CO_2 levels.

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