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Rodent Middens

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Introduction

The study of Pleistocene terrestrial environments has tended to focus mainly on the middle and high latitude regions where water-lain deposits (lake sediments, peat bogs, fluvial deposits) tend to be well preserved. By their very nature, most desert and semi-arid regions offer few if any archives of waterlain sediments for such studies. However, an important, if unexpected archive of Pleistocene desert environments does exist, in the form of rodent middens. Rodent middens are produced by *Neotoma* (packrats) and *Erethizon* (porcupine) in North America; *Lagidium* (viscacha), *Phyllotis* (leaf-eared mice), *Abrocoma* (chinchilla rats) and *Octodontomys* (mountain degu) in South America; *Procapra* (rock hyrax) and *Petromus* (Dassie rat) in Africa and the Middle East;

Alticola (mountain voles) and *Ochotona* (pikas) in central Asia, and *Leporillus* (stick-nest rats) in Australia. The studies of South American middens have mostly concerned pollen analysis, although a few plant macrofossil records have been developed (Betancourt *et al.*, 2000; Latorre *et al.*, 2002). The studies of hyrax middens from the Middle East and desert regions of Africa have focused mainly on pollen (Scott and Vogel, 2000). The few studied Stick-nest rat middens in Australia are all of late Holocene age (Pearson, 1999). Little research has been done on porcupine middens in North America, although these middens are known to persist as long as 25,000 years in arid conditions (Betancourt *et al.*, 1986). The middens of North American packrats have yielded by far the most well-studied records of late Pleistocene plant macrofossils. This article focuses primarily on this remarkable record.

North American Packrat Middens

Packrats, or woodrats, are the native North American rats of the genus *Neotoma* (Fig. 1). There are 21 species in this genus. These rats are broadly distributed, ranging from Arctic Canada to Nicaragua. They are a very successful group, and only a few species inhabit desert and semi-arid regions. While packrats are not strict herbivores, plants are by far the most important part of their diets. Packrats live in dens. Regardless of size, each den is occupied by one individual, or the female and her young. These dens range from piles of sticks



Figure 1 Photograph of a packrat (*Neotoma*), the principle agent of plant materials that become incorporated into packrat middens (photo courtesy of Corel Corporation).



Figure 2 Packrat (*Neotoma*) midden sample from a rock shelter at Emery Falls, Grand Canyon, Arizona. Photo by Thomas Van Devender. The shiny surface is amberat (dried packrat urine). Note fossil conifer needles that have weathered out from the broken edge of the midden.

under shrubs or trees to more elaborate shelters in caves and rock shelters. In the arid Southwest, these dens often include tightly-packed bundles of cactus stems that deter predators. Besides bedding material and food plants, packrats also accumulate other objects from the surrounding landscape. These objects, plus packrat feces, are cemented together by successive layers of dried rat urine to form a midden (Fig. 2). The crystallized urine layers encapsulate plant materials and rat feces to form a hardened mass, called amberat. When protected from direct rainfall and high humidity, amberat is extremely resistant to decomposition. It secures biological specimens (plant parts, bones, insects, etc.) into a kind of desiccated time capsule, documenting the ancient life of the region. Middens of late Holocene age have been found throughout the western United States and southwestern Canada (Hebda *et al.*, 1990). In the arid regions of the southwestern United States and northern Mexico, many packrat middens have remained intact beyond the limit of the radiocarbon dating method (> 45,000 years).

Packrat ecology has been described by Vaughan (1990). Packrats require succulent plants for food, and they must have shelter, as they do not have the metabolic mechanisms for water retention found in some other rodents. The dens are often built in rock shelters, crevices, and caves, where there is a microclimate that is significantly buffered from ambient climatic conditions. The annual variation of temperatures in packrat dens from mid- to high latitudes is as little as 15 °C. Packrat middens accumulate as long as a den is occupied. In sheltered localities, these middens may accumulate for millennia, as favorable denning sites are inhabited by succeeding generations of packrats. Packrat middens are an unusual source of

fossils, because the packrat is the primary agent that accumulates the materials found in middens. They eat a wide variety of plants, and the unconsumed pieces of these plants eventually form the bulk of the plant macrofossils in midden records. Because of the rodent's food preferences, plant macrofossil records from middens do not represent the full spectrum of regional vegetation; nevertheless, the variety of plant species found in these assemblages can be truly remarkable. Dial and Czaplewski (1990) discussed the problems of potential bias in packrat midden plant macrofossil assemblages. Their study concluded that if several middens are studied from a given region, then the contemporaneous plant species diversity of that region may be fairly represented in the suite of midden samples. A study of paired samples of modern vegetation communities and paired samples of ancient communities was used to investigate the probability that the absence of a plant taxon from a packrat midden implies absence from the ancient plant community where the packrat lived (Nowak *et al.*, 2000). The probability of the occurrence of a false inference was calculated to be from 7–11%, depending on the taxon. Lyford *et al.* (2004) studied the contents of 59 modern packrat (*Neotoma cinerea*) middens in escarpments and canyons in three states in the Rocky Mountain region. They found that these middens are highly reliable sensors for the presence of key woody plant species, such as *Juniperus osteosperma* (Utah juniper) and *J. scopulorum* (Rocky Mountain juniper), but that other conifers were occasionally absent from modern middens if their presence in the local vegetation cover was less than 20% of the canopy cover.

How Middens Are Analyzed

Packrat midden analysis methods have been described by Spaulding *et al.* (1990). Most ancient packrat middens are indurated (hardened almost to the consistency of rock), and resemble blocks of asphalt. Amberat forms a tough, outer rind that resists erosion and decomposition (Fig. 1). When moist, amberat is sticky. It is this stickiness that often cements middens to the walls of caves or rock shelters. Midden samples are taken by the removal of discrete horizontal sections of midden, often using hammers and chisels. Each sample is radiocarbon-dated, because successive layers in a midden may have been deposited at widely-spaced time intervals, or occasionally in random order. Radiocarbon dates are often obtained from packrat fecal pellets, or from plant macrofossils. The majority of middens are of Holocene and late Wisconsin age (Fig. 3).

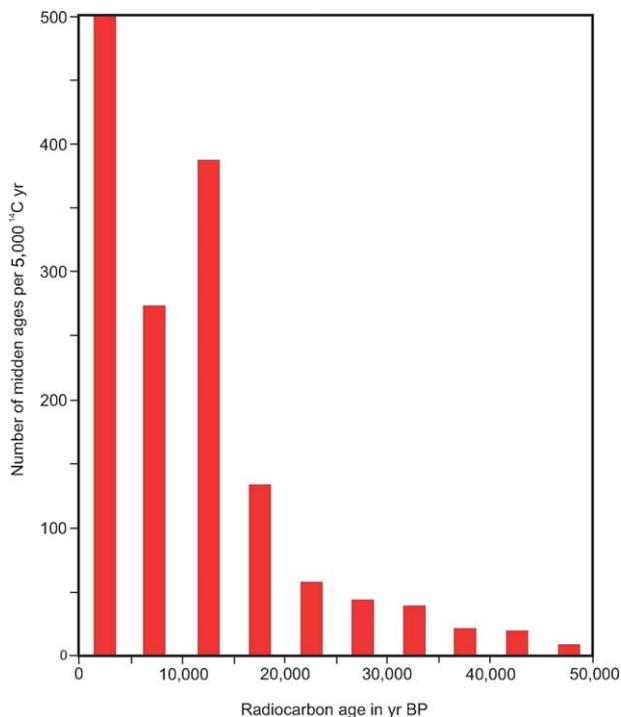


Figure 3 Distribution of radiocarbon ages of packrat middens from the southwestern United States and northern Mexico, after Thompson *et al.*, 2004.

Following rehydration in a laboratory, the samples are wet-screened to remove fine sediment, then dried and sorted under a low-power microscope. The plant macrofossils are picked out and sorted from this dried matrix. Macrofossils from individual species of plants are sometimes submitted for AMS radiocarbon dating (*see* AMS Method).

Plant macrofossils from middens are frequently identified to the species level. Midden plant macrofossil analysis is generally done on a presence/absence basis for each identified taxon. Occasionally, a subjective quantification of the remains is conducted, either through application of a relative abundance scale (rare, common, etc.), or through specimen counts and dry weights of materials. The results of plant macrofossil analyses are often tabulated in terms of relative species abundance. They are separated into categories such as rare, common, abundant, and very abundant.

Distribution of Fossil Sites in the Arid Southwest

Figures 4 through to 7 illustrate published packrat midden records from southwestern North America. Dozens of sites have been studied in each of the major desert regions discussed below, and more than a thousand radiocarbon dates have been obtained from regional midden samples. Most of the midden

samples discussed here have been taken from canyons and rocky hillsides, just above the desert floor. In the American Southwest, no Pleistocene middens have been sampled at elevations greater than 2,500 m. The elevational distribution of midden samples reflects regional physiography. Sites south of 36° latitude generally occur at elevations below 1,500 m, while more northerly sites reflect a broader range of elevations.

Regional Studies

Chihuahuan Desert

The Chihuahuan Desert is an interior continental desert, stretching from southeastern Arizona in the northwest to northern Zacatecas, Mexico in the southeast (Fig. 4). The desert lies in the rainshadow of the Sierra Madre Occidental to the west and the Sierra Madre Oriental to the east. Sub-freezing temperatures are not uncommon in winter, and Arctic air mass incursions may bring very cold weather to even the southernmost parts of the desert. Today the southern Chihuahuan Desert supports subtropical vegetation, rich in succulent scrub species. This flora diminishes to the north, giving way to more cold-tolerant desert grassland. The plant macrofossil record developed from Chihuahuan Desert packrat middens reveals a series of environmental changes through the late Pleistocene and the Holocene. These changes brought about major shifts in plant distributions, both within the desert (*i.e.*, elevational shifts) and beyond its boundaries (*i.e.*, regional extirpations and the invasion of new species). The plant macrofossil samples studied from this desert range in age from > 43,300 years BP to recent. Regional plant macrofossil records are discussed by Van Devender (1990a).

In the northern Chihuahuan desert, pinyon-juniper-oak woodland dominated limestone slopes during the middle to late Wisconsin interval (42,000 to 12,750 cal years BP). At the northern edge of the desert (Rough Canyon, New Mexico), Rocky Mountain juniper (*J. scopulorum*) began to decline at 14,000 cal years BP, as Holocene warming started and it was regionally extirpated by 12,400 cal years BP (Betancourt *et al.*, 2001). An early Holocene oak-juniper woodland was replaced by desert-grassland after about 9,250 years BP. At Rough Canyon, elements of the modern desert vegetation began dominating packrat midden floras after 5,750 years BP (Betancourt *et al.*, 2001). By about 4,700 cal years BP, the common elements of the Chihuahuan Desert flora had become established throughout the northern Chihuahuan Desert region, forming a relatively

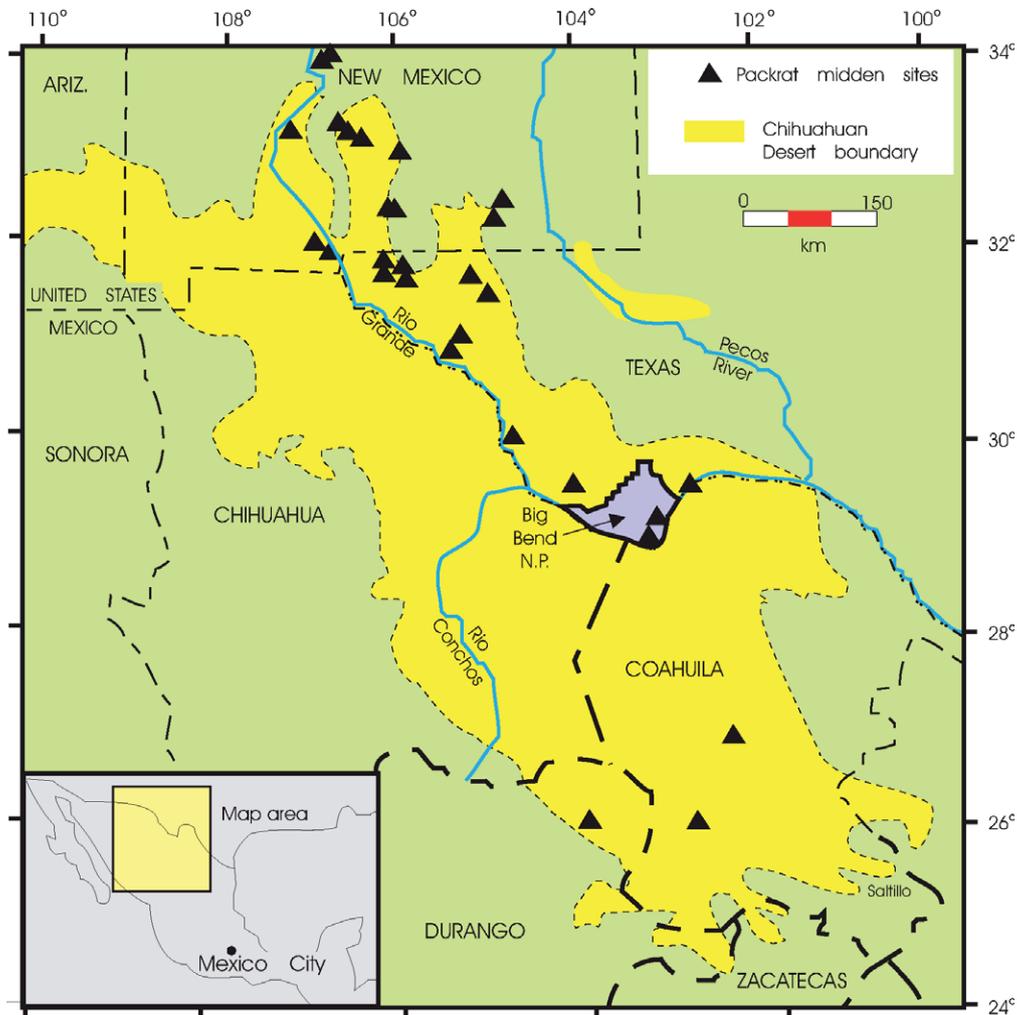


Figure 4 Map of the Chihuahuan Desert region, showing location of packrat middens from which fossil analyses have been published (triangles).

modern desert-scrub vegetation on rocky slopes. This vegetation continues to be regionally dominant today.

In the central Chihuahuan Desert, in and around Big Bend National Park, Texas, the middle Wisconsin vegetation (40,000–26,500 years BP) was a pinyon-juniper-oak woodland on the uplands, and juniper grassland on the lowlands. By late Wisconsin times (prior to 25,000 years BP), papershell pinyon (*Pinus remota*) became important in the upland flora, and pinyon-juniper-oak woodland spread into lowland regions, indicating relatively mild winters, cool summers, and greater precipitation than today. The boundary between late Wisconsin and early Holocene environments (between 13,100 and 12,100 cal years BP) is well marked in the vegetation, with the demise of papershell pinyon and increase of shrub oak (*Quercus pungens*) before 9,200 cal years

BP, followed by a succulent desert-scrub vegetation, including lechuguilla (*Agave lechuguilla*), catclaw acacia (*Acacia greggii*), honey mesquite (*Prosopis glandulosa*), and prickly pear cactus (*Opuntia* spp.). Vegetation diversity increased in the mid-Holocene, signaling the shift to subtropical climatic conditions. More mesic vegetation communities developed here in the last 1,000 years. By the middle Holocene, the vegetation in the lowlands of Big Bend was essentially modern desert-scrub.

In the southern Chihuahuan Desert of Mexico, the late Wisconsin vegetation on limestone slopes was a woodland dominated by juniper and papershell pinyon in association with succulents such as sotol (*Dasylirion*) and beaked yucca (*Yucca rostrata*). Pinyon pine declined after 16,000 cal years BP, as succulents increased. Between 13,600 and 10,550 cal years BP the regional vegetation shifted

to Chihuahuan desert-scrub. The paleobotanical record from this region shows unique combinations of floristic elements. Late glacial floras included both conifers and desert succulents, but macrofossils of temperate plants disappeared from regional records during the middle and late Holocene. A mosaic of temperate and xeric habitats has been available to the regional biota, even during the last 1,000 years, when other regions of the Chihuahuan Desert have experienced extremes of aridity.

Sonoran Desert

This desert comprises the arid, subtropical region centered around the head of the Gulf of California (Fig. 5), encompassing parts of Sonora and Baja California in Mexico, and southern Arizona and California in the United States. All parts of the Sonoran Desert are occasionally subject to winter freezes, although rarely for more than one night at a time. Most of the large, columnar cacti that characterize the Sonoran Desert are not able to tolerate prolonged freezing. Rainfall ranges from a bi-seasonal pattern with summer monsoon moisture in Sonora and Arizona to a winter rainfall pattern along the west coast of Baja California. Changes in large-scale atmospheric circulation patterns during the Wisconsin glaciation caused changes in Sonoran Desert regional climates, especially in precipitation patterns and the frequency of winter freezes.

Unlike the Chihuahuan Desert, the plant macrofossil record from Sonoran Desert packrat middens indicates that regional vegetation succession from the late Wisconsin through the Holocene made a single,

continuous progression toward modern plant communities. The regional paleobotanical record has been summarized by Van Devender (1990b). The chronological sequence of plant communities during the last 20,000 years is similar to the modern vegetational gradient from the tops of mountains to valley floors. This history is summarized in Table 1. Central and southern Arizona were clothed with a variety of woodlands in the late Wisconsin. In upland regions, juniper or juniper-oak woodlands persisted until the early Holocene. Juniper died out in the Sonoran Desert after 10,000 cal years BP. The vegetation of lowland Sonoran regions has been desert-scrub since the early Holocene. Desert-scrub communities, including species found today in the Mojave Desert, persisted in the harsh lowlands of the lower Colorado River valley throughout the late Pleistocene. It is thought that this region may have served as a refugium for North American desert plants for much of the Quaternary. Typical Mojave Desert species migrated north along the Colorado River and crossed over it only during the warmest (interglacial) periods. The ecotone (ecological boundary) between the Sonoran and Mojave Deserts has essentially remained in its current position since 10,000 cal years BP. After 4,500 cal years BP, modern vegetation became established throughout the Sonoran Desert.

Based on the plant macrofossil evidence, late Wisconsin climate in the Sonoran Desert had cooler-than-modern summers and a dominance of winter precipitation. While winters may have been generally cooler, it appears that freezing conditions were actually rarer than today, a remarkable finding, given the degree of climatic cooling associated with North American glacial climates in regions further north. Early Holocene Sonoran climates were transitional between late Wisconsin and modern climates. Regional summer temperatures probably remained cooler, based on the persistence of conifers in the uplands. Parts of south-central Arizona received up to 30% more precipitation than today in the early Holocene. A relatively modern climate was established after 10,000 cal years BP, characterized by hot summers. Mid-Holocene plant macrofossil assemblages indicate greater species richness than today, probably because of increased rainfall. While the packrat midden results are internally consistent throughout the Sonoran Desert, none of the regional paleoclimatic reconstructions based on these fossil data have supported the results of general circulation model simulations for the early and middle Holocene (Van Devender *et al.*, 1994). By 4,500 cal years BP, a completely modern climatic regime was established in the Sonoran Desert.

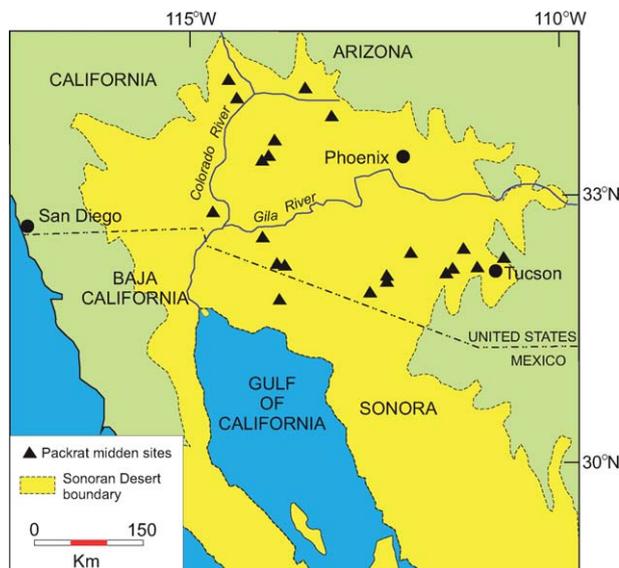


Figure 5 Map of the Sonoran Desert region, showing location of packrat middens from which fossil analyses have been published (triangles).

Table 1 Summary of Changes of Sonoran Desert Vegetation Inferred from Packrat Midden Data (after Elias, 1995)*Region Time Interval Vegetation***Central Arizona**

Uplands late Wisconsin Pinyon-juniper-oak woodland (550–1,550 m)
 Early Holocene Juniper-oak woodland with Sonoran desert-scrub
 Late Holocene Sonoran desert-scrub with increasing subtropical elements
 Lowlands late Wisconsin Juniper woodlands and/or Mohave desert-scrub (<600 m)
 Early Holocene onwards Sonoran desert-scrub

Southern Arizona

Uplands late Wisconsin Pinyon-oak-juniper woodland with Joshua tree (550–1,550 m)
 After 13,000 cal years BP Xeric juniper woodland with shrub oak or chaparral
 After 10,000 cal years BP Juniper disappears from entire region
 Lowlands late Wisconsin Xeric juniper woodland with Joshua tree, yucca, beargrass (600–300 m)
 Early Holocene desert-scrub common
 After 4,500 cal years BP Modern Sonoran desert-scrub

Baja California

Lowlands early Holocene abundant Boojam tree; buckwheats and Mormon tea (0–400 m) in desert-scrub community
 Late Holocene Boojam tree less abundant; buckwheats and Mormon tea disappear; increasing succulents

Mojave Desert

The Mojave is a small, topographically complex desert, situated in southern Nevada and adjacent California and Arizona (Fig. 6). The modern vegetation of the southern Mojave Desert (south of 36° N latitude) is dominated by creosote bush (*Larrea divaricata*), white bursage (*Ambrosia dumosa*), and pygmy-cedar (*Peucephyllum schottii*). The northern Mojave region is generally higher in elevation, and the modern vegetation here is a temperate desert-scrub, including blackbrush (*Coleogyne ramossissima*), Joshua tree (*Yucca brevifolia*), ground-thorn (*Menodora spinescens*), boxthorn (*Lycium* spp.), and goldenbushes (*Haplopappus* spp.). The higher mountains in southern Nevada

support pinyon-juniper woodlands above 1,800 m elevation, giving way to fir-pine forest above 2,200 m. Bristlecone pine (*Pinus longaeva*) dominates subalpine landscapes above 2700 m.

The late Wisconsin and Holocene vegetation history of the Mojave Desert has been discussed by Spaulding (1990, 1995), and is summarized in Table 2. The northern Mojave region has yielded more packrat midden studies than the southern region. During the late Wisconsin period, woodlands extended downslope on to the Mojave lowlands. These were ‘pygmy’ woodlands, composed primarily of juniper (mixed with pinyon pine at elevations below 1,500 m), shrub oak, and Joshua tree in some regions. During the last glacial maximum in the northern Mojave, elevations above 1,600 m had populations of limber pine (*Pinus flexilis*), replaced at times by white fir (*Abies concolor*). The lower reaches of the Grand Canyon lie in the southeastern corner of the Mojave Desert. During the late Wisconsin, this region supported more succulent species, including barrel cacti and yuccas.

By 11,600 cal years BP, a major shift in Mojave vegetation was underway: desert-scrub vegetation spread across the lowlands, at the expense of semi-arid woodland. However, the transition from glacial to postglacial vegetation was not smooth; it was marked by multiple incursions of new taxa and extirpations of others. Not all of the newly invading species remained throughout the Holocene. The immigration of warm-adapted species from their southern refugia took place in stages. On the other hand, widespread desert vegetation apparently developed earlier in the Mojave than in the Sonoran or

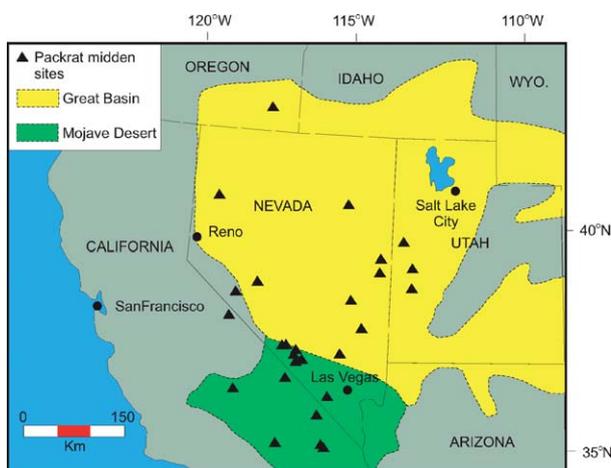


Figure 6 Map of the Mojave Desert and Great Basin regions, showing location of packrat middens from which fossil analyses have been published (triangles).

Table 2 Summary of Changes of Mojave Desert Vegetation Inferred From Packrat Midden Data (after Elias, 1995)*Region Time Interval Vegetation***Southern and Central Mojave**

Lowlands late Wisconsin Juniper woodland (<1,000 m)

Early Holocene desert-scrub widespread by 11,500 cal years BP; succulents and grasses increasing

Uplands late Wisconsin Juniper-pinyon woodland (1,000–1,800 m)

Early Holocene Woodland persists at higher elevations and moist slopes

Mid-Holocene desert-scrub rich in species

Late Holocene downward shift of blackbrush desert-scrub

Northern Mojave

Uplands late Wisconsin desert-scrub in dry locations, with Mormon tea, shadscale, (1,000–1,800 m) rubber rabbitbrush, and snowberry; juniper woodland in most regions; at higher elevations, limber pine in drier sites and white fir in mesic sites

Early Holocene Woodland persists on some slopes; after 8,700 cal years BP, then replaced by creosote bush and Joshua tree scrub

Mid-Holocene desert-scrub lacking in diversity

Late-Holocene rich desert-scrub communities at lower elevations and pinyon-juniper woodlands at higher elevations

Chihuahuan deserts, with the earliest occurrences documented from middens dating to 18,000 cal years BP. By 8,600 years BP, woodlands had been replaced by desert vegetation throughout the lower elevations of the Mojave. An interval of increased aridity is marked by vegetation changes in most regions of the Mojave during the mid-Holocene, but regional packrat midden evidence suggests that effective moisture subsequently increased between 4,200 and 1,400 cal years BP. This increase was probably due to a combination of increased precipitation and decreased temperatures. Conifers retreated up mountain slopes in the Mojave region during the last 1,400–500 years, signaling a return to hotter, drier conditions.

Great Basin

The Great Basin is a large, arid region between the Rocky Mountains and the Sierra Nevada (Fig. 6). This enormous, closed basin is made up of broad valleys of sagebrush steppe, dissected by more than one hundred narrow mountain chains that trend north to northeast. During the last glaciation, immense lakes covered the Great Basin lowlands, and glaciers flowed down from high mountain valleys. In the modern vegetation, sagebrush and shadscale (*Atriplex confertifolia*) dominate the low elevation steppe vegetation. Pinyon-juniper woodland covers most low mountain slopes in the southern two-thirds of the region, while juniper woodland characterizes the northern third. Montane forests of ponderosa pine (*Pinus ponderosa*), white fir, and Douglas fir grow in the mountains of the eastern and southern sectors. The montane zone in the central and northern Great Basin is covered by sagebrush grassland. Some isolated mountain ranges are covered by mountain mahogany (*Cercocarpus*) woodland. Sub-Alpine forests of bristlecone pine, limber

pine, and Englemann spruce (*Picea engelmannii*) occur in the higher mountain ranges, and small pockets of Alpine tundra grow on isolated peaks.

The late Pleistocene and Holocene vegetational history of the Great Basin has been discussed by Thompson (1990), and is summarized in Table 3 (see Western North America). Many plant species that lived in the Great Basin during the Pleistocene have their northern limits today in the Mojave Desert; other plants grew as much as 1,000 m downslope from their modern ranges. Unlike some other deserts, there is no evidence that extra-limital plant species immigrated into the Great Basin during the late Pleistocene. Instead, regional floras suffered a reduction in species diversity, as many of the modern taxa were absent.

The packrat midden records show that sub-Alpine conifers, especially limber pine, expanded their ranges downslope by as much as 1,000 m during the late Wisconsin interval. Curiously, the modern dominants of the montane zone (spruce and fir) were absent from the region during much of the late Pleistocene. Many persisted south of the Great Basin, in southern Nevada and southeastern California. In the western Great Basin, juniper dominated lower elevation woodlands in areas adjacent to pluvial lakes. Although Utah juniper (*Juniperus osteosperma*) was likely the dominant species at these sites, possible hybrids of western juniper (*Juniperus occidentalis*), Rocky Mountain juniper (*Juniperus scopulorum*) and California juniper (*Juniperus californica*) have been found in some middens. Sagebrush and other steppe species expanded their ranges in the late Wisconsin, both in latitude and elevation. They spread south to the Mojave and Sonoran deserts, and into adjacent mountain ranges. The drier regions of the northern Great Basin were dominated by shadscale.

Table 3 Summary of Changes in Great Basin Vegetation Inferred From Packrat Midden Data (after Elias, 1995)*Time Interval Vegetation***Late Wisconsin (26,000–17,000 cal years BP)***Uplands:*

Sub-Alpine conifers grow as much as 1,000 m downslope from modern limits; dominant trees: bristlecone pine, limber pine, prostrate juniper, and Englemann spruce in some locations; many shrubs and trees common today are absent, including Douglas fir, white fir, and Rocky Mountain juniper.

These shift south, into the Mojave Desert and elsewhere

Steppe regions:

Sagebrush and other steppe species present across entire range of elevations in Great Basin, up to sub-Alpine (as ground cover under coniferous forests).

Steppe species include sagebrush, rabbitbrush, horsebrush, snake-weed, and snowberry steppe species spread south into Mojave and Sonoran deserts, and other regions.

Late Glacial (17,000–11,500 cal years BP)

Limber pine, prostrate juniper, Englemann spruce, and some shrubs decline from 16,000–13,000 cal years BP, replaced by snake-weed, rock spiraea Bristlecone and limber pine persist at late Wisconsin levels until after 11,500 cal years BP

Mesic-adapted plants at many elevations replaced by thermophiles starting at 16,000 cal years BP In southern Great Basin, a major shift to desert vegetation before 13,000 cal years BP

Early Holocene (11,500–7,800 cal years BP)

Bristlecone and limber pines absent from western Utah and eastern Nevada by 9,600 cal years BP. Limber pine and Douglas fir replaced by Utah juniper and Gambel oak in southeastern Nevada by 10,000 cal years BP.

Mid-Holocene (7,800–4,500 cal years BP)

Rapid transition to modern vegetation zones between 7,800 and 6,900 cal years BP. Pinyon-juniper woodland established in several mountain ranges, characterized by Utah juniper and single-needle pinyon pine. Midden assemblages include a number of species that are rare or absent from Great Basin today.

Late Holocene (4,500 cal years BP–present)

Few changes in regional vegetation. Ranges of sagebrush and shadscale steppe contract; upper treeline retreats to mid-Holocene levels Lower treeline drops about 170 m between 4,500 and 2,000 cal years BP, then retreats to modern levels during last 2,000 years

The downslope extension of bristlecone and limber pines might have produced a contiguous forest zone stretching from the eastern shore of pluvial Lake Lahontan to the Rockies, but edaphic factors probably prevented conifer establishment in some regions. These vast coniferous woodlands became fragmented as lower treeline advanced upslope in response to climatic warming at the end of the last glaciation. The shift from Pleistocene to Holocene vegetation regimes took place in different ways at different sites. In the boundary region between the Mojave Desert and Great Basin, the major vegetation change took place by 13,000 cal years BP. In the north, this shift was completed between 10,000 and 7,800 cal years BP.

The Great Basin has a large number of endemic grasses and other herbs. The packrat midden record suggests that this is due to a combination of factors. Range fragmentation led to genetic isolation and rapid evolution, at least at the subspecific level. Also, new habitats opened up as the huge pluvial lakes receded and climates changed at the end of the last glaciation. During the Holocene, semi-arid lowlands have acted as biotic barriers, much as pluvial lakes did during the Pleistocene. Lyford *et al.*

(2002) extended Holocene midden research into the northern edge of the Great Basin in southern Montana. They were able to document the timing of a regional shift from cooler and moister to hotter and drier climates, based on the replacement of boreal and montane juniper species by the Great Basin juniper, *J. osteosperma*. This replacement occurred by 4,700 ¹⁴C years BP, and was followed by another cool, moist interval (4,400–2,700 ¹⁴C years BP) during which the lower treeline shifted downslope once again.

The Colorado Plateau

This plateau is a well-marked physiographic province that covers nearly 400,000 km² of the Four Corners region (Fig. 7). Plateau elevations range from 1,000 to 4,600 m, with much of the plateau below 1,800 m. Topography strongly affects regional climates, now and in the late Pleistocene. Modern vegetation zones are shown in Figure 8. These zones do not fall in simple elevation bands, because local bedrock type strongly affects the vegetation.

More than 180 packrat middens have been analyzed from sites on the Colorado Plateau. The

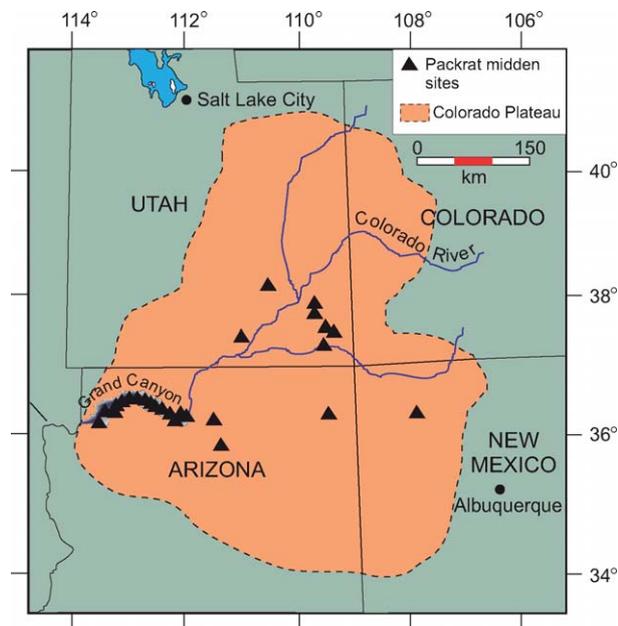


Figure 7 Map of the Colorado Plateau region, showing location of packrat middens from which fossil analyses have been published (triangles).

middens occur only in regions with sandstone and limestone bedrock. The plant macrofossil record of the region has been discussed by Betancourt (1990) and is summarized in Figure 8. During the late Wisconsin, upper treeline on the Colorado Plateau was significantly depressed, and Alpine tundra regions may have supported more sage cover than is

found there today. Today Alpine tundra is found in only three high mountain regions, at elevations above 3,660 m. Late glacial coniferous woodlands extended down to 2,000 m elevation in mesic canyon habitats. In the San Juan Mountains and Glen Canyon, coniferous woodlands with limber pine, Douglas fir (*Pseudotsuga menziesii*), junipers, and Colorado blue spruce (*Picea pungens*) grew down to 1,300 m elevation on rocky sites. Regional lowlands (<1,300 m elevation) were covered in desert-scrub with junipers and sagebrush.

Plant macrofossil records from the Grand Canyon indicate that the ranges of regional plant species are now 700–900 m higher and 400–700 km further upstream than they were in the late Wisconsin interval (Cole, 1990a) (Fig. 9). Cole's (1985) work on the paleobotany of the Grand Canyon also suggested that plant migration lagged significantly behind climate change at the end of the last glaciation. For instance, the upslope immigration of some species to their modern zones was not completed until the mid-Holocene; some plants, such as ocotillo (*Fouquieria splendens*), may still be adjusting to past climate fluctuations. These assertions sparked a heated debate among paleobotanists (Markgraf, 1986; Cole, 1986). The unexpected associations of species in early Holocene plant macrofossil assemblages may be partly due to unique climatic conditions, involving the dynamics of monsoonal moisture and shifts in the timing of summer warmth. Betancourt (1990) suggested that the length and

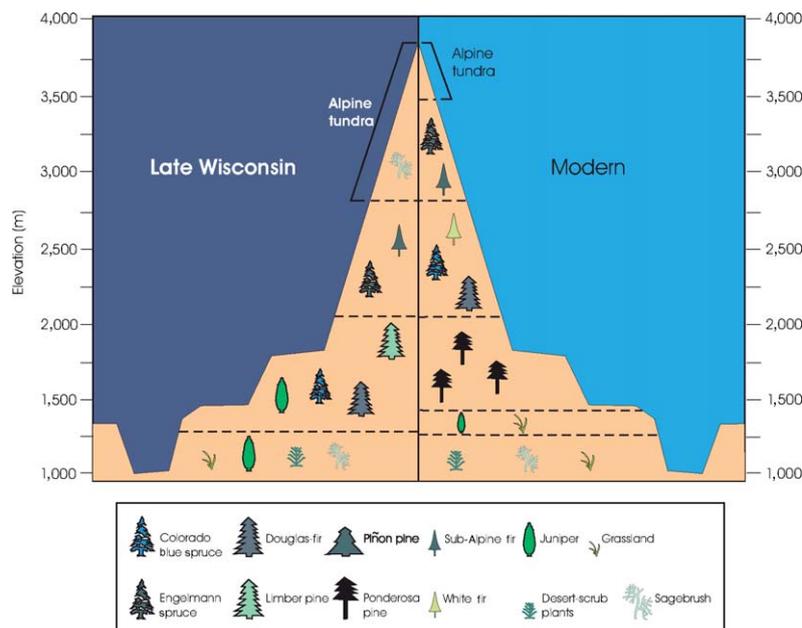


Figure 8 Diagrammatic drawing showing principal vegetation zones of the Colorado Plateau during late Wisconsin and modern times, after Betancourt, 1990.

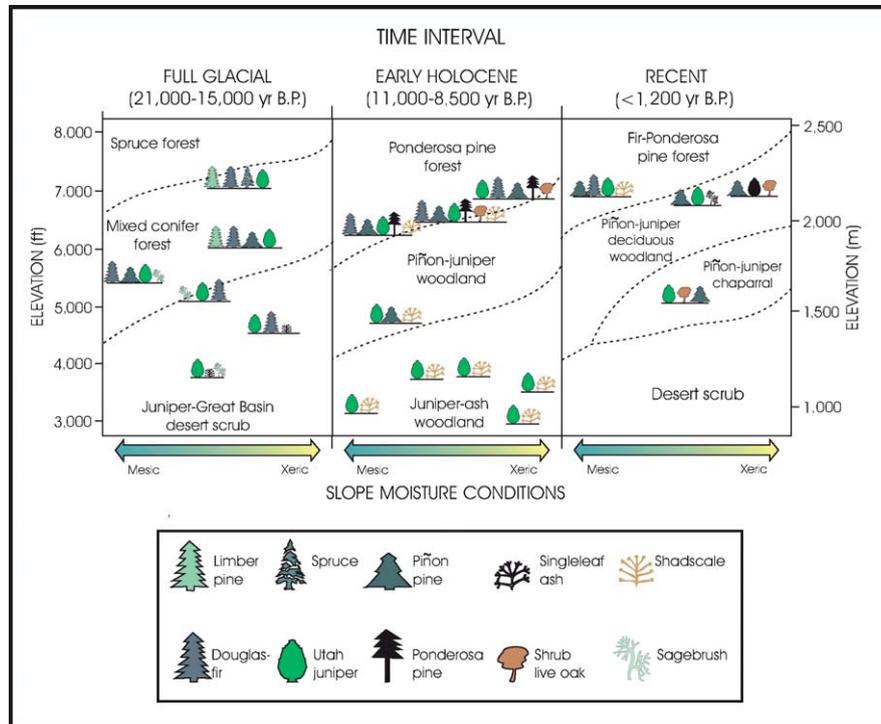


Figure 9 Diagrammatic drawing showing principal vegetation zones of the Grand Canyon during Full Glacial, early Holocene, and modern times, after Cole, 1990b.

difficultly of the various migration corridors leading to the Grand Canyon may have played a significant role in the postglacial establishment of new species. Cole (1990a) concluded that the biological phenomena, rather than unusual climatic conditions, are the cause of the peculiar plant associations of the Grand Canyon in the early Holocene. In his view, ‘as the complexities of plant population dynamics in the Grand Canyon become better understood, the biologically-oriented theories will gain ground.’

Major Implications of Packrat Midden Studies

The plant macrofossil record is providing valuable data on past and present ecosystems of the arid southwest. The fossil record shows that environmental change during the Pleistocene was substantial, even in regions such as the arid southwest that were far-removed from continental ice sheets. The midden record offers good evidence for individualistic responses to major climate changes that brought about uneven displacement of species, and anomalous associations in which some species do not appear to belong in the communities where they were found.

The age and origin of southwestern desert biological communities are important questions in the field of biogeography. About 1,200 of the 5,500 species of southwestern plants are considered endemic to that region, a far higher proportion than elsewhere in North America. Even though many of these plants evolved locally, the packrat midden data suggest that desert plant communities are very recent and very dynamic. One of the reasons the midden data are so important is that they offer tangible evidence of the history of species in this region. For instance, based on modern data, creosote bush was thought by some to have immigrated from South America during the Holocene. However, the fossil evidence shows that it grew at least as far north as the Arizona-Sonora border during the middle of the last glaciation. We are not currently able to verify the exact whereabouts of southern refugia for the desert biota in Mexico, because many regions hypothesized to have been refugia are now in the tropical or subtropical zones, where preservation of middens is extremely limited.

Many intriguing questions remain to be addressed by the plant macrofossil record. For instance, the late Wisconsin pygmy conifer woodlands that covered much of the lower elevations of the American

Southwest remained intact until after 11,000 years. Was this long-term ecosystem stability a product of climatic stability across a wide region? What brought about the demise of the lowland woodlands? One way of approaching these questions is the analysis of stable isotopes from the cellulose preserved in woody plant macrofossils. In particular, analysis of changes in the concentration of the deuterium may help to clarify the climate regimes under which these plants grew, and to define the climatic changes that forced their retreat from the desert lowlands. Another difficult question concerns a major switch in pinyon pines at the end of the Pleistocene. Colorado pinyon (*Pinus edulis*) and single-needle pinyon (*Pinus monophylla*) became the dominant pinyon pine species in the Holocene, at the expense of papershell pinyon and another single-needle pinyon, *Pinus californiarum* var. *fallax*, that were dominant in the late Pleistocene. Why this reversal of roles? One approach to the problem of population dynamics of pinyon pines is through the study of ancient DNA. Gene amplification techniques are being applied to pinyon wood, cones, and needles preserved in middens, to unravel the genetic relationships between ancient populations and their modern descendants (Betancourt *et al.*, 1991). Modern pinyon pine ranges are far from static. Both single-needle pinyon and Colorado pinyon are still migrating. The northernmost population of Colorado pinyon became established in north-central Colorado only 400 years ago. The same is true of single-needle pinyon, which arrived at its current northwestern limit near Reno, Nevada within the last 700 years.

Summary

The fossil record developed from packrat middens in the arid southwest is a unique resource for investigating the pace and direction of biotic changes. Indeed, without the packrat midden data, we would know little about the biotic history of this region where lake sediments are scarce and peat bogs almost non-existent. The midden data have shown that late Pleistocene landscapes of the southwest were radically different from today, with coniferous woodlands covering much of the lowland regions that now support only desert-scrub. This change was not just a downslope shift of intact communities; it brought together new associations of plants and animals in an ever-changing dynamic that is still at work today (Van Devender, 1985). Arid-land biotic communities viewed as 'stable' from our short-term perspective are actually in a constant state of flux. Each new environmental change brings a different cast of

characters to the biological stage. In some regions, like the Great Basin, the same players appear in succeeding intervals. In other regions, such as the Sonoran and Chihuahuan deserts, new players appear from time to time, often at the expense of others. The fossil record has much to say to both the paleontological and modern ecological research communities; we are just starting to come to grips with its message.

See also: Plant Macrofossil Introduction. Pollen Methods and Studies: Reconstructing Past Biodiversity Development. Radiocarbon Dating: AMS Method.

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Surface Samples, Taphonomy, Representation

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Plant macrofossils preserved in lake sediment are frequently identified and counted as a means of reconstructing the vegetational communities of a lake and surrounding areas. However, many factors affect the relationships between macrofossil assemblages and plant communities. This article explores those factors and the types of studies that clarify them.

In an ideal system, each individual plant of a species would produce a standard quantity of preservable macrofossils. (The term macrofossil is here used to indicate identifiable plant parts that are large enough to be visible without magnification and have the potential to become incorporated into lake or peatland sediment.) These macrofossils would disperse in a predictable fashion, uniformly incorporate into sediment across a lake basin, and be lost to predators and decomposition in consistent proportions, all regardless of individual basin morphology. Macrofossil assemblages could then be used to reconstruct past vegetational communities by means of precise mathematical inference models for each macrofossil type, which might appear as follows:

$$V_A = (N_A \div (P_A - L_A)) \times D_A \times b \times S$$

where V_A is the proportion of local vegetation represented by plant taxon A; N_A is the number of macrofossil type A found in standard volume of sediment; P_A is the annual production of macrofossil type A; L_A is the mean annual loss from sediment of macrofossil type A by decomposition, predation, etc.; D_A is the mean dispersal distance from source plants for macrofossil type A; b is the basin coefficient accounting for basin characteristics such as fetch, wind direction, and slope; and S is the sample location within the basin.

Alas, natural systems do not work with mathematical uniformity but are notoriously quirky and constantly changing. An additional factor could be added to the previous formula:

U = all unknown factors that paleoecologists have not even begun to anticipate.

Macrofossils do not meet the first and most important requirement for quantitative paleoenvironmental reconstruction (Birks, 1995); they are not systematically (linearly or unimodally) related to the