7-1-2014

Establishment of Larrea tridentata at the northern edge of the modern Mojave Desert: Insights from Neotoma paleomiddens

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Recommended Citation

Steinberg, Clare. "Establishment of Larrea tridentata at the northern edge of the modern Mojave Desert: Insights from Neotoma paleomiddens." (2014). https://digitalrepository.unm.edu/biol_etds/104

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Establishment of *Larrea tridentata* at the northern edge of the modern Mojave Desert: Insights from *Neotoma* paleomiddens

by

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B.S Evolution, Ecology, and Biodiversity
University of California, Davis, 2010

Submitted in Partial Fulfillment of the
requirements for the Degree of

Master of Science
in Biology

The University of New Mexico
Albuquerque, New Mexico

July, 2014

ACKNOWLEDGMENTS

Special thanks to my advisor, Dr. Felisa Smith, for pushing me to take on a challenging and worthwhile thesis, and for her support and patience. Thanks to my committee members Dr. Astrid Kodric-Brown and Dr. Don Natvig for their support and optimism.

Much gratitude to the members of the Smith lab for their support, friendship, encouragement, and faith.

Finally, thank you to my family, John, Kati, and Kelly Steinberg, for their extreme patience, unwavering support, and love over the last few years.

I love you all.

Establishment of *Larrea tridentata* at the northern edge of the modern Mojave Desert: Insights from *Neotoma* paleomiddens

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ABSTRACT

Shifting climates affect the composition of biological communities. If environmental conditions change sufficiently, new species can invade, leading to large-scale community turnover. Understanding how and why such shifts occur is crucial in this era of anthropogenic global change. Paleontological studies provide a valuable long-term perspective of the dynamics of community turnover. Here, we examine changes in the plant community over the past 34 thousand years in what is now the northern Mojave Desert. This time period includes the last glacial maximum as well as numerous smaller climatic fluctuations in the Holocene and the end of the Pleistocene. We quantified plant macrofossils recovered from 48 ancient *Neotoma* middens collected in Titus Canyon in Death Valley, California, ranging in age from 33.5 to 0.05 ka. Using this unique fossil record, we are able to document the invasion and establishment of the important desert shrub creosote (*Larrea tridentata*) into the northern Mojave Desert. Overall, we are able to characterize the ecosystem shift in dominant shrubs from juniper (*Juniperus osteosperma*) to creosote bush (*Larrea tridentata*). Interestingly, we find that most secondary plant species do not follow dominant shrubs. Instead, shifts in these plants most likely depend on their own physiological limits. Our results may help predict responses of desert communities to ongoing climatic fluctuations.

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INTRODUCTION

Creosote bush (*Larrea tridentata*) is the dominant plant across three of the five major deserts in North America. However, it is a relatively recent invader of the habitats where it is now ubiquitous. When and how did creosote proliferate and establish itself after its arrival in North America? The answer to this question is not only relevant for understanding the history of North American deserts, but is also important for understanding the consequences of global climate change; as ecosystems become hotter and drier, creosote scrublands are expanding and replacing more mesic desert communities (Baez and Collins 2008). Recent experimental data suggest that creosote can more readily cope with projected future extreme drought and heat conditions than many other native plants (Beatley 1974, McAuliffe and Hamerlynck 2010, Jin and Evans 2010, Medeiros and Pockman 2011, Newingham et al. 2012). Thus, examination of the initial invasion of creosote into North America can facilitate our understanding of how modern desert communities are changing under current warming trends.

The presence of creosote in a habitat has both positive and negative consequences for local floral and faunal diversity. In the Chihuahuan Desert, replacement of grasslands by encroaching creosote scrubland results in a decrease in overall plant diversity (Baez and Collins 2008) and an increase in average soil temperature (He et al. 2010). Because the roots of creosote allelopathically inhibit root growth of neighboring plants (Mahall and Callaway 1992), it can outcompete native plants.

Moreover, creosote has a high secondary metabolite load, which is highly unpalatable to most herbivores. Conversely, because creosote is one of the few large shrubs able to grow in North America's most xeric deserts, it provides important cover for many animals, including domestic sheep, small mammals, and reptiles. Its root systems likewise provide soil stability for burrowing animals like the desert tortoise (Marshall 1995). Further, nitrogen, phosphates, chlorine, and other nutrients concentrate around large shrubs including creosote, creating "fertility islands" (Schlesinger et al. 1996). Creosote plants can act as nurseries for small native plants and seedling, providing nutrient-rich soil as well as protection from the heat and desiccating effects of the direct desert sun (Schafer et al. 2012). This effect is particularly important in many of the most xeric North American desert communities where creosote is the only shrub, or one of a few species of shrubs.

A combination of molecular, fossil, and ecological evidence all suggest creosote arrived in North America through a single long-distance dispersal event. Creosote's closest relative, *L. divaricata*, is endemic to Argentina, and the three other members of the genus are also South American natives (Raven 1963, Wells and Hunziker 1976), suggesting a South American origin. When creosote arrived, however, is less clear; different data yield different estimates. Molecular studies put the divergence of *L. tridentata* and *L. divaricata* at ~ 0.52-1.57 ma (Laport et al. 2012) or 4.2-8.4 ma (Lia et al. 2001) based on nuclear and cpDNA sequences, or 0.6 – 1.2 ma based on allozyme data (Cortes & Hunziker 1997). Certainly, it is possible that the initial speciation event occurred in South America, and ancestral *L. tridentata* persisted there for some time before migrating to North America and subsequently becoming extirpated in South America.

In contrast, fossil evidence indicates a much more recent arrival of creosote. In North America, woodrat (*Neotoma* spp.) paleomiddens provide the best record for late Quaternary desert vegetation. All woodrat species construct dens or houses, which may contain multiple debris piles, or "middens" (Smith and Betancourt 2006). If protected from water, these piles can be preserved for thousands of years, hence the term "paleomiddens". Along with woodrat pellets and other refuse, paleomiddens include fragments of local flora, which are encased in desiccated and crystallized woodrat urine, or "amberat". To date, the oldest creosote fossils were recovered from a *Neotoma* paleomidden from Big Bend, Texas in the Chihuahuan Desert, dated at 26.4 ka. However, the taphonomy of this record has been called into question. The old date may be a result of younger midden material mixing with older material. Not only is the next oldest record in Big Bend considerably younger (10.1 ka), the creosote macrofossils were not directly dated (Van Devender 1990a). The next oldest paleomidden record is 18.7 ka from the Tinajas Altas Mountains near Yuma, Arizona in the Sonoran Desert (Van Devender 1990b).

Regardless of the initial migration date, we can reconstruct the historical dispersal pattern of creosote using extant genomic variation. Although typically considered a single species, creosote is actually a complex of three genomically distinct races whose ranges correspond with the borders of the Chihuahuan, Sonoran, and Mojave deserts. Chihuahuan creosote are diploid (n=13), while Sonoran are tetraploid (n=26), and Mojave creosote are hexaploid (n=39)(Yang 1970, Hunter et al. 2001, Laport and Minckley 2013). Because *L. divaricata* is diploid, the most parsimonious hypothesis is that Chihuahuan creosote is the most basal of the complex. Thus, the most likely dispersal scenario is that creosote established first through the Chihuahuan Desert, then spread north and west through the Sonoran and Mojave Deserts as climatic conditions changed during the late Quaternary.

Creosote expanded steadily from its site of initial colonization in the south to its modern range over thousands of years (Table 1). In the Chihuahuan Desert, creosote is present in paleomiddens dated 11.6 and 12.6 ka from Rough Canyon, NM, and ubiquitous beginning 5.4 ka (Betancourt et al. 2001). It was certainly ubiquitous throughout the Chihuahuan desert region by 4 ka. Middens from the Peloncillo Mountain and Playas Valley at the Northwestern edge of the Chihuahuan suggest creosote became ubiquitous by 4 ka, and by 4-5 ka in the Sevilleta Long Term Ecological Research site and Sacramento Mountains in the northernmost reaches of the Chihuahuan (Holmgren et al. 2007).

Interestingly, paleomidden evidence indicates creosote became a dominant shrub much earlier in the Sonoran Desert than in the Chihuahuan. In Guadalupe Canyon in northern Baja California, Holmgren (2014) found creosote in middens dated 18.4 and 18.0 ka. In the Tinajas Mountains, which are less than 100 km southeast of Yuma, Arizona, Van Devender 1990 likewise found trace amounts of creosote in paleomiddens dated 18.7 ka. By 15.7 ka, creosote macrofossils are common in Tinajas middens. On Picacho Peak, California, just north of Yuma, Arizona, Van Devender found consistent and strong presence of creosote beginning over 12 ka, and in the Whipple Mountains near the northern extant of the Sonoran from 10.5 ka. The fact that the oldest records of creosote come from the Sonoran Desert and not from the Chihuahuan Desert may indicate that the first North American colonization occurred in the Sonoran, and that diploid creosote was extirpated there some time after its initial expansion. However, there is a large dearth of collection of Mexican paleomiddens. Analysis of Mexican middens may provide more support for the Chihuahuan founding population hypothesis suggested by genomic variation.

It took longer for creosote to expand into the Mojave Desert. Despite its ubiquitous presence today, the earliest records for creosote in the Mojave date to only 8.7 ka in the Marble Mountains (Rowlands 1878). At the northern edge of the Mojave, Spaulding (1990) records creosote at Point of Rocks in the Amargosa Desert at 3.7 ka, and Spaulding (1980) records it at 3.9 ka at Eureka View. However, most other studies of the northern Mojave don't record creosote until ~2-3 ka (Spaulding 1980, Wells and Woodcock 1985, Cole and Webb 1985, Buckley and Willis 1969).

In this study, we use plant macrofossils found in woodrat paleomiddens to reconstruct the history of North American creosote at what is today the northern edge of the Mojave. We employ a chronosequence of 48 radiocarbon-dated middens recovered from Titus Canyon in Death Valley, California, ranging in age from over

33,000 to 50 calendar years, and from 300 to 1600 m in elevation (Fig. 1). Today, the bottom of Titus Canyon is home to the creosote bush desert scrub communities that dominate the Mojave desert, while juniper-piñon woodlands typical of Great Basin communities are found above ~1800 m (Koehler et al. 2005). Thus, Titus Canyon represents an important ecotone between two major North American ecosystems, and it rests close to the northern limit of creosote today.

Using this well-resolved sequence of middens, we aim to answer the following questions about the evolutionary history of creosote in the Mojave Desert:

(1) *When did creosote reach the northern extent of its range?* Previous studies assume creosote marched steadily north as the climate became hotter and drier after the end of the last glacial maximum and the Younger Dryas, each plant dispersing its seeds only short distances from itself. If this is true, creosote should appear in our record no earlier than it was found in paleomiddens collected in the central and southern Mojave. However, it is also possible that creosote hop-scotched its way across its range, dispersed by birds as the first seed from South America might have been. In that case, we might see creosote arriving earlier in our record than in some of the more southern Mojave sites.

(2) *How does the species of woodrat responsible for constructing a midden influence the plant community preserved? Specifically, how variable are middens' representations of plant communities between woodrat species?* Previous work shows that two species of woodrat are responsible for

creating these middens (Smith et al. 2009). *Neotoma cinerea* built our older middens, mostly associated with juniper woodlands, and *Neotoma lepida* built most of our young middens, which includes most of those containing creosote. Studies of modern woodrats suggest that midden contents provide a fairly comprehensive account of local woody plants within 30 m of a den (Frase and Sera 1993, Nowak et al. 2000, Lesser and Jackson 2011). Dial and Czaplewski (1990) found that sympatric woodrat species mostly recruit the same plant species, but may do so at different proportions. The plant recruitment habits of *N. lepida* and *N. cinerea* have not been directly compared. To make inferences about changes in the presence, absence, and proportion of plant species over time, we must first determine whether or not it is reasonable to compare the macrofossils found in middens built by different species of woodrats.

(3) *How do the responses of different woodrat and plant species to climate change compare?* Smith et al. (2009) found that *N. cinerea* retreated to higher elevations and ultimately was extirpated in Titus Canyon as climate warmed during the Holocene, at which time it was replaced by *N. lepida.* How does this extirpation and species replacement relate to the dynamics of the plant communities over this time period? Are there other factors that may explain the changes in woodrat populations?

(4) *What did the plant community in the Mojave look like before the arrival of creosote?* We speculate that creosote desert scrub may have displaced a different and distinct type of xeric plant community that existed before the

arrival of creosote and after the end of the last glacial maximum. If so, that community may have been structured the same way as the creosote community with one or two dominant shrubs, or the resident species may have shared the landscape more evenly. This community may have even included plants that are today extirpated from Titus Canyon.

(5) *How does the invasion of creosote into a community change the patterns of plant diversity?* In the Chihuahuan Desert, the replacement of grasslands by creosote desert scrubland results in a decrease in overall floral diversity (Baez and Collins 2008). Is the effect similar in the Mojave?

(6) *How does plant diversity respond to temperature variability?* Over the past 33,000 years, there have been many periods of both stable and changing temperature. We hypothesize that all community types will be relatively static over periods of little temperature change, but the disturbance caused by periods of changing temperatures will result in more variable community composition over those periods.

MATERIALS AND METHODS

1. Death Valley Climate and Topography

Death Valley is one of the hottest and driest places on earth: summer high temperatures often exceed 49°C in the shade, and average rainfall is only 5cm yr^{-1} (National Park Service). The topography is likewise dramatic. At an elevation of - 86 m, Badwater Basin in the middle of the valley is the lowest point in North America, while the Amargosa Mountains running along the east side of the valley peak at 2663 m, and the Panamint Range to the west reaches 3368 m. As moisture blows in from the ocean to the west, the air currents experience an impressive and sudden drop in elevation as they reach Death Valley, creating a considerable rain shadow that is responsible for the dry conditions.

Middens were collected in Titus Canyon, a steep and narrow gorge running east to west through the Grapevine Mountains, the northernmost mountains within the Amargosa Range (Fig 1). The upper drainage, known as Upper Titus Canyon, runs from the top of the surrounding mountains at ~ 2000 m west down to the mouth of the main canyon at about 1190 m. The westernmost ~ 2.5 km of Titus form a slot canyon, less than six meters wide in some places. Where it opens abruptly onto the valley, the floor of the western mouth of the canyon is ~200 m in elevation. Imposing cliffs of olive-colored conglomerate and tuffaceous sandstone characterize the upper elevations of the canyon (>1200-1400 m). Dolomite and limestone beds and tightly cemented breccia primarily form the lower elevations. Most middens were collected in dolomite and limestone caves and crevices. (Smith et al. 2009)

2. Modern Plant Communities

Titus Canyon represents a dramatic ecotone between two major deserts. The plant communities of Death Valley and the mouth of Titus Canyon are associated with the Mojave Desert, while the upper canyon and the tops of the Grapevine Mountains host communities typical of the southern Great Basin. On the peaks above Upper Titus Canyon, *Juniperus osteosperma* and *Pinus monophylla* dominate in the juniper-piñon woodlands typical of the Great Basin. Juniper remains dominant above ~1900 to 2000 m, while piñon is restricted to only the very tops of the peaks. Below ~1800 m on gentle slopes and flats, *Coleogyne ramosissima* (blackbrush), considered a high-elevation Mojave desert species (Schramm 1982) is dominant. On rockier slopes and dry, saline soils at the same elevation, shadescale (*Atriplex confertifolia*) (found in both deserts) and big sagebrush (*Artemisia tridentata*) (considered a low-elevation Great Basin species (Beatley 1975)), are the primary shrubs. On the steepest mid-elevation slopes, *Atriplex* spp., pygmycedar (*Peucephyllum schottii*), and brittlebrush (*Encelia farinosa*) are the most notable species.

Below 1600 m, true Mojave communities take hold, characterized primarily by creosote bush (*Larrea tridentata*). At the high end of its elevational range, important creosote associates include blackbrush and shadescale. *Ambrosia dumosa* (white bursage) typically associates with the middle elevations of creosote's range, and desert holly (*Atriplex hymenelytra*) with creosote's middle to low elevations.

3. Woodrats and Paleomiddens

Paleomiddens formed by woodrats of the genus *Neotoma* provide an unparalleled record of biological information. The 21 extant species of *Neotoma* occupy a remarkable range of habitats in North and Central America, reaching to within two degrees of the Arctic Circle and as far south as the tropics of Nicaragua, with the greatest species richness in central Mexico (Hall 1981). As protection from predators and temperature extremes, all species build dens out of sticks, plant fragments, and detritus. These dens are typically found in rock crevices, caves, or under dense patches of vegetation. A den typically includes several debris piles, or “middens”, formed of fecal pellets, food waste, and other detritus piled together. Over time, woodrat urine permeates a debris pile, desiccates, and hardens, forming a hard, asphalt-like substance called amberat. If protected from the elements, a midden encrusted in amberat can survive for tens of thousands of years with the relics of its creator safely preserved inside. Dens may be used sequentially by many woodrats, so one amberat-preserved deposit may include several decades of debris from its resident community. From these ancient middens, we can recover plant macrofossils, pollen, feathers, bones, teeth, and even archeological artifacts (Vaughan 1990). Because woodrats generally forage within 30 m of their dens (Finley 1990, Lyford et al. 2004), analysis of plant macrofossils gives a good representation of plants found in close proximity of a midden.

4. Woodrat Species

Two species of woodrat were responsible for building paleomiddens in Titus Canyon: *Neotoma lepida*, the desert woodrat and *N. cinerea*, the bushy tailed woodrat. *N. lepida* is a much smaller animal (~ 85–240 g) (Smith et al. 2009) and inhabits xeric areas in southeastern Oregon, southern Idaho, Utah, and across Nevada, southern California, and Baja Mexico (Verts and Carraway 2002). This range corresponds with the Mojave Desert and the western half of the Sonoran

Desert. It is found in a variety of communities, including juniper-piñon woodlands, creosote bush scrub, chaparral, Joshua tree woodlands, scrub oak woodlands, and cholla cactus gardens. Necessary to its habitat are structures that provide protection from predators and harsh weather, such as rock crevices, rock piles, and shrubs and trees where animals can build dens that provide protection from predators and thermal extremes (Verts and Carraway 2002). *N. lepida* will build large dens in these places, often enforced with cactus or yucca for structural stability and predator discouragement. Over its range, *N. lepida* displays significant dietary variability (Verts and Carraway 2002), but locally it tends to specialize on available plants, such as *Quercus turbinella* (scrub oak), *Juniperus*, *Ephedra*, *Eriogonum*, *Stanleya pinnata* (prince's plume), *Artemisia tridentata*, and, most notably, creosote bush, which it has locally adapted to metabolize (Mangione et al. 2000, Haley et al. 2008), despite creosote's high resin content.

N. cinerea is a much larger animal (~ 200-600 g) (Smith et al. 2009). As the most boreal species of the genus, *N. cinerea* is much more cold tolerant and less heat tolerant than *N. lepida*. Today it is found as far north as the Yukon of Canada and as far south as central Arizona, ranging to the coasts of Northern California, Oregon, Washington, and British Columbia, and east into North Dakota, South Dakota, and Nebraska. It can be found in a wide variety of communities, including alpine talus, spruce-fir forest, piñon-juniper woodland, shortgrass prairie, and Great Basin desert scrub habitats (Smith 1997). Like other woodrats, *N. cinerea*'s successful occupation of habitat is limited by access to den sites. However, *N. cinerea* is almost exclusively limited to rock-based dens (or unoccupied human habitations), and therefore availability of rock shelters may be more important than vegetation for determining where *N. cinerea* may be found. Like *N. lepida, N. cinerea* eats a wide variety of foliage across its range, but tends to specialize locally (Smith 1997). Plants that it has been documented to prefer at various places across its range include aspen (*Populus tremuloides*), choke-cherry (*Prunus virginiana*), rabbitbrush (*Chrysothamnus*), currant (*Ribes cereum*), *Pinus* spp., *Juniperus* spp., saltbrush (*Atriplex* spp.), pricklypear cactus (*Opuntia* spp.), mountain mahogany (*Cercocarpus ledifolius*), and sagebrush (*Artemisia tridentata*). Creosote is notably absent from this list (Smith 1997).

In Death Valley today, *N. lepida* can be found across the valley floor and up to ~1800 m, where temperatures drop below its thermal tolerance. *N. cinerea* is only found at about ~ 1900-2000 m on the west side of Death Valley, and may be limited by abiotic factors at both its upper and lower elevational boundaries (Smith et al. 2009). During the Pleistocene, *N. cinerea* ranged as far south as northern Mexico (Smith 1997) and inhabited the lower elevations of Death Valley, as well as much of the Amargosa Range, including Titus Canyon (Smith et al. 2009). *N. cinerea* was extirpated from the Amargosa Range in the middle to late Holocene (Smith et al. 2009).

Both species preferentially build dens in protected rock crevices that promote long-term protection and formation of paleomiddens. While thermal limitations and interspecific competition prevent the two species from living sympatrically (Smith et al. 2009), some paleomiddens may contain material from more than one species if a species replacement occurred during the period of midden deposition. Comparisons of modern midden plant contents to local plant communities indicate that large, woody shrubs and trees within 30-50 m of a den are almost always represented in midden contents. However, the chance that a smaller herbaceous plant growing within 30 m of a den is also found within that den's midden may be as low as 20-40%. Grasses are generally very poorly represented (Frase and Sera 1993, Lyford et al. 2004, Lesser and Jackson 2011).

5. Data Collection and Generation

Paleomidden Collection and Processing

As described elsewhere (Smith et al. 2009), a total of 94 paleomiddens were collected in Death Valley National Park, California in 2006, 2007, and 2009. The middens were recovered along a ~ 15 km stretch of Titus Canyon between 200 and 1600 m, mostly in recessed limestone and dolomite caves or crevices. Only indurated (cemented) middens were collected. All middens were carefully examined for signs of amberat rehydration before removal. Sites were geo-referenced and permanently marked with metal tags, and topography, aspect ratio, relief, and nearby modern vegetation were recorded. After removal, middens were carefully cleaned in the field to remove surface contamination and to verify that each sample represented a cohesive temporal unit. Large caves often contained multiple middens. Unless radiocarbon dating or pellet measurements indicated that they were built during the same time periods, each sample was processed separately.

In the lab, middens were further cleaned and prepared for analysis. Each midden was weighed, and vouchers were removed for archival purposes and for use in future pollen analysis. The remaining material was soaked in covered 14.1 L buckets of water for 5-14 days. The dissociated material was power-washed and wet-sieved to remove most non-organic material. The matrix was dried at ~60˚C in a forced-draft oven for 1-2 days. This material was then sifted through a series of standard 1 mm (No. 10) and 2 mm (No. 18) stainless steel mesh geological sieves, and each fraction was hand-sorted to remove fossil woodrat pellets. Midden processing methods generally followed the well-established methods described by Spaulding (1990). See Smith et al. (2009) for more details on the collection and processing of these middens.

Radiocarbon Dating of Samples

Age of midden deposition was determined through radiocarbon dating. We selected 49 middens for dating based on their size, elevation, integrity, and surface macrofossils. For each, an aliquot of ~10g of untreated pellets were sent to the University of Arizona National Science Foundation Accelerator Facility or the Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine for radiocarbon dating. A tandem accelerator mass spectrometer (TAM) was used to determine dates. We converted radiocarbon ages to calendar years (years before 1950 AD) using the CalPal2007_HULU calibration curve from the online Cal-Pal 2007 program (Cologne 2007). Carbon-14 dates and calendar ages are listed in Table 2. Unless otherwise noted, calendar age is used throughout this document.

Macrofossil Data Collection

Material of the largest particle size (>2 mm) contained the highest density of identifiable macrofossils, so this was used for macrofossil analysis. We note that >2 mm particle material was largely void of identifiable macrofossils from grasses and other annual plants with small seeds and non-diagnostic leaf structure. Material of <1 mm likely includes seeds from such plants, and may be used in future further analysis of the plant communities described in this paper. Of the 49 dated middens, 48 had sufficient material available for macrofossil analysis.

To ensure adequate sampling effort, we performed a methods test to determine the appropriate amount of midden material to sample. This test also determined the most appropriate way to calculate macrofossil proportions: by number of macrofossils per total number of macrofossils, by number of macrofossils per gram, or by number of macrofossils per milliliter. Two middens with different dominant shrubs (TiC 1, a creosote-dominated midden, and TiC 4c, a juniper-dominated midden) were chosen. We chose three plant species from each midden to sample: the dominant species, a common species, and a rare species. For each midden, we took four well-mixed aliquots 45- 60 mL of >2 mm midden material. Each aliquot was spread on a 19 cm diameter plate with a 2 cm x 2 cm grid, a fraction at a time. Under a Nikon SMZ1500 microscope at 0.75–2x magnification, four of the squares on the grid were carefully examined for the plant macrofossils of the chosen species. This was repeated until the entire aliquot had been plated and sampled.

We calculated the cumulative number of macrofossils of each type per total number of macrofossils, cumulative number of particles of each macrofossil type per gram, and cumulative number of particles of each macrofossil type per milliliter. For each measure, we used a rarefaction curve to determine minimum sampling effort necessary to accurately detect presence and proportion of common and rare macrofossils. Based on our results, we determined that number of macrofossils of a given type per total number of macrofossils recovered is the most consistent measure of macrofossil proportions. We also determined that macrofossils recovered from a single aliquot of 45 mL of >2mm material generally are representative of both number and proportion of plant species present in the larger sample. (Fig 2)

For each midden, the >2 mm fraction was weighed, and at least 10% of the mass and a minimum of 90 mL was removed for plant macrofossil analysis. This ensured that at least twice the necessary minimum volume determined by our methods test was sampled for each midden. Fractions of this aliquot were spread on a 19 cm diameter plate with a 2 cm X 2 cm grid. Four of the squares on the grid were carefully examined under a Nikon SMZ1500 microscope at 0.75–2x magnification, and all plant macrofossils deemed potentially identifiable were removed. The entire plate was quickly scanned for additional non-pellet trace animal matter, such as bones, teeth, feathers, and exoskeleton fragments. This process was repeated until the entire aliquot had been plated and sampled. Plant macrofossils were sorted by species, photographed, tallied, and placed in labeled envelopes. Non-pellet trace animal matter was recorded and placed in vials. Woodrat molars were used to substantiate diagnosis of woodrat species.

To identify macrofossils, we compared them to previously identified modern plants and macrofossils. Modern samples were collected from Death Valley and obtained from the Museum of Southwestern Biology at the University of New Mexico. Photographs of modern plants and ancient macrofossils were obtained from the Macrobotanical Digital Library. When morphology could not differentiate between species, we used ranges of modern species as listed on Calflora.org to further determine likely identification. Plants were identified to the lowest taxonomic level possible. Not all macrofossil types were identifiable. However, all distinct types were recorded for use in diversity analyses. We assigned each type of macrofossil from each midden a “certainty score”. These ranged from 1 to 3, with 3 indicating high certainty about the identification and 1 indicating low certainty.

Woodrat Species Identification

The woodrat species responsible for building each midden was identified in an earlier study by estimating body size of each woodrat from measurements of fossil pellet size (Smith et al. 2009). These identifications were independently verified using morphology of molars (M1) recovered from middens. To characterize woodrat species for middens whose mean pellet size did not give a clear identification, we further examined the statistical movements of woodrat pellet size distributions for each midden. In a few instances, a bimodal distribution was found, suggesting a species replacement was likely within the ~20 year deposition interval. In most cases, molars supported previous pellet-based identifications or clarified instances where pellet size did not give a clear identification. In several middens (TiC 4c, 18.4 ka, 1250 m; TiC 12 bottom c, 33.4 ka, 889 m; TiC 12 top e, 29.1 ka, 1249 m; TiC 15 take 2A, 0.4 ka, 582 m; TiC 16, 4.15 ka, 1015 m; TiC 17 take 3a, 16.5 ka, 1030 m; UTiC 2a, 9.5 ka, 1576 m), we also recovered non-*Neotoma* teeth.

Temperature Data Calculations

As a temperature proxy, we used mean global temperature estimates derived from analysis of oxygen isotopes in ice cores recovered by the Greenland Ice Sheet Project 2 (GISP2) (Alley 2004). This northern hemisphere proxy allowed us to estimate temperatures at time of each midden's deposition. For our analysis, we converted the GISP2 data from historical temperatures in Greenland to historical temperatures relative to modern temperatures. To do this, we converted each data point to an anomaly from the average temperature of modern Greenland, which we approximated by taking the average of all the data within the last 1000 calendar years. This follows the method set up by Jouzel et al., al (2007). The Greenland Ice Sheet data is the best temperature proxy available for the entire time interval spanned by our set of middens. While it does not capture fine-scale regional or local dynamics, this data does provide a broad picture of climate change over the late Quaternary for the northern hemisphere.

To estimate the temperature variability during the time of midden deposition, we calculated the difference between the maximum and minimum relative temperature values within ± 50 years of each midden's deposition. These 100-year intervals centered on each midden's C^{14} calendar date.

Precipitation Data Calculations

We obtained a very rough estimate of average precipitation at time of midden deposition using modern minimum precipitation requirements of plants found in each midden. Minimum precipitation within a given plant species' range was obtained from Calflora.org, which calculates those numbers from average monthly precipitation from 1971-2000 over 30 arc-second PRISM derived grids. These data were not available for every plant taxa we identified. For indentified genera and subfamilies, we used mean minimum precipitation for species we deemed to plausibly be found in the midden record based on modern range. To verify that juniper and creosote are not the primarily drivers of any trends over time, we also calculated mean minimum precipitation for plants in each midden excluding juniper and creosote.

6. Statistical Analysis

To analyze differences in diversity over time, between (i) middens made by difference species of woodrats, (ii) between plant communities, and (iii) during periods of temperature fluctuation, we calculated two measures of alpha diversity for all middens: a simple tally of the number of macrofossil types per midden, and the Shannon-Wiener diversity index. The Shannon-Wiener diversity index, or the Shannon heterogeneity index, is a metric that takes into account both number and evenness of species within a given community. It is a simple and commonly-used metric in the field of community ecology (Hubalek 2000). All distinct macrofossil types, whether identified or unidentified to genus, were included in the analysis.

We note several important factors that could cause plants identified within each midden to not perfectly reflect plant species presence, absence, or proportion: ease of plant identification due to strength and number of diagnostic characteristics, frequency of plant fractionation, and higher likelihood of identifying common and familiar species over uncommon species.

In general, these factors lead to over-representation of common species in the dataset. In particular, juniper is both easily identifiable and prone to fracturing, so it is likely over-represented in the data. To mitigate some of this effect, we calculated the Shannon-Wiener index on the unaltered macrofossil dataset, as well as on several permutations of the dataset: using the macrofossil data with each midden's most common macrofossil species excluded from analysis, and with juniper and creosote excluded.

To analyze differences in average diversity between middens made by different woodrat species, we compared alpha diversity measures for middens deposited by *N. cinerea* versus those for middens deposited by *N. lepida*. A two-tailed t-test was performed between these two groups for each of the alpha diversity measurements. To verify that differences in alpha diversity were not due to plant community type, we performed the same test, but only for juniper middens. Sample size was not adequate to do this test for creosote and NJNC middens.

We employed ANOVA and paired t-tests of alpha diversity measures between plant community types to examine differences in diversity between community types. We also performed regressions of alpha diversity versus temperature variability to determine if those variables are correlated.

Finally, we analyzed changes in precipitation over time. We performed an ANOVA and paired t-tests of mean minimum precipitation requirements of plants found in each midden versus plant community type, and a two-tailed t-test of mean minimum precipitation versus woodrat species. We also performed a two-tailed t-test of precipitation in juniper middens built by *N. cinerea* versus juniper middens built by *N. lepida*.

RESULTS

1. Macrofossil Identifications

From our middens, we were able to identify 18 genera and two subfamilies (Figs 6, Tables 3 & 7). Of these, we were able to identify 11 to the species level (Fig 4). We recognized an additional 41 macrofossil types that we were not able to identify to any valuable taxonomic level (Fig 5). These we recorded for use in alpha diversity analyses. Seven of these unidentified types comprised at least 20% of the macrofossils in at least one midden, and 24 of the 41 unidentified types were found in three or more middens.

Of the 20 indentified taxa, there were a few ambiguities (table 3). Because it is common in the Amargosa range today, Utah juniper (*Juniperus osteosperma*) is the most likely species of juniper found in most middens. However, we found one berry in UTIC 11a (9.6 ka, 1559 m) whose morphology does not match that of Utah juniper (Fig 4a, 4c). It is most likely *J. californica*, which grows at higher elevations than Utah juniper in the Panamint Mountains. Identification of juniper macrofossils is problematic, but further analysis of stomata may be more diagnostic of species (Betancourt et al. 2001). The three youngest *Pinus* samples (UTiC 10: 11.6 ka; TiC 11c-2: 13.1 ka; and TiC 11c-3: 15.5 ka) have round needles and are certainly *Pinus monophylla*, which is found in the high elevations of the Amargosa and Panamint mountain ranges today. The needles from the six older *Pinus*- containing middens have triangular cross-sections and are clearly a different species. *P. flexilis is* currently found in the highest elevations of the nearby Panamint Range, and it is likely that these needles belong to that species. However, the needles of *P. edulis* also have triangular cross-sections, and that species is found in the Mojave National Preserve less than 300 km southeast of Titus Canyon. Mehringer and Ferguson (1969) also found *P. aritata*, which is today primarily restricted to the Rocky Mountains of Colorado and New Mexico, in middens dated 23.6 and 28.7 ka from Clark Mountain in the Mojave National Preserve. Mehringer and Ferguson (1969) required observations of cross-sections of stomatal cells to differentiate *P. flexilis* from *P. aritata*.

It is also likely several of the genera we identified include multiple species. Within *Atriplex,* we likely recovered *A. confertifolia*, which is present in Titus Canyon today, as well as *A. canescens*, which is found at high elevations in the mountains surrounding Death Valley. *A. hyemelytra* currently reaches its maximum elevation at the mouth of Titus Canyon, so it may be present in young low-elevation middens as well. Additionally, at least 6 species of *Ephedra*, 29 species of *Eriogonum* (buckwheat), 9 species of *Ericameria* (goldenbrush), 4 species of *Encelia*, 23 species of *Cryptantha* (forget-me-not), 6 members of the subfamily Opuntioidea (prickly pear and cholla cactus), and 2 species of *Purshia* grow in Death Valley and the surrounding mountains and may be present in this record.

Middens grouped remarkably cleanly by community type: there is essentially no overlap between middens containing juniper, middens containing creosote, and middens containing neither species (Table 3, Fig 3a). Furthermore, middens grouped cleanly with age and elevation: only juniper middens are present until about 13 ka, at which time juniper retreated to high elevations. Creosote suddenly appeared in abundance ~4.5 ka. Juniper and creosote co-occur in only one midden (TiC 11c-3, 15.5 ka), but because we recovered only two particles of creosote, and because this midden is significantly older than the next oldest creosote-containing midden, it is likely that the creosote represents modern contamination. Between the retreat of juniper and the arrival of creosote, we recovered trace amounts (1-3 macrofossils) of juniper from a single midden (UTiC 6, 8.5 ka) and trace amounts of creosote in another (TiC 11b, 6.3 ka).

Because of the clear separation of creosote and juniper, we hereafter refer to middens with more than trace amounts of juniper or creosote as “juniper middens” and “creosote middens”, respectively. We refer to middens without more than trace amounts (1-3 macrofossils) of creosote or juniper as “NJNC middens”, for “non-juniper, non-creosote”.

Juniper is overwhelmingly dominant where it is found, constituting 50- 98% of macrofossils in 25 of the 26 juniper middens, with a mean of 78%. TiC 18c is the only juniper midden for which juniper is not the most common species, comprised of 16% juniper and 50% of unknown 2. We identified 17 taxa and 32 unidentified macrofossil types other than juniper in the middens with a significant juniper presence, with 3-16 non-juniper taxa/types identified for each juniper midden.

Thirteen of these taxa/types were found only in juniper-dominated middens. Between the retreat of juniper and the arrival of creosote, we recovered trace juniper (3 macrofossils) from one NJNC midden (UTiC 6, 8.5 ka). This midden is only ~0.4 ka younger than the youngest juniper midden and 63 m lower in elevation.

Creosote is not as consistently dominant as juniper where it is found. It constitutes 11 – 78% of macrofossils in the 11 creosote middens, with a mean of 40%. In 4 of the creosote middens, creosote is *not* the most common macrofossil. In UTiC 9, which was deposited above creosote's modern elevational range, *Ephedra, Sphaeralcea ambigua*, and unknown 6 are all more common than creosote. Pygmycedar is the most common plant in TiC 15b (2.5 ka, 582 m) and TiC 8 bottom b (4.7 ka, 1229 m), and unknown 5 is the most common plant in TiC 15 take 2a (0.4 ka, 582 m). Thirteen identified taxa and 20 unidentified types are found in middens with a significant creosote presence. Four unidentified types are found only in creosote middens. *Chaenactis* is the only indentified taxa found only in creosote middens. It is represented by a single seed found in a single midden.

In the absence of creosote and juniper, we found several other shrubs in abundance. Pygmycedar is the most common macrofossil in the 10 NJNC middens, comprising 11- 79% of macrofossil in the 8 middens in which it is found. *Ericameria* spp. are the most common macrofossil in 2 NJNC middens, and *Atriplex* (probably *A. confertifolia*) in one other. We found 16 indentified taxa and 22 unidentified types in NJNC middens. Only 4 unidentified types and no indentified taxa were found exclusively in NJNC middens. Ten taxa/types were found in juniper and NJNC middens only, and 2 taxa/types were found in creosote and NJNC middens only.

Most macrofossils were found in middens deposited by both species of woodrats. *Ambrosia dumosa* is the only identified taxa found in middens made only by *N. lepida*. This is likely because *A. dumosa* prefers climates hotter than *N. cinerea'*s thermal maximum, not a dietary prejudice on the part of the woodrats. No identified taxa was found only in middens deposited by *N. cinerea*. Nineteen unidentified macrofossil types were found in middens deposited by a single species. Of these, thirteen were only found in one midden. Four of these were found in 2-4 *N. cinerea* middens, and three were found in 2-7 *N. lepida* middens.

2. Woodrat Identification

The 48 middens studied were more or less evenly split between the two woodrat species (Fig 3b). A few were ambiguous. For example, TiC 13b (1216m, 9.7 ka, NJNC) had a mean maximum pellet width that is slightly small for *N. cinerea* but slightly large for *N. lepida.* Since no teeth were recovered from this midden, we did not include this midden in analyses related to woodrat species. *N. cinerea* was almost always associated with juniper middens, although two *N. cinerea* middens did contain significant portions of creosote. Only one *N. cinerea* midden is an NJNC midden. Conversely, *N. lepida* was not as restricted to one plant community type. We attribute 6 juniper middens, *9* creosote middens, and 9 NJNC middens to *N. lepida*.

We also find a demarcation in the ages of the middens associated with each woodrat species. *N. cinerea* built most of the oldest middens in this record, and, like juniper, it seems to have moved up in elevation after the warming period leading into the Holocene. However, it lingered at lower elevations longer than juniper did: the youngest two *N. cinerea* middens (TiC 8a Top 2, 3.7 ka, 1220 m; and TiC 16, 4.15 ka, 1015 m) are found at middle-elevations in Titus Canyon and contain creosote. *N. lepida* built most of the younger and lower-elevation middens in the record. *N. lepida* is present as early as 24.7 ka (TiC 10d, 1200 m), but it does not become common until ~ 13 ka.

N. lepida is likewise found in middle elevations of Titus Canyon well before the Holocene and the retreat of juniper. The oldest two *N. lepida* middens (TiC 10d, 24.7 ka, 1200 m; and TiC 18c, 23.6 ka, 1114 m) are found at elevations similar to the elevations of the *N. cinerea* middens found before and after them.

Several identifications were somewhat ambiguous. Pellet size distributions of TiC 8a Top 2 (37.1 ka, 817 m), a *N. cinerea* midden, and TiC 8 bottom b (4.7 ka, 1220 m), a *N. lepida* midden, show some signs of mixing with each other. Because TiC 8a top 2 contains mostly larger *N. cinerea*-sized pellets and TiC 8 bottom b contains mostly smaller *N. lepida*-sized pellets, and because they are relatively close in age, we included these two middens in statistical analyses for both plants and woodrats. Additionally, distribution of pellets in TiC 16, the youngest midden containing *N. cinerea* pellets, indicates a replacement event of one species by the other during midden deposition. Because TiC 16 is the second youngest midden with evidence of *N. cinerea*, and because it is only one of two middens containing both creosote and evidence of *N. cinerea*, we treated TiC 16 as a *N. cinerea* midden for statistical analyses.

3. Precipitation

In general, older middens and higher-elevation middens contained plants with higher precipitation requirements. Our data indicate that slightly more mesic plants became more prevalent in the canyon ~25-19 ka, which corresponds with the last glacial maximum. Increasingly arid plants began appearing ~17 ka. Very arid plants took over at the beginning of the Holocene, ~13ka, especially at lower elevations. (Fig 3c)

4. Alpha Diversity Analyses

To evaluate difference in diversity between middens deposited by different woodrat species, we performed a similar comparison between alpha diversity and woodrat species for each midden (Table 4, Fig 7). A two-tailed equal variance t-test indicates a significant difference between *N. cinerea* and *N. lepida* middens for plant species per midden at $P<0.10$ and for Shannon-Weiner diversity with all species included at $P<0.01$. No significant difference between *N. cinerea* and *N. lepida* middens was detected for Shannon-Weiner diversity excluding juniper and creosote and Shannon-Weiner diversity excluding each midden's most common macrofossil.

To account for differences in diversity between middens deposited by different woodrat species that is caused by differences in community, we performed a similar two-tailed equal variance t-test of alpha diversity values between juniper middens built by *N. cinerea* and juniper middens built by *N. lepida* (Table 4). (Because only two juniper middens and one NJNC midden were built by *N. cinerea*, we do not have adequate sample sizes to perform similar tests for differences in diversity between either juniper or NJNC middens built by different woodrat species.) No significant difference was detected for any alpha diversity measure, and all p-values exceeded 0.82.

To evaluate differences in diversity before and after the arrival of creosote, we compared alpha diversity between community types (Fig 9, Table 5). We performed an f-test and two-tailed equal variance t-tests for each pair of community types for each of the four measures of alpha diversity we calculated. F-ratios indicated a significant difference at $P<0.10$ between community types for Shannon-Weiner alpha diversity with all species included. T-tests indicate a significant difference between juniper and creosote middens and between juniper and NJNC middens for Shannon-Weiner diversity with all species included at $P<0.01$, and between juniper and creosote for count of species per midden at $P<0.05$. However, there were no significant differences between community types when Shannon-Weiner diversity was calculated excluding creosote and juniper data and when calculated excluding each midden's most common species.

To evaluate how temperature variability affects diversity of a system, we compared temperature variability estimates to each of the four alpha diversity measures (Fig 10, Table 6). Middens for which less than three GISP2 data points were available within the 50± year period around the midden's date of deposit were eliminated from this analysis, leaving 27 middens. We performed linear analyses of temperature variation versus each of the four alpha diversity measures. The R^2 value was insignificant for all four analyses. We performed similar analyses for temperature variability versus alpha diversity for middens of each of the three plant community types; again, in no case was the R^2 value significant.

DISCUSSION

Our study documents significant changes over time in the Titus Canyon plant community driven by climate change and the invasion of a new species. As climate warmed at the end of the Pleistocene, juniper-dominated communities retreated up in elevation and were replaced by more arid-adapted plants. However, the appearance of creosote lagged several thousand years behind the onset of warmer temperature regimes. With the establishment of creosote in Titus Canyon came the formation of the modern Mojave community.

Surprisingly, the appearance of creosote did not significantly change what plant species were found in the middens and therefore the communities, but only to a change in the proportions of each species found in the middens. In general, other shrub species became less prevalent after the arrival of creosote. Overall, we did not find that either changes in climate or invasion of creosote significantly impacted alpha diversity.

Bushy-tailed woodrats (*N. cinerea*) also retreated to higher elevations as temperatures warmed, though not as quickly as juniper and associates did. *N. cinerea* was eventually replaced by the desert woodrat, *N. lepida*, though not until after the arrival of creosote. Our data suggests that incorporating middens from two different rat species did not significantly impact our conclusions.

1. Titus Canyon Plant Community Dynamics

This midden record provides a particularly good means to examine shifts in plant communities over long periods of time. The 33,000 year age distribution of our midden series begins during a cooling period, the ice sheets reaching their height during the last glacial maximum 26-19 ka at the end of the Pleistocene. The record ranges through the warming period at the end of the Pleistocene interrupted by the Dryas stadials, the short and cold period of the Younger Dryas between about 12.8 and 11.5 ka (Alley et al. 2003), and into the modern temperature regimes of the Holocene beginning 11.5 ka. The middens are spread remarkably evenly through this time period, although they are still affected by the “pull of the recent”, or bias towards younger samples that have had less time to degrade, that plagues most paleontological studies (Fig 3).

The upward shift in elevation of juniper beginning ~12-11 ka corresponds with the period of warming at the end of the Younger Dryas that led into the Holocene. The appearance of creosote, on the other hand, does not correspond to any known widespread environmental change. It therefore seems likely that the expansion of creosote's range lagged behind the expansion of suitable habitat. Alternatively, creosote may have required the extirpation of some extant vegetation before it could expand its range.

However, we believe the latter scenario is unlikely. Before the arrival of creosote and after the retreat of the juniper community, many of the more heat-tolerant and arid plant species present in Titus Canyon today appeared or became more populous in Titus Canyon. All identified taxa found in NJNC middens are also found in creosote and/or juniper middens, and only four unidentified macrofossil types are exclusive to NJNC middens. Furthermore, ~60% of macrofossils found in NJNC middens are also found in *both* creosote and juniper middens. The NJNC communities may not have an exact modern analog, but aside from an absence of creosote, NJNC communities were not very different from modern mid to low-elevation Titus assemblages. Competition from invading creosote resulted in a rearrangement of plants in the community, but no widespread extirpation of shrub species.

Conversely, only one plant is strictly associated with creosote: white bursage (*Ambrosia dumosa*), a lowland middle-Mojave species. Its presence may indicate a change in community due to the presence of creosote. On the other hand, both creosote and white bursage have a minimum annual precipitation requirement of ~7.62 cm, which is ~5 cm less than the next most arid plants we identified. The presence of creosote and white bursage may indicate that conditions became more arid. If that is the case, than changes in the plant community after the arrival of creosote may be due to changes in precipitation, rather than a change caused by creosote. Our estimates of average precipitation indicate that the creosote communities in our record had lower mean minimum precipitation requirements than the NJNC midden's communities (Fig 11). However, our analysis does not provide any indication of whether precipitation *actually* decreased around the time of creosote's arrival, or if the expansion of all arid plants simply lagged behind climatic warming, following the pattern seen by creosote.

The pattern of precipitation reflected by the plant species in this record generally reflect temperature: cooler periods are associated with more mesic species, and warmer temperatures with more arid species (Fig 11). Between ~24 and 19 ka, mean minimum precipitation requirements increased slightly. This period precisely corresponds with the Last Glacial Maximum. Mean minimum precipitation requirements decrease at the end of the Younger Dryas and beginning of the Holocene with the retreat of juniper. About 8 ka, mean minimum precipitation decreases slightly again. This later increase in aridity is not correlated with any major global shifts in temperature. However, this increased aridity may loosely correlate with the arrival of creosote. He et al. (2010) found that nighttime air temperature is substantially higher in creosote scrubland than in grassland in the Chihuahuan Desert. Thus, this shift in temperature may be due to changes in microclimates created by dominant plants rather than in global climatic changes.

Our record documents the establishment of creosote at the northern edge of the Mojave Desert at 4.7 ka (Figs 3, 6). This extends the earliest records of persistent creosote populations there ~ 1000 years beyond the dates that Spaulding (1990) and Spaulding (1980) previously found at 3.7 and 3.9 ka, respectively. The earliest record of creosote in the Mojave is 8.7 ka from the Marble Mountains in the southern Mojave (Spaulding 1990), a date well into the Holocene. This suggests that it took creosote at least 4 ka to expand ~400 km to its current northern border. This relatively consistent record of steady northward expansion combined with the lag in expansion into newly available habitats suggests that creosote has historically expanded slowly, dispersing short distances , as opposed to hop-scotching its way through its range via long-distance dispersal. The original long-distance migration of creosote from South America to Central and North America does not seem to represent characteristic movement of creosote.

The consistent presence and high abundance of creosote in our midden record after its arrival in Titus Canyon, despite fluctuating environmental conditions (Fig 10), suggests that creosote is robust and persistent within the modern range of arid conditions over long periods of time. In this modern period of climate change and the likely increasing frequency in extreme weather patterns (Hartmann et al. 2013), the hardiness of creosote may help stabilize disturbed communities.

The fact that we found only one plant that was not present in both creosote and NJNC middens, combined with the lack of significant difference in alpha diversity indices between NJNC and creosote middens, suggests that creosote does not have any significant effect on overall plant alpha diversity. Interestingly, our analysis indicates that juniper communities may also have a lower mean number of species and a slightly lower mean alpha diversity than lower elevation arid communities. However, the lower diversity we detect may be an artifact of the less-reliable herbaceous and gramminoid macrofossil record recovered from standard paleomidden macrofossil analyses like ours. More analysis of grasses and perennial plants is necessary to determine overall effect of creosote on plant community diversity.

Additionally, we did not detect any significant differences in alpha diversity due to disturbance caused by variable temperature, nor does our data suggest a decrease in diversity associated with a more arid plant community (Fig 9, 10, 11). Again, more study of herbaceous and gramminoid plants is necessary to confirm this result. Furthermore, a better proxy for precipitation independent of plant species is required to draw any conclusions about the effect of precipitation on plant diversity.

2. Woodrat Dynamics

We find that *N. cinerea* and *N. lepida* give similar representations of plant communities through time. We did not detect any clear differences in proportion of macrofossils between *N. cinerea* and *N. lepida* middens, and most plant taxa and macrofossil types we identified are found in both types of middens. Because most *N. cinerea*-built middens are juniper-dominant, significant differences in alpha diversity between woodrat species can be explained as a reflection of the lower alpha diversity detected in juniper middens by those two measures. The high P-values for t-tests between *N. cinerea* and *N. lepida* juniper middens for all alpha diversity measures lead us to feel confident that any differences in plant recruitment between *N. cinerea* and *N. lepida* are negligible. We therefore find it appropriate to use middens from the two species to create one record of plant communities over time.

The pattern of woodrat species movement over time and elevation is not quite as clean as that of the plant communities. *N. cinerea* is strongly allied with juniper in this record. It is therefore not surprising that it is also responsible for building most of the pre-Holocene middens. However, while juniper moved uphill immediately after the warming period leading into the Holocene, *N. cinerea* persisted in middle elevations (~10,000-13,000 m) until at least 3.7 ka (e.g. TiC 8a top 2, 1220 m). Furthermore, while juniper still grows in the high elevations of the Amargosa Mountains today, *N. cinerea* has been extirpated. *N. cinerea* has a lower temperature tolerance than most other species of *Neotoma*, with a maximum tolerated July average temperature of ~25°C (Smith 1997). Because it persisted in Titus Canyon well into the Holocene despite summer highs regularly above this temperature, temperature is probably not the only variable driving the distribution of *N. cinerea* in the Amargosa Mountains.

Why didn't *N. cinerea* move up in elevation with juniper in the Holocene? Topography may be a limiting factor: limestone caves are particularly plentiful ~1000-1300 m in the Amargosa, but suitable caves and crevices are less plentiful above that elevation. Deep caves may have provided a retreat from warmer temperatures that allowed *N. cinerea* to persist so long into the Holocene. Grayson (2000) reported similar persistence of *N. cinerea* in the Great Basin during the early Holocene.

Conversely, *N. lepida* seems to show little preference for elevation or plant community, having built approximately the same number of juniper, creosote, and NJNC middens, as well as both the highest (1583 m) and lowest (298 m) elevation middens in this record. Whole most of the Pleistocene middens in this record were built by *N. cinerea*, two middens from the wet and cold period of the last glacial maximum were built by *N. lepida*, as well as most of the middens in the much warmer and dryer Holocene. This suggests that this species is not heavily constrained by either temperature or aridity in Titus Canyon. Additionally, because *N. lepida* builds dens in shrubs and trees as well as rock structures, it is likely not as limited by topography as *N. cinerea*. Smith et al. (2009) observed that *N. cinerea* easily out-competes *N. lepida* due to its significantly larger size and more aggressive nature. This suggests that *N. lepida* is well adapted to the range of conditions found in Titus Canyon over the last 35 ka, and that it has primarily been constrained by the limits of *N. cinerea*'s range.

3. Conclusions

To date, our midden record is one of the largest collections from a single location. It is also one of only a few to be analyzed for both plant macrofossils and for woodrat evolution and species replacements. Consequently, this record provides a fine-grained examination of the shifts in plant communities over an important temporal interval.

Understanding how arid communities react to long-term warming is essential for predicting how modern communities will react to modern climate change. Despite documenting fundamental changes in the dominant plants, our study suggests that overall diversity remains relatively consistent over long periods of time under large-scale climatic warming. Furthermore, the invasion of creosote into new habitats does not decrease diversity long-term, despite creosote's strong competitive characteristics. To confirm the resilience of North American desert communities to climate change, future study of grass and small annual plant abundance and diversity is necessary.

Additionally, it should be noted that both species of woodrat responded to climate change by migrating as well as by adapting *in situ*. Using this midden series, Smith et al. (2009) analyzed changes in woodrat body size and found that both species became smaller as conditions warmed. Analysis of plant adaptations over long periods of time is necessary to gain a fuller understanding of how communities react to climate change. Macrofossils may be useful for analysis of desert adaptations, such as stomatal and cuticle morphology.

Paleomiddens provide important snapshots of desert communities over long periods of time, and these snapshots can help us make predictions about the future of modern communities. The analytical potential of paleomiddens has not been fully explored. In the light of modern anthropogenic environmental change, it is essential to use all tools available to understand how biological communities respond to disturbances like climatic warming and invasion of new species.

Figure and Tables

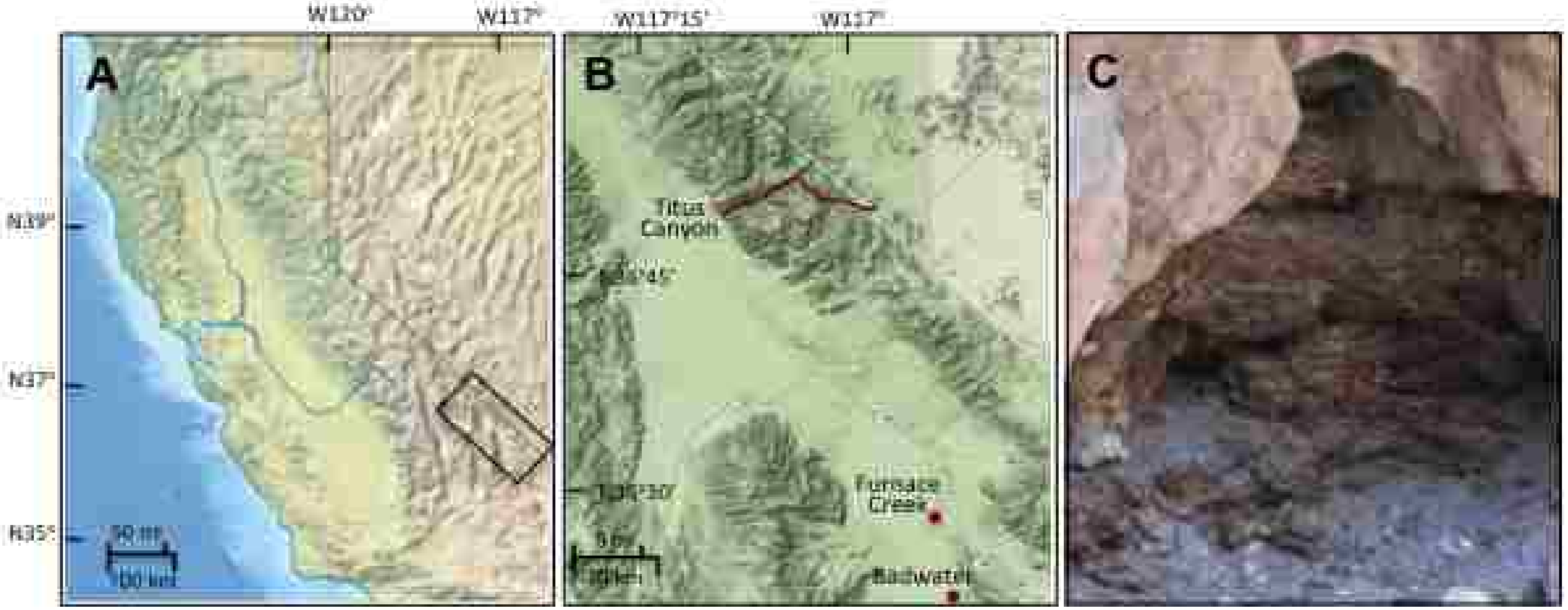

Figure 1: Map of Titus Canyon and picture of midden
(a) Map indicating location of Death Valley (b) Map indicating location of Titus Canyon in the Amargosa Mountains on the northeast side of Death Valley (c) Photograph of indurated paleomidden in Titus Canyon. Large size and layers indicate that this crevice was used by many woodrats over a long period of time.

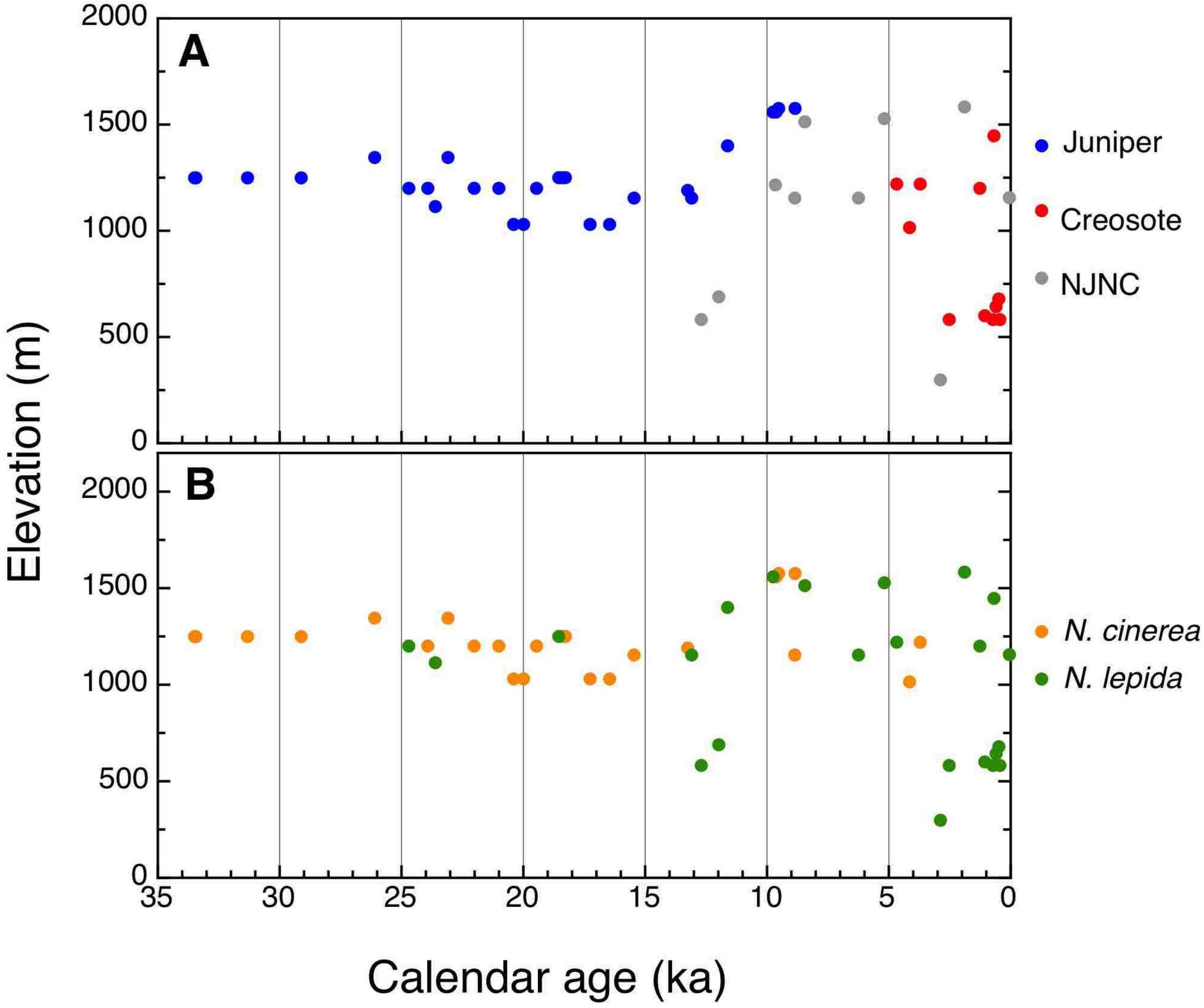

Figure 2: Age and elevation of Titus Canyon middens
(a) Points are color-coded by vegetation type. Blue indicates middens with more than trace amounts of juniper (>6 macrofossils). Red indicates middens with more than trace amounts (>6 macrofossils) of creosote. Gray indicates middens containing no more than trace amounts of either juniper or creosote. (b) Points are color-coded by the species of woodrat that deposited the midden. Yellow indicates *Neotoma cinerea* and green indicates *N. lepida.*

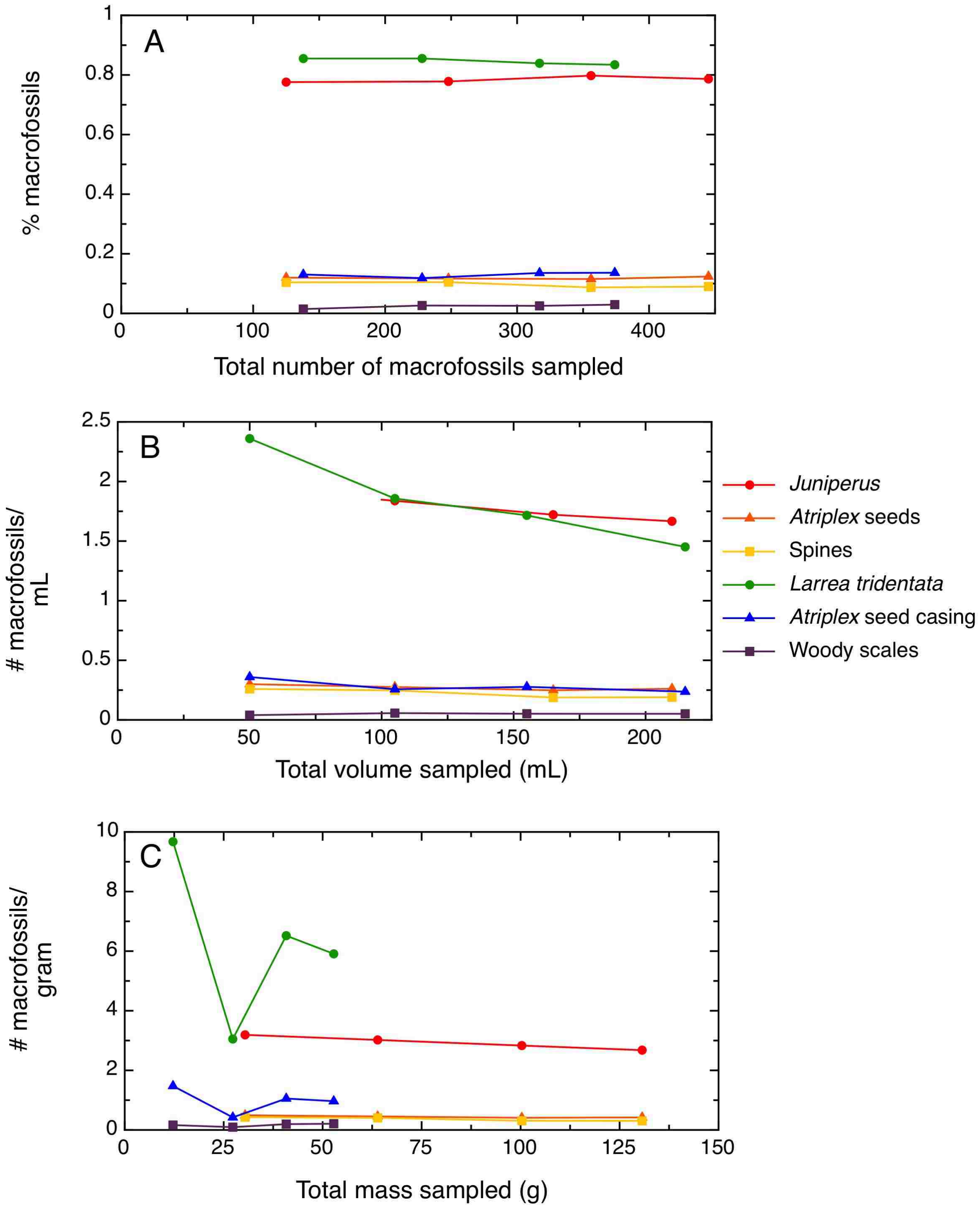

Figure 3: Tests for appropriate sample size

Six macrofossil types were sampled and tallied to determine minimum necessary sampling effort. (a) Percent macrofossils was calculated using number of macrofossils of given type divided by total number of macrofossils sampled. (b) Number of macrofossils per total volume sampled versus total volume of midden material sampled. (c) Number of macrofossils per gram total midden material sampled versus total mass of midden material sampled

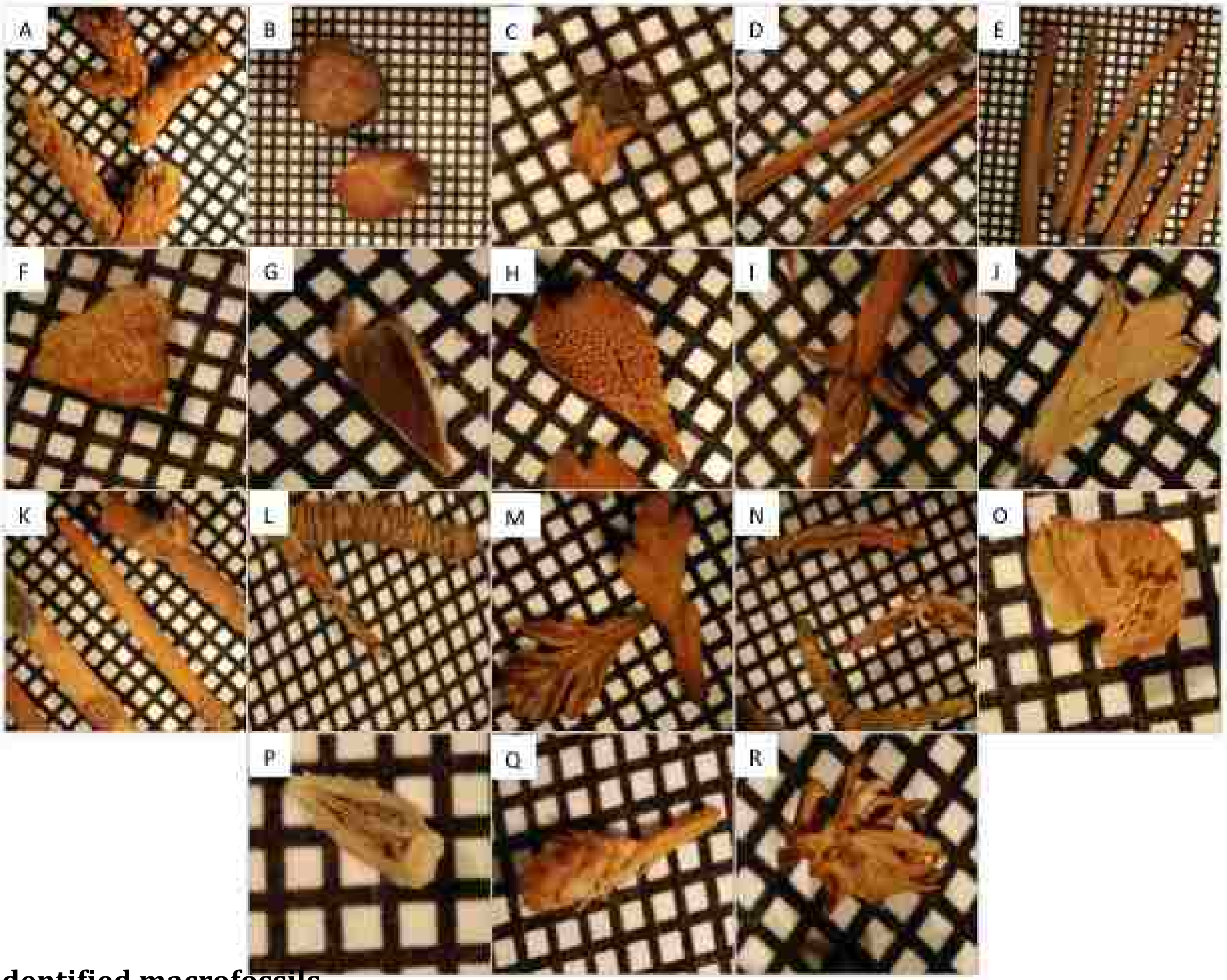

Figure 4: Identified macrofossils

(a) *Juniperus osteosperma* twigs (b) *J. osteosperma* fruit (c) *J. californicus*? (d) *Pinus flexilis*? (e) *Pinus monophylla* (f) *Atriplex* (g) *Encelia* (h) *Ericameria* (i) *Ribes cereum* (j) *Artemisia tridentata* (k) *Ephedra* (l) *Cercocarpus ledifolius* (m) *Purshia* (n) *Eriogonum* (o) *Sphaeralcea ambigua* (p) *Cryptantha* (q) *Peucephyllum schottii* (r) *Ambrosia dumosa*

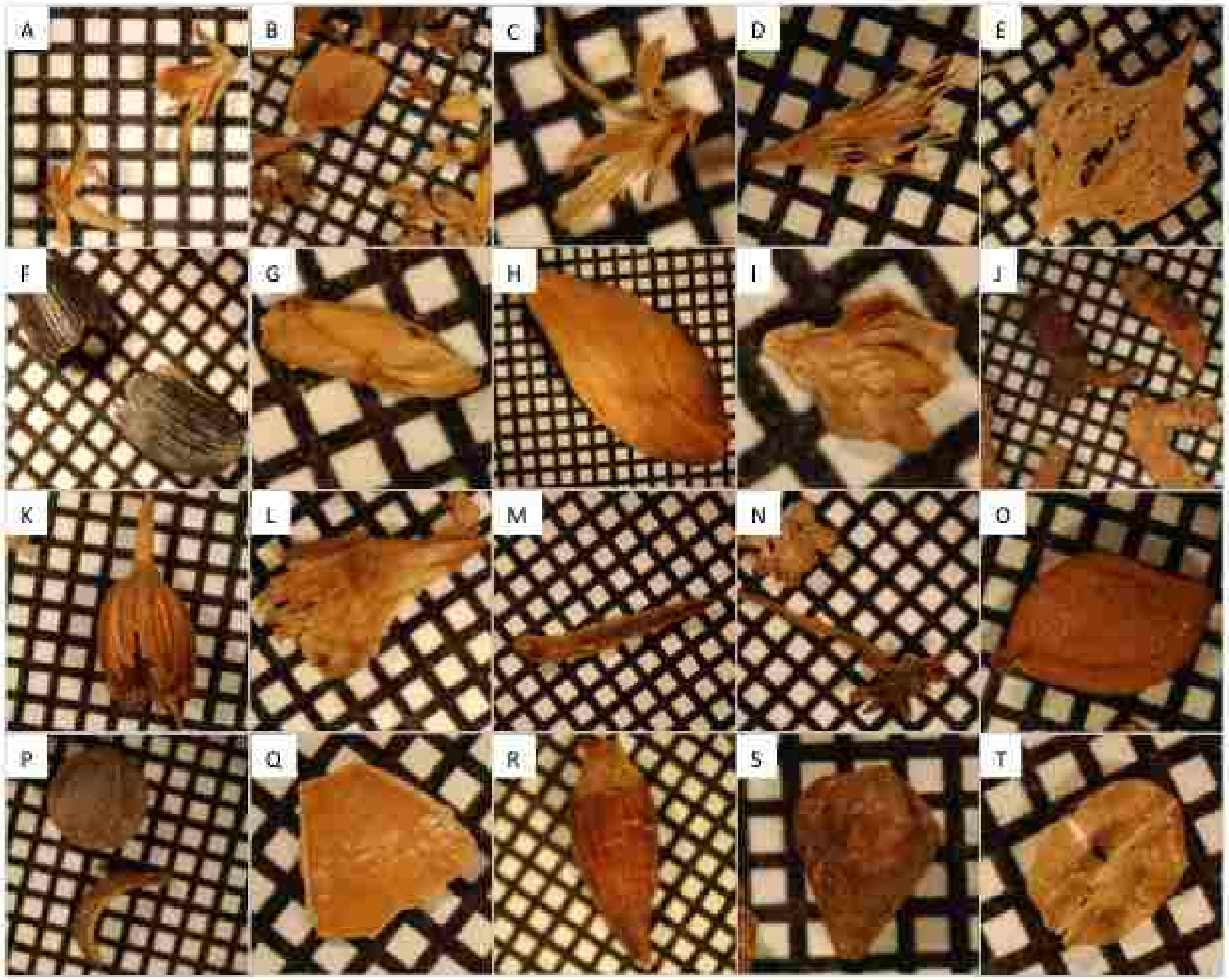

Figure 5: Unidentified macrofossil types 1-20
Numbers correspond to number assigned to unknown macrofossil type. Unidentified types 21- 41 are not pictured. Ten or fewer macrofossils were found across entire record for those types not pictured.

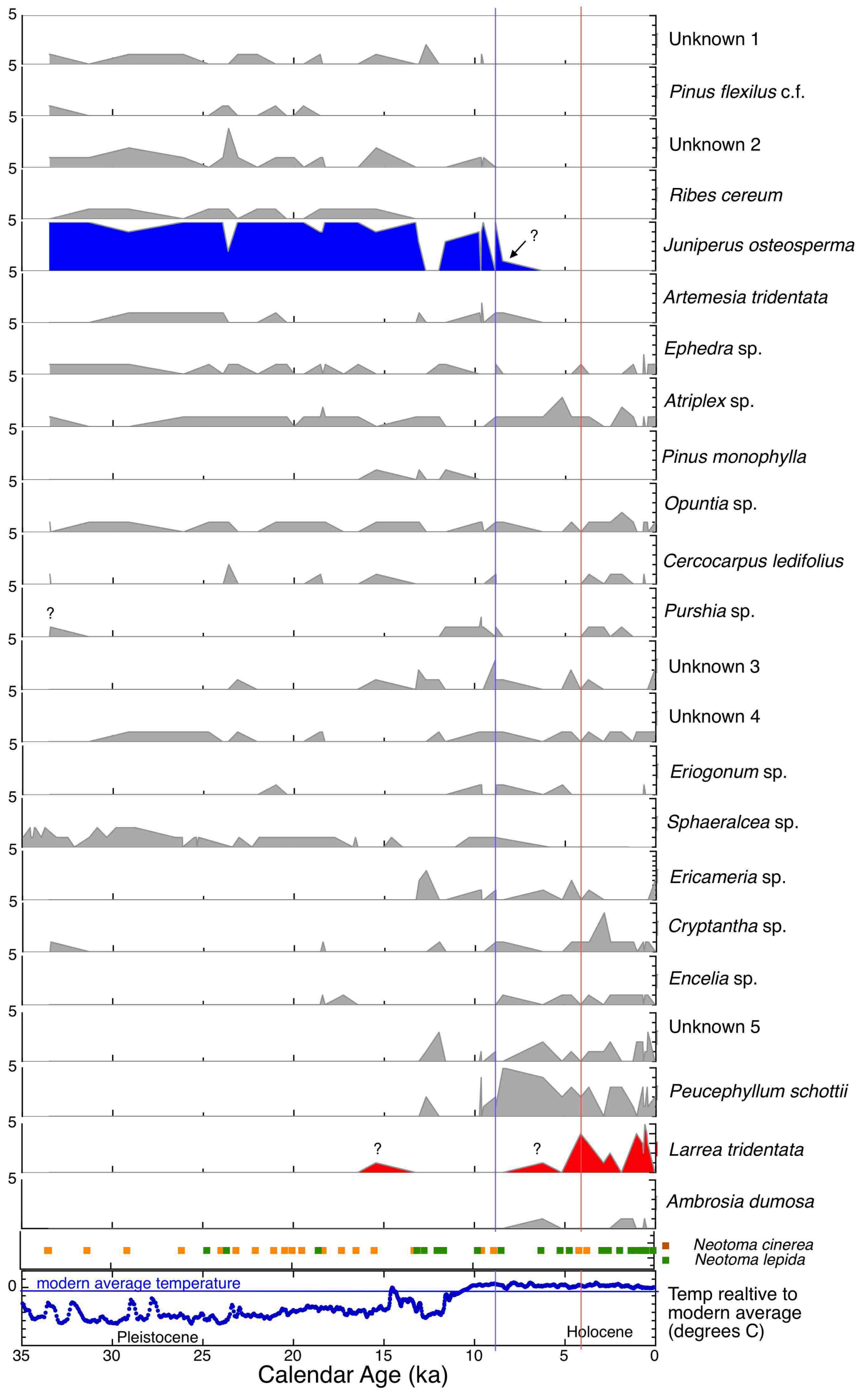

Figure 6: Proportions of macrofossils over time

For the purposes of this graph, each plant was given a score between 1 and 5 for each midden: 5 if the plant comprises > 75% of macrofossil in given midden, 4 > 50%, 3 > 25%, 2 > 10%, and 1 > 0. Question marks indicate probable contamination, and in each of these cases we found less than 5 macrofossils of a given species. The vertical blue line indicates the youngest midden with a significant proportion of juniper, and the red vertical line indicates the oldest midden with a significant proportion of creosote. Plant species are arranged by average age of the middens from which each species was recovered.

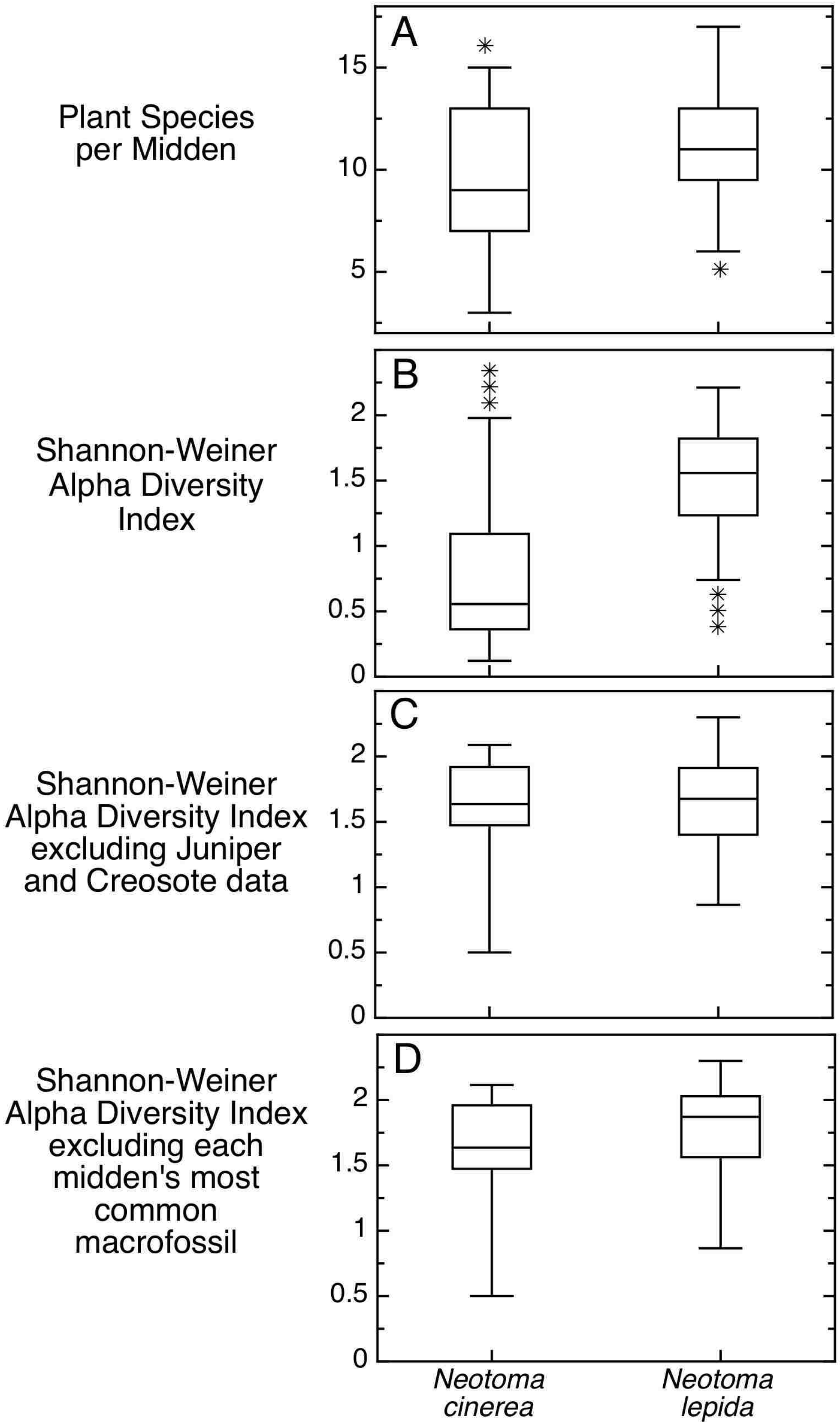

Figure 7: Alpha diversity of middens by woodrat species
Maximum, upper quartile, mean, lower quartile, and minimum are indicated by each box plot. A significant difference of P<0.1 is indicated by one star, and of P<0.01 by three stars..

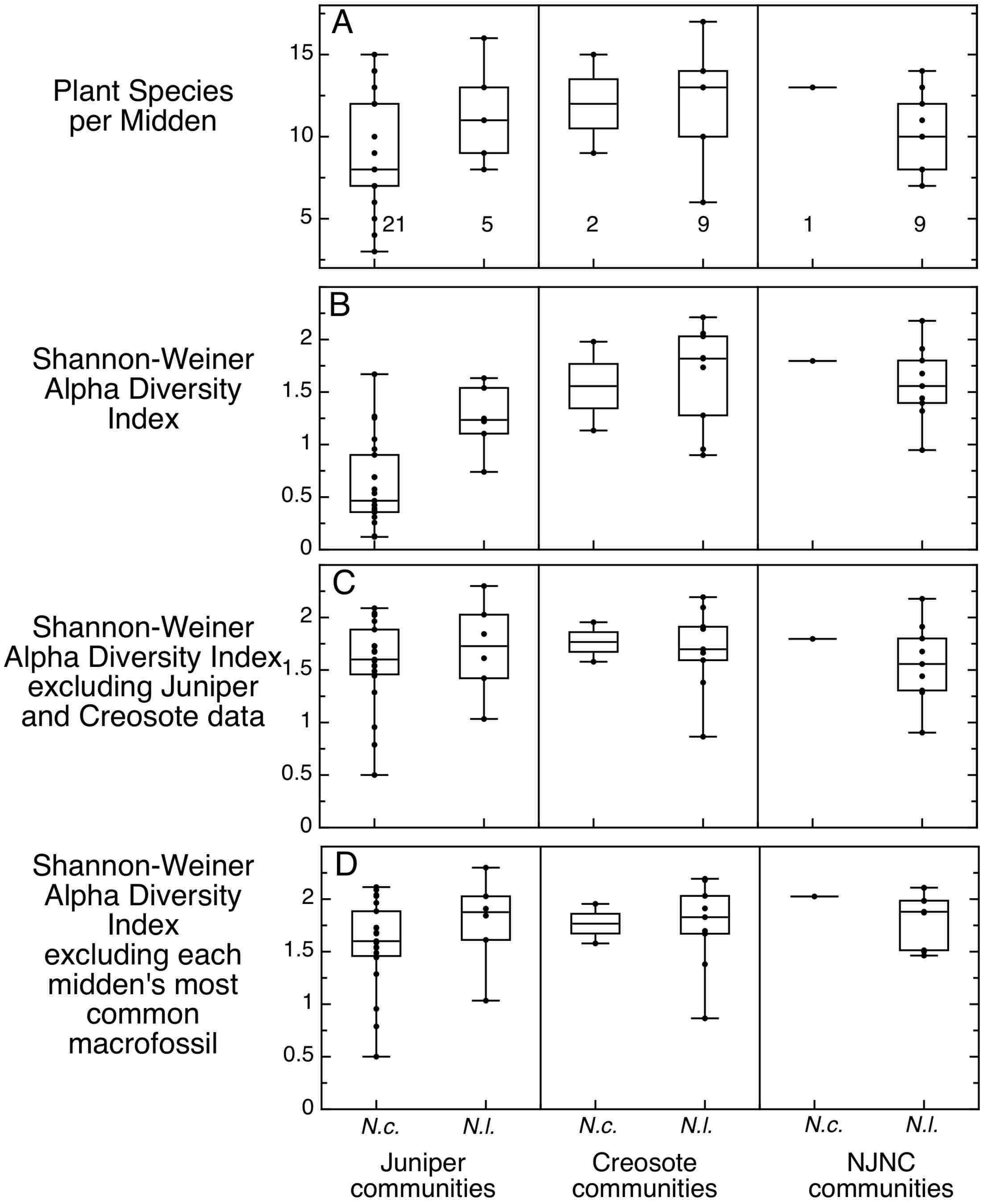

Figure 8: Alpha diversity of middens by woodrat species and plant community
Maximum, upper quartile, mean, lower quartile, and minimum are indicated by each box plot. T-tests were performed for juniper communities; no significant differences were found.

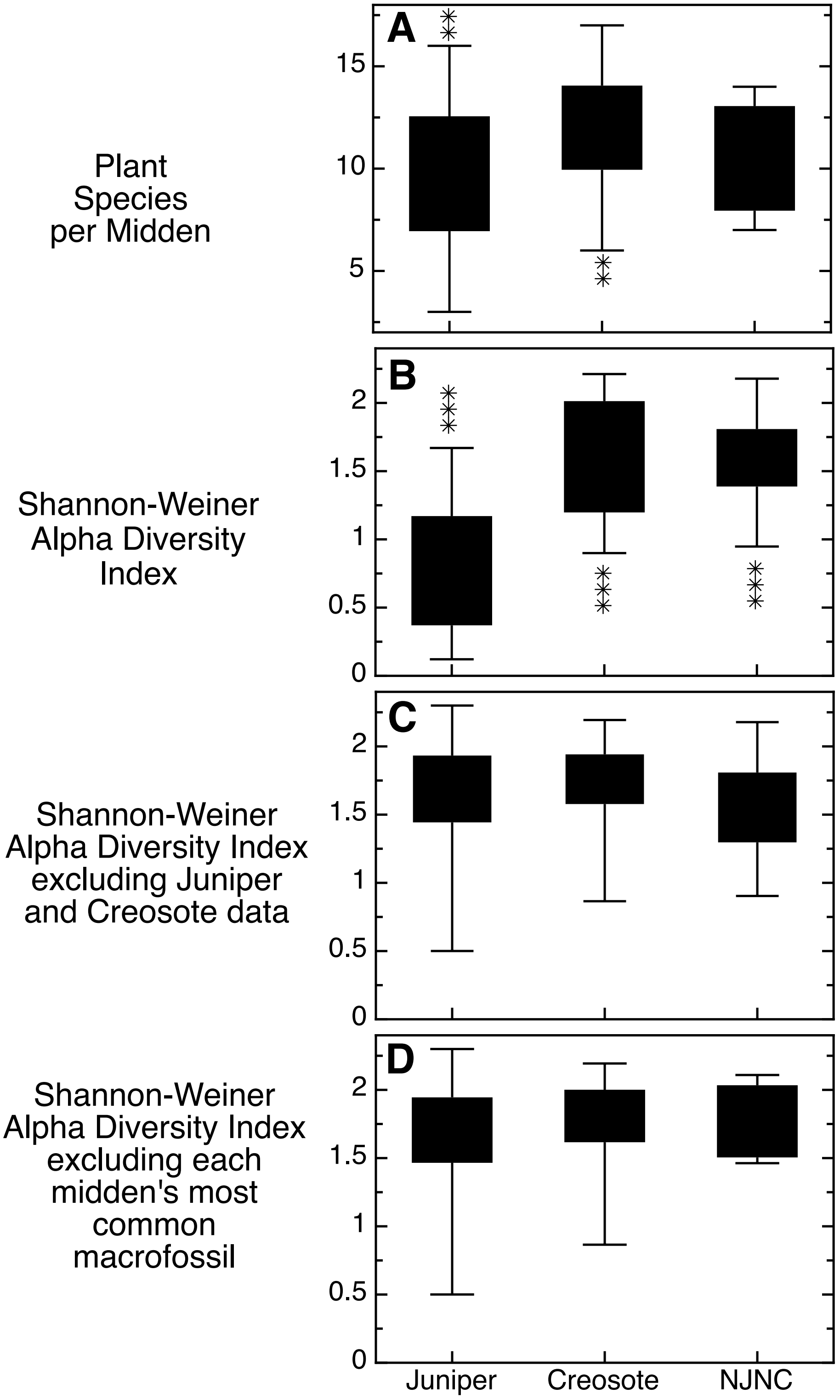

Figure 9: Alpha diversity by plant community
Maximum, upper quartile, mean, lower quartile, and minimum are indicated by each box plot. Significant t-test values of $P<0.05$ are indicated by two stars and of $P<0.01$ by three stars.

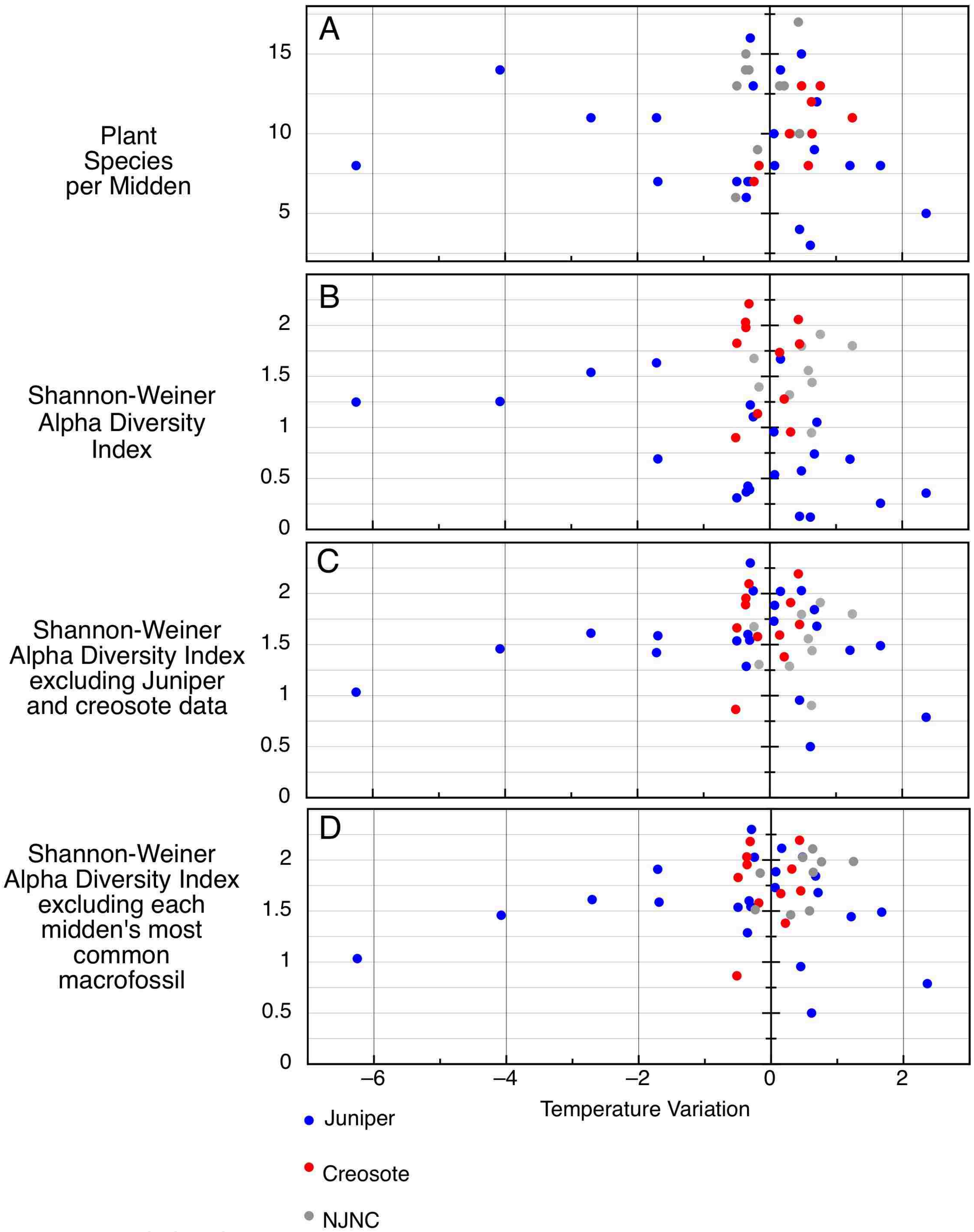

Figure 10: Alpha diversity versus temperature variation

Colors indicate plant community type. Blue indicates middens with more than trace amounts of juniper (>6 macrofossils). Red indicates middens with more than trace amounts (>6 macrofossils) of creosote. Gray indicates middens containing no more than trace amounts of either juniper or creosote.

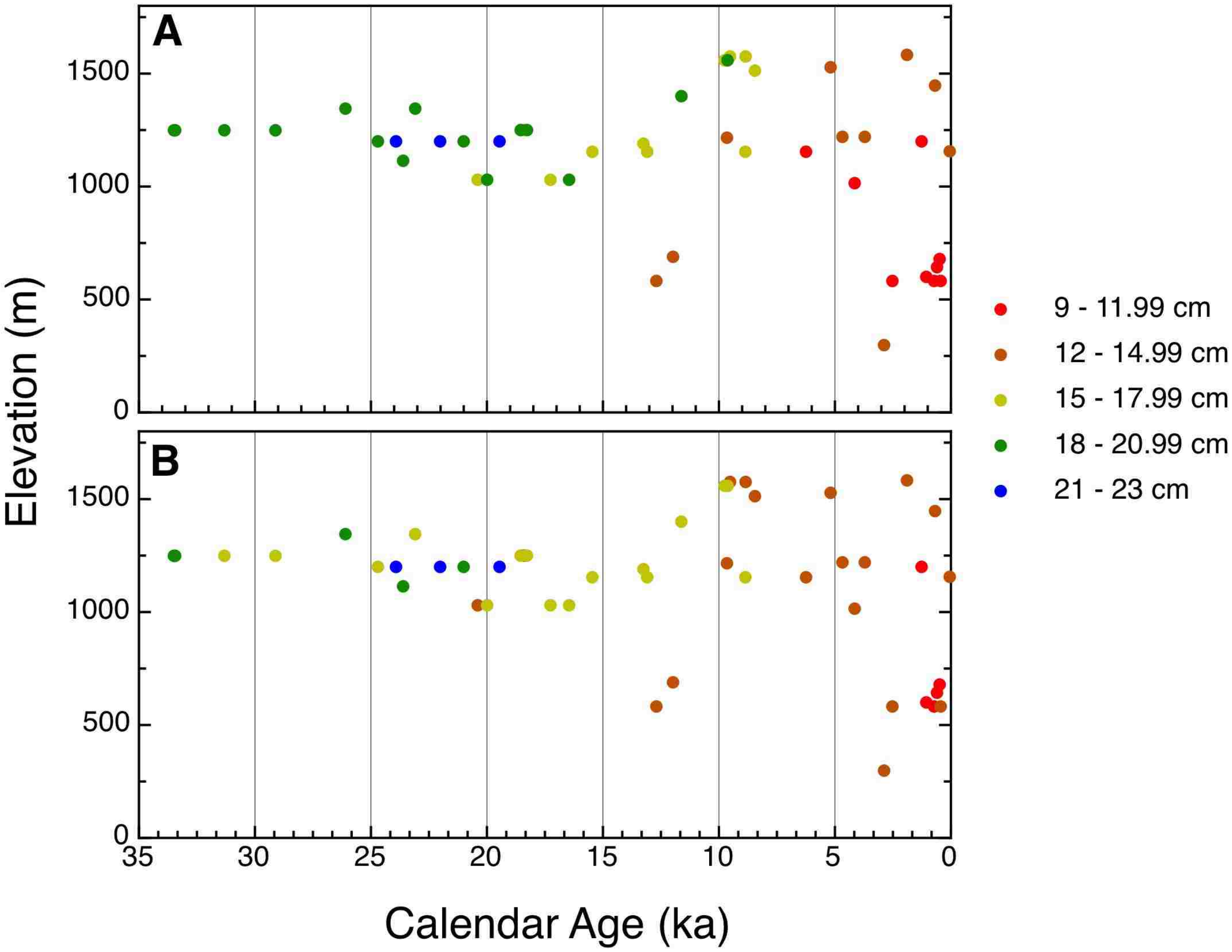

Figure 11: Mean minimum precipitation requirements of plants found in middens
Mean minimum precipitation requirements of plants found in middens is indicated by color. (a) All plants are included in calculations of mean minimum precipitation requirements of plants. (b) Creosote and juniper are excluded from calculations of mean minimum precipitation requirements of plants.

Table 1: Earliest paleomidden records of creosote

Earliest records of creosote from various paleomidden collection sites across the Chihuahuan, Sonoran, and Mojave Deserts.

Location	Desert	Latitude	Longitude	Elevation (m)	Age	Source
Rio Grande Village area, Big Bend, TX	Chihuahuan	29°11-16' N	102°58'-103°01'W	60-835	26.5	Van Devender, 1990a
Tinajas Altas Mountains *near* Yuma, AZ	Sonoran	32°16-20'N	114°02-07'W	330	18.7	Van Devender 1990b
Guadalupe Canyon, north-eastern Baja California, Mexico	Sonoran	32°10'8.5N	115°44'36.5W	155	18.4	Holmgren 2014
Tinajas Altas Mountains *near* Yuma, AZ	Sonoran	32°16-20'N	114°02-07'W	550	15.7	Van Devender 1990b
Whipple Mountains, San Bernadino Co., CA	Northern Sonoran	34°13'N	114°22'W	320	13.5	Rowlands 1978
Rough Canyon, NM	Chihuahuan	N32°22.7'	W105°52.83'	1490	12.6	Betancourt et al. 2001
Picacho Peak, Imperial Co., CA	Sonoran	32°58'N	114°38'W	285	12.5	Van Devender 1990b
Picacho Peak, Imperial Co., CA	Sonoran	32°56-58'N	114°38-39'W	240-300	12.4	Van Devender 1990b
Rough Canyon, NM	Chihuahuan	N32°22.39'	W105°54.07'	1500	11.6	Betancourt et al. 2001
Butler Mountains, Yuma Co., AZ	Sonoran	32°21'N	114°12'W	240-255	11.2	Van Devender 1990b
Picacho Peak, Imperial Co., CA	Sonoran	32°56-58'N	114°38-39'W	240-300	11.2	Van Devender 1990b
Whipple Mountains, San Bernadino Co.	Northern Sonoran	34°13-16'N	114°22-25'W	320	11	Van Devender 1990b
Whipple Mountains, San Bernadino Co.	Northern Sonoran	34°13-16'N	114°22-25'W	320-525	10.8	Van Devender 1990b
Wellton Hills, AZ	Sonoran	32°36'N	114°08'W	160-80	10.7	Van Devender 1990b
Butler Mountains, Yuma Co., AZ	Sonoran	32°21'N	114°12'W	240-255	10.3	Van Devender 1990b
Butler Mountains, Yuma Co., AZ	Sonoran	32°21'N	114°12'W	240-255	10.2	Van Devender 1990b
Rio Grande Village area, Big Bend, TX	Chihuahuan	29°11-16' N	102°58'-103°01'W	60-835	9.8	Van Devender 1990a
Marble Mountains	Southern Mojave	34°40'N	115°35W	840	8.7	Spaulding 1990

Maravillas Canyon Cave, Black Gap Wildlife Management Area, TX	Chihuahuan	29°33' N	102°50'W	610	8.2	Van Devender 1990b
Silurian Valley	Mojave	35°22'30"N	116°05'W	400	7.7	Koehler et al. 2005
Chocolate Mountains, Riverside Co., CA	Sonoran	33°30'N	115°40	250	7.6	Rinehart and McFarlane 1995
Granite Mountains	Mojave	35°26'N	116°34'W	1220	6.7	Koehler et al. 2005
Waterman Mountains	Eastern Sonoran	32°20'3"N	111°27'W	795	6.1	Van Devender 1990b
Sunset Cove, CA	Mojave	34°30'N	116°59-117°00W	972	5.9	King 1976
Lucerne Peak, CA	Mojave	34°30'N	117°00W	1097	5.8	King 1976
Nelson Basin	Mojave	35°21'N	116°44'W	1010	5.3	Koehler et al. 2005
Rhodes Canyon, San Andres Mountains, NM	Chihuahuan	33°11'N	106°36-39'W		4.3	Van Devender 1990a
Lucerne Valley, CA	Mojave	34°30'N	116°50W	1006	4.3	King 1976
Eureka View, CA	Mojave	37°20'N	117°47'W	1465	3.9	Spaulding 1980
Hueco Mountains, TX	Chihuahuan	31°43'-53'N	105°59'-106°09'W	1270-1495	3.7	Van Devender 1990a
Point of Rocks	Mojave	36°24	116°17'W	900-910	3.7	Spaulding 1990
Lucerne Valley, CA	Mojave	34°30'N	116°50'W	1006	3.6	King 1976
Puerto Blanco Mountains, Yuma Co., AZ	Sonoran	31°58-59'N	112°47-48'W	535-605	3.4	Van Devender 1990b
Skeleton Hills, NV	Mojave	36°35-36'N	116°18-22'W	910-940	2.6	Spaulding 1990
Greenwater Valley, Inyo Co., CA	Mojave	36°10	116°36	1350	2.3	Cole and Webb 1985
Greenwater Valley, Inyo Co., CA	Mojave	36°10	116°36	1350	2.1	Cole and Webb 1985
Panamint Range, Inyo Co., CA	Mojave	36°35N	117°20W	260	1.9	Wells and Woodcock 1985
Fortymile Canyon, NV	Mojave	36°57-37°01N	116°17-22'W	925-1050	1.8	Spaulding 1990
Death Valley, CA	Mojave	36°15'52N	116°45'39W	-73	0.9	Buckley and Willis 1969
Isleta Pueblo, NM	Chihuahuan	34°56'N	106°43'W	1535	0 (Not present >0.17, present today)	Van Devender 1990a

Table 2: Titus Canyon middens

Age, elevation, woodrat, and plant summaries for each Titus Canyon midden

Calendar Age (ka)	Elevation (m)	Woodrat Species	% Juniper	% Creosote	Plants comprising >20% of midden	Proportions of plants comprising >20% of midden	Mean global temperature relative to modern at midden deposition
52	1156	*lepida*	0	0	*Ericameria*, Other	0.21, 0.20	0.13
443	582	*lepida*	0	0.29	Other, Creosote	0.35, 0.29	-0.23
487	679	*lepida*	0	0.57	Creosote, *P. schottii*	0.57, 0.27	-0.19
601	643	*lepida*	0	0.78	Creosote	0.78	-0.18
685	1447	*lepida*	0	0.11	Other	0.24	-0.06
727	582	*lepida*	0	0.28	Creosote, *P. schottii*	0.28, 0.27	-0.08
1062	600	*lepida*	0	0.68	Creosote, other	0.68, 0.21	0.65
1265	1200	*lepida*	0	0.36	Creosote	0.36	-0.16
1895	1583	*lepida*	0	0	*Peucephyllum schottii*	0.37	0.77
2523	582	*lepida*	0	0.22	*P. schottii, Creosote*	0.36, 0.22	1.20
2883	298	*lepida*	0	0.03	*Cryptantha*	0.611	1.20
3713	1220	*cinerea*	0	0.30	Creosote, *P. schottii*	0.3, 0.28	1.41
4150	1015	*cinerea*	0	0.68	Creosote	0.68	1.34
4677	1220	*lepida*	0	0.15	*Peucephyllum schottii*	0.3	0.09
5187	1528	*lepida*	0	0	*Atriplex, P. schottii,* Other	0.29, 0.24, 0.23	1.66
6246	1154	*lepida*	0	0.01	*Peucephyllum schottii*	0.57	0.74
8447	1513	*lepida*	0.01	0	*Peucephyllum schottii*	0.79	1.19
8849	1576	*cinerea*	0.89	0	*Juniperus osteosperma*	0.89	2.04
8861	1154	*cinerea*	0	0	Other	0.45	2.14
9522	1576	*cinerea*	0.92	0	*Juniperus osteosperma*	0.91	1.17
9628	1559	*cinerea*	0.72	0	*Juniperus* spp.	0.72	1.36
9655	1216	*cinerea*	0	0	*Peucephyllum schottii*	*0.59*	1.61
9751	1559	*lepida*	0.74	0	*Juniperus osteosperma*	0.73	1.77
11618	1400	*lepida*	0.46	0	*Juniperus osteosperma,* Other	0.45, 0.39	-6.96

11979	689	*lepida*	0	0	Other	0.44	-15.39
12697	582	*lepida*	0	0	*Ericameria*, Other	0.41, 0.24	-18.10
13092	1154	*lepida*	0.47	0	*Juniperus osteosperma*	0.47	-10.99
13255	1190	*cinerea*	0.92	0	*Juniperus osteosperma*	0.92	-13.31
15456	1154	*cinerea*	0.54	0.02	*Juniperus osteosperma*	0.54	-13.70
16459	1030	*cinerea*	0.92	0	*Juniperus osteosperma*	0.92	-14.73
17261	1030	*cinerea*	0.83	0	*Juniperus osteosperma*	0.83	-13.43
18274	1250	*cinerea*	0.94	0	*Juniperus osteosperma*	0.94	-12.51
18413	1250	*cinerea*	0.63	0	*Juniperus osteosperma*	0.63	-12.39
18544	1250	*lepida*	0.73	0	*Juniperus osteosperma*	0.73	-13.28
19457	1200	*cinerea*	0.92	0	*Juniperus osteosperma*	0.92	-13.50
19991	1030	*cinerea*	0.98	0	*Juniperus osteosperma*	0.98	-13.90
20398	1030	*cinerea*	0.95	0	*Juniperus osteosperma*	0.95	-14.24
21004	1200	*cinerea*	0.76	0	*Juniperus osteosperma*	0.76	-16.71
22018	1200	*cinerea*	0.98	0	*Juniperus osteosperma*	0.98	-17.21
23092	1345	*cinerea*	0.84	0	*Juniperus osteosperma*	0.84	-16.90
23612	1114	*lepida*	0.16	0	Other	0.51	-18.67
23919	1200	*cinerea*	0.89	0	*Juniperus osteosperma*	0.89	-21.17
24701	1200	*lepida*	0.84	0	*Juniperus osteosperma*	0.84	-19.20
26100	1345	*cinerea*	0.78	0	*Juniperus osteosperma*	0.78	-16.80
29116	1249	*cinerea*	0.60	0	*Juniperus osteosperma*, Other	0.60, 0.24	-14.98
31318	1249	*cinerea*	0.94	0	*Juniperus osteosperma*	0.94	-20.33
33439	1249	*cinerea*	0.92	0	*Juniperus osteosperma*	0.92	-11.08
33491	1249	*cinerea*	0.91	0	*Juniperus osteosperma*	0.91	-9.91

Table 3a: Identified Macrofossils found in middens

J.o. = *Juniperus osteosperma, L.t.* = *Larrea tridentata,* Aga = Agavoideae, *A.d.* = *Ambrosia dumosa, A.t.* = *Artemisia tridentata, Atr* = *Atriplex, C.l.* = *Cercocarpus ledifolius, Cry* = *Cryptantha, Enc* = *Encelia, Eph* = *Ephedra, Eric* = *Ericameria, Erio* = *Eriogonum,* Opu = Opuntioideae, *P.s.* = *Peucephyllum schottii, P.f.?* = *Pinus flexilis* c.f., *P.m.* = *Pinus monophylla, Pur* = *Purshia mexicana & P. tridentata, R.c.* = *Ribes cereum, S.a* = *Sphaeralcea ambigua*

Midden ID	*J.o*	*L.t*	Aga	*A.d*	*A.t*	*Atr*	*C.l*	*Cry*	*Enc*	*Eph*	*Eric*	*Erio*	Opu	*P.s*	*P.f?*	*P.m*	*Pur*	*R.c*	*S.a*
TiC 1		159		22		25		2	6	26			5	44					83
TiC 2	379					26							1						2
TiC 4a	228					3				1			6					2	
TiC 4b	211		22			4	11			2			7					9	
TiC 4c	194					43		1	1				1					4	1
TiC 6	304					4												1	
TiC 8a top 2		168				21	1	7	2		53		2	157			4		42
TiC 8 bottom b		95				16		27	8		83		1	197					32
TiC 9c-2			1			2				4	34		1	18					3
TiC 10a	371				35	11				2		8	3		9			8	
TiC 10c	182					3							2		8				
TiC 10c-1	110				2	2							3		2			1	
TiC 10d	109				7	4				1			3					1	2
TiC 11a-1					7	2	1	12			4		8	24					
TiC 11b		1		1		12					2			82					16
TiC 11c-2	129				22	6					49		8			1			1
TiC 11c-3	51	2					6						5			8		1	1
TiC 12 bottom a	490					1		1		3					2		2		
TiC 12 bottom b	794					4	2			2			12		2				
TiC top d	554									3			3					2	
TiC top e	297				2					20			15					1	
TiC 13b			2								14	13	6	150			36		
TiC 14		1						22					3				1		

TiC 15a			2			5					56			25					
TiC 15b		66					1	8	9				3	108					29
TiC 15 take 2a		62				1		2	1	2				19					25
TiC take 2d		32						3	1					31					17
TiC 16		127				4		1		6				19					23
TiC 17 a&b	212												4						
TiC 17 take 2	196					9			1									5	2
TiC take 3a	300					10				5								2	2
TiC take 3b	555					13				1			2						1
TiC 18c	30					8	23			3			10		3			4	
TiC 21a		283						4	4				1	134					13
TiC 22						3		5		6									7
TiC 23a		276		4				3	12				2	3					20
TiC 24		185							2										25
UTiC 1 back	153					1				4									
UTiC 1 front	265				19	18													1
UTiC 2a	195													1			4		4
UTiC 2b	592				32	6		1		4		4	3	6			5		6
UTiC 3a				1		17	4	3	2				25	47			1		12
UTiC 6	3				8	1		5	1			15	12	260					9
UTiC 9		17				6	2			27		8	1	14					23
UTiC 10	74									8						5	8		
UTiC 11a	395		1		74								3				6		20
UTiC 11b	195		8		15						1	5	1				15		2
UTiC 12a						46			8			4		38					19

Table 3b: Unidentified macrofossils

Number of each unidentified macrofossil type (1-32) found in each midden

Unknown #:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
TiC 1							6	28					5	23	2		3				2											
TiC 2												6																				
TiC 4a																									1							
TiC 4b	3	7		5						4											2	1										1
TiC 4c		16		4				11		29		1																				
TiC 6	2																															
TiC 8a top 2			44	12	20		17						10																			
TiC 8 bottom b			127	29	20					7			7																		4	
TiC 9c-2			19	9				24	33		6							4				4										
TiC 10a	13	38								1																						
TiC 10c																									1							
TiC 10c-1		1																						2								
TiC 10d	1			2																												
TiC 11a-1			63	4	11			1		1																						
TiC 11b	1				28									1																		
TiC 11c-2			47							1				2														6				
TiC 11c-3	3	13	1				1			1											1					1						
TiC 12 bottom a	1	19							2		2	4										1		2			1					
TiC 12 bottom b	7	26							3	1	9	3																		3		
TiC top d		9							1	1	8	5										1		2	1							
TiC top e	4	119		1					1	7	15	10									1											1
TiC 13b		3		8	16					5																						
TiC 14					2	3												2														
TiC 15a	32		7		2		6																									
TiC 15b				5	52	1	8						6	5																		
TiC 15 take 2a				5	75		18							2	2						1											
TiC take 2d				2	15		11						3	1																		
TiC 16							3																			3				1		

TiC 17 a&b		1																														
TiC 17 take 2															19											2						1
TiC take 3a												1								5												
TiC take 3b		3																		6		1										
TiC 18c		98								4		9													1							
TiC 21a				21	22								6	1	5						1						2					
TiC 22			8	1	50		13	2								18					1											
TiC 23a				13	18										4																	
TiC 24				2	56										1																	
UTiC 1 back	7	10	2	5																												
UTiC 1 front	20	4		3																				3					6			
UTiC 2a		2		1													6															
UTiC 2b			2	1														2			1	1										
UTiC 3a				9			4								1		2															
UTiC 6			4	9													1															
UTiC 9				4			37																9		4		3					
UTiC 10							2		62																							1
UTiC 11a	22			4		4											3	5	8													
UTiC 11b		14		1		1		1											5													
UTiC 12a				7				36																								

Table 4: Alpha diversity statistics by woodrat species

Pailr-wise two-tailed, equal-variance t-tests for differences in alpha diversity between middens built by *N. cinerea* and middens built by *N. lepida.*

	Plant Species per Midden	Shannon-Weiner Alpha Diversity	Shannon-Weiner Diversity excluding juniper and creosote	Shannon-Weiner Diversity excluding each midden's most common macrofossil
T-test for *N. cinerea/lepida* (equal variance)	0.09	<0.0001	0.61	0.14
T-test for Juniper middens: *N. cinerea* vs. *lepida* (equal variance)	0.93	0.8242	0.83	0.96

Table 5: Alpha diversity statistics by plant community

F-test and pair-wise two-tailed, equal-variance t-tests for differences in alpha diversity between middens containing different plant communities

	Plant Species per Midden	Shannon-Weiner Alpha Diversity	Shannon-Weiner Diversity excluding juniper and creosote	Shannon-Weiner Diversity excluding each midden's most common macrofossil
F Ratio for community types	2.2421, Prob>F= 0.12	21.3052, Prob>F= 0.0001	0.3498, Prob>F= 0.71	1.3076, Prob>F= 0.28
T-test for J/C	0.04	<0.0001	0.45	0.35
T-test for J/NJNC	0.48	<0.0001	0.91	0.13
T-test for C/NJNC	0.27	0.89	0.47	0.60
T-test for Juniper middens: *N. cinerea* vs. *lepida* (equal variance)	0.93	0.82	0.83	0.96

Table 6: Alpha diversity versus temperature variation

Regression analyses of alpha diversity versus temperature variation for each midden

	Plant Species per Midden	Shannon-Weiner Alpha Diversity	Shannon-Weiner Diversity excluding juniper and creosote	Shannon-Weiner Diversity excluding each midden's most common macrofossil
Slope, R-squared for all middens	-0.163, 0.005	-0.059, 0.020	0.019, 0.005	0.031, 0.012
Slope, R-square for juniper middens (x=8)	-0.019, >0.001	-0.107, 0.469	0.023, 0.021	0.023, 0.0.21
Slope, R-square for creosote middens (x= 11)	1.279, 0.024	-0.063, 0.003	0.270, 0.076	0.186, 0.033
Slope, R-square for NJNC middens (x=8)	4.444, 0.514	0.009, 0.0001	0.048, 0.003	0.283, 0.182

Table 7: Mean minimum precipitation of plants found in middens versus plant community and woodrat species

F-test and pair-wise two-tailed, equal-variance t-tests for differences in mean minimum precipitation between middens containing different plant communities and built by different woodrat species

	Mean Minimum Precipitation for all plants in middens	Mean Minimum Precipitation excluding juniper and creosote
F Ratio for community types	104.8078, Prob> F<0.0001	45.6795, Prob>F <0.0001
T-test for J/C	<0.0001	<0.0001
T-test for J/NJNC	<0.0001	<0.0001
T-test for C/NJNC	<0.001	0.03
T-test for *N. cinerea/lepida* (equal variance)	<0.0001	<0.0001
T-test for Creosote middens: *N. cinerea* vs. *lepida* (equal variance)	0.49	0.83

Table 8: Plant possibly species found in middens

Asterisks next to species names indicates that species is most likely present in the record. "J", "C", and "NJNC" columns indicate whether that taxa is found in juniper, creosote, or NJNC middens. In "In Death Valley Today" column, "cf" indicates presence recorded by Calflora.org, and "dvp" indicates presence recorded by dvplants.com.

Family	Genus	species	Common Name	Habitat (Calflora.org)	Growth type	In Death Valley today	J	C	NJ NC	Most prevalent species in any middens?
Amaranthaceae	***Atriplex***						X	X	X	UTiC 12a
		*canescens**	Fourwing saltbush	Alkali Sink, Creosote Bush Scrub, Piñon-Juniper Woodland, Coastal Strand, Valley Grassland, Chaparral, Coastal Sage Scrub	Shrub	X (cf, dvp)				
		*confertifolia**	Shadscale	Shadscale Scrub, Creosote Bush Scrub, Sagebrush Scrub	Shrub	X (cf)				
		hymenelytra	Desert holly	Creosote Bush Scrub	Shrub	X (cf, dvp)				
		polycarpa	Allscale	Creosote Bush Scrub, Shadscale Scrub, Sagebrush Scrub, Alkali Sink	Shrub	X (cf)				
		truncata	Wedgescale	Creosote Bush Scrub, Piñon-Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest, wetland riparian	Annual herb	X (cf)				
Asparagales, subfamily Agavoideae			Agave, yucca, Joshua tree		Perennial herb, Shrub	X (dvp)	X	X		No
Asteraceae	***Ambrosia***							X	X	No
		*dumosa**	White bursage	Creosote Bush Scrub, Joshua Tree Woodland	Shrub	X (cf, dvp)				
		eriocentra	Wooly bursage	Creosote Bush Scrub, Piñon-Juniper Woodland, Joshua Tree Woodland	Shrub					

	ilicfolia	Hollyleaf bursage	Creosote Bush Scrub	Shrub					
Artemisia						X	X		No
	arbuscula	Black sagebrush	Sagebrush Scrub, Northern Juniper Woodland, Piñon-Juniper Woodland	Shrub					
	bigelovii	Bigelow sagebrush	Piñon-Juniper Woodland	Shrub	X (cf)				
	lucoviciana	Mugworm	Sagebrush Scrub, Yellow Pine Forest, Red Fir Forest, Creosote Bush Scrub, Piñon-Juniper Woodland	Perennial herb	X (cf)				
	spinescens	Budsage	xeric conditions, semiarid valley bottoms, benches, and foothills throughout interior of western US (http://www.fs.fed.us/global/iitf/pdf/shrubs/Artemisia%20spinescens.pdf)	Shrub	X (cf)				
	*tridentata**	Common sagebrush	Sagebrush Scrub, Yellow Pine Forest, Northern Juniper Woodland, Piñon-Juniper Woodland, Coastal Sage Scrub, Joshua Tree Woodland	Shrub	X (cf, dvp)				
Encelia						X	X	X	No
	actoni	Acton encelia	In California, between 220 and 2370 m	Shrub	X (cf)				
	*farinosa**	Brittlebush	Creosote Bush Scrub, Coastal Sage Scrub	Shrub	X (cf, dvp)				
	frutescens	Bush encelia	Creosote Bush Scrub	Shrub	X (cf, dvp)				
	virginensis	Virgin River encelia	Creosote Bush Scrub	Shrub	X (cf)				
Ericameria						X	X	X	TiC 9c2, TiC 15a
	cooperi	Cooper's goldenbrush	Creosote Bush Scrub, Joshua Tree Woodland	Shrub	X (cf)				
	cuneata	Desert rock goldenbush	Yellow Pine Forest, Piñon-Juniper Woodland	Shrub	X (cf, dvp)				

		laricifolia	Turpentine brush	Creosote Bush Scrub, Piñon-Juniper Woodland	Shrub	X (cf)				
		lunearifolia	Narrowleaf goldenbush	Chaparral, Creosote Bush Scrub, Piñon-Juniper Woodland, Joshua Tree Woodland	Shrub	X (dvp)				
		nana	Rubberweed	Piñon-Juniper Woodland	Shrub	X (cf)				
		nauseosa	Rubber rabbitbrush	In California, between 50 and 3290 meters	Shrub	X (cf)				
		paniculata	Mojave rabbitbrush	Creosote Bush Scrub	Perennial herb	X (cf)				
		parryi	Parry's rabbitbrush	In California, between 970 and 3700 m	Shrub	X (cf)				
		teretifolia	Green rabbitbrush	Sagebrush Scrub, Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Shrub	X (cf)				
	Peucephyllum	*schottii*	Pygmycedar	Creosote Bush Scrub	Shrub	X (cf, dvp)	X	X	X	TiC 8 bottom b, TiC 11b, TiC 13b, UTiC 6
Boraginaceae	***Cryptantha***						X	X	X	
		ambigua	Wilke's cryptantha	Sagebrush Scrub, Yellow Pine Forest, Northern Juniper Woodland, Red Fir Forest	Annual herb					
		angustifolia	Panamint cryptantha	Creosote Bush Scrub	Annual herb	X (cf)				
		barbigera	Bearded Forget-me-not	Creosote Bush Scrub, Piñon-Juniper Woodland	Annual herb	X (cf)				
		cinerea	James' cryptantha	Sagebrush Scrub, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Perennial herb					
		circumscissa	Western Forget-me-not	Creosote Bush Scrub, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Piñon-Juniper Woodland	Annual herb	X (cf, dvp)				
		clokeyi	Clokey's cryptantha	Creosote Bush Scrub	Annual herb	X (cf)				

confertiflora	Basin yellow cryptantha	Sagebrush Scrub, Piñon-Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest	Perennial herb	X (cf, dvp)
crymophila	Subalpine cryptantha	Subalpine Forest	Perennial herb	
decipiens	Granel Forget-me-not	Creosote Bush Scrub, Foothill Woodland, Valley Grassland, Joshua Tree Woodland	Annual herb	X (cf)
dumetorum	Flexous Forget-me-not	Creosote Bush Scrub	Annual herb	X (cf)
echinella	Prickly cryptantha	Yellow Pine Forest, Piñon-Juniper Woodland, Red Fir Forest	Annual herb	X (cf)
flavoculata	Rough seed cryptantha	Piñon-Juniper Woodland, Sagebrush Scrub	Perennial herb	X (cf)
glomeriflora	Truckee cryptantha	Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Annual herb	
gracilis	Slender Forget-me-not	Joshua Tree Woodland, Piñon-Juniper Woodland, Creosote Bush Scrub	Annual herb	X (cf, dvp)
hoffmannii	Hoffmann's Virgin River cryptantha	Piñon-Juniper Woodland, Bristlecone Pine Forest	Perennial herb	X (cf)
holoptera	Rough stemmed Forget-me-not	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf)
humilis	Roundspike cryptantha	Red Fir Forest, Lodgepole Forest, Subalpine Forest	Perennial herb	X (cf, dvp)
inaequata	Panamint cryptantha	In California, between 80 and 1720 m	Annual herb	X (cf)
intermedia	Clearwater cryptantha	Coastal Sage Scrub, Yellow Pine Forest, Northern Oak Woodland, Foothill Woodland, Chaparral, Piñon-Juniper Woodland	Annual herb	

maritima	Guadalupe Island cryptantha	Creosote Bush Scrub, Joshua Tree Woodland, Coastal Sage Scrub	Annual herb	X (cf)
micrantha	Purple rooted Forget-me-not	Creosote Bush Scrub, Yellow Pine Forest, Piñon-Juniper Woodland, Coastal Sage Scrub	Annual herb	
mohavensis	Mojave cryptantha	Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	
nevadensis	Nevada Forget-me-not	Sagebrush Scrub, Creosote Bush Scrub, Foothill Woodland, Valley Grassland, Northern Juniper Woodland, Piñon-Juniper Woodland, Joshua Tree Woodland	Annual herb	X (cf)
nubigena	Sierra cryptantha	Subalpine Forest, Alpine Fellfields	Perennial herb	
oxygona	Sharp nut cryptantha	Joshua Tree Woodland, Piñon-Juniper Woodland, Chaparral, Valley Grassland	Annual herb	
pterocarya	Winged Nut Forget-me-not	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	X (cf)
racemosa	Woody Forget-me-not	Creosote Bush Scrub, Joshua Tree Woodland	Perennial herb	X (cf, dvp)
recurvata	Curve nut cryptantha	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf)
roosiorum	Bristlecone cryptantha	Subalpine Forest	Perennial herb	
scoparia	Desert cryptantha	Sagebrush Scrub, Piñon-Juniper Woodland, Northern Juniper Woodland	Annual herb	
tumulosa	New York Mountain cryptantha	Creosote Bush Scrub, Piñon-Juniper Woodland	Perennial herb	X (cf, dvp)
utahensis	Scented Forget-me-not	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf, dvp)

		virginensis	Virgin River cryptantha	Sagebrush Scrub, Bristlecone Pine Forest, Piñon-Juniper Woodland	Perennial herb	X (cf, dvp)				
		watsonii	Watson's cryptantha	Piñon-Juniper Woodland, Subalpine Forest	Annual herb	X (cf)				
Cactaceae, Subfamily Opuntioideae			Prickly pear cactus, cholla cactus				X	X	X	UTiC 3a
	Cylindropuntia	*acanthocarpa*	Buck horn cholla	In California, between 160 and 1720 m	Perennial herb (stem succulent)	X (cf)				
		echinocarpa	Wiggins' cholla	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Shrub (stem succulent)	X (cf)				
		ramosissima	Branched pencil cholla	Creosote Bush Scrub, Joshua Tree Woodland	Shrub (stem succulent)	X (cf)				
	Grusonia	*pulchella*	Sagebrush cholla	Creosote Bush Scrub, Sagebrush Scrub	Shrub (stem succulent)					
	Opuntia	*basilaris*	Beavertail pricklypear	Creosote Bush Scrub, Joshua Tree Woodland, Chaparral, Southern Oak Woodland, Coastal Sage Scrub, Piñon-Juniper Woodland, Valley Grassland	Shrub (stem succulent)	X (cf, dvp)				
		engelmannii	Cactus apple	In California, between 560 and 1540 m	Shrub (stem succulent)					
		phaeacantha	Mojave Prickly Pear	Joshua Tree Woodland, Piñon-Juniper Woodland	Shrub (stem succulent)	X (cf)				
		polyacantha	Plains pricklypear	In California, between 860 and 2980 m	Shrub (stem succulent)	X (cf)				

Cupressaceae	***Juniperus***						X		(trace)	TiC 2, TiC 4a, TiC 4b, TiC 4c, TiC 6, TiC 10a, TiC 10c, TiC 10c1, TiC 10d, TiC 11c2, TiC11c3, TiC 12 bottom a, TiC 12 bottom b, TiC 12 top d, TiC 12 top e, TiC 17 a&b, TiC 17 take 2, TiC 17 take 3a, TiC 17 take 3b, UTiC 1 back, UTiC 1 front, UTiC 2a, UTiC 2b, UTiC 10, UTiC 11a, UTiC 11b
		*californica**	California juniper	Piñon-Juniper Woodland, Joshua Tree Woodland, Foothill Woodland	Shrub	X (cf, dvp)				
		grandis	Sierra juniper	In California, between 1130 and 3290 meters	Tree	X (cf)				
		occidentalis	Western juniper	Northern Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest	Tree	X (cf)				
		*osteosperma**	Utah juniper	Piñon-Juniper Woodland	Tree, Shrub	X (cf)				
Ephedraceae	***Ephedra***						X	X	X	No
		aspera	Mormon tea	Creosote Bush Scrub, Joshua Tree Woodland	Shrub					
		californica	California jointfir	Creosote Bush Scrub, Chaparral	Shrub	X (cf)				
		fasciculata	Arizona jointfir	Creosote Bush Scrub	Shrub	X (cf)				
		funerea	Death Valley jointfir	Creosote Bush Scrub	Shrub	X (cf)				
		nevadensis	Nevada jointfir	Creosote Bush Scrub, Joshua Tree Woodland	Shrub	X (cf)				
		trifurca	Longleaf jointfir	Creosote Bush Scrub	Shrub	X (cf)				
		viridis	Mountain ephedra	Creosote Bush Scrub, Piñon-Juniper Woodland	Shrub	X (cf, dvp)				
Grossulariaceae	***Ribes***						X			No

		*cereum**	Wax current	Piñon-Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest, Alpine Fellfields	Shrub	X (cf, dvp)				
		lasianthum	Alpine gooseberry	Red Fir Forest, Lodgepole Forest, Subalpine Forest	Shrub					
		montigenum	Alpine Prickly Current	Red Fir Forest, Lodgepole Forest, Subalpine Forest, Alpine Fellfields	Shrub	X (cf)				
		velutinum	Desert gooseberry	Sagebrush Scrub, Piñon-Juniper Woodland, Yellow Pine Forest	Shrub	X (cf)				
		viscosissimum	Sticky Current	Sagebrush Scrub, Yellow Pine Forest, Northern Juniper Woodland, Red Fir Forest, wetland riparian	Shrub					
Malvaceae	***Sphaeralcea***						X	X	X	No
		*ambigua**	Desert Mallow	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland, Yellow Pine Forest	Perennial herb	X (cf, dvp)				
		rusbyi	Rusby's globemallow	Creosote Bush Scrub, Joshua Tree Woodland	Perennial herb	X (cf)				
Pinaceae	***Pinus***						X			No
		albicaulis	White pine	Subalpine Forest	Tree					
		balfouriana	Foxtail pine	Subalpine Forest	Tree					
		*fexilis**	Limber pine	Lodgepole Forest, Subalpine Forest, Bristlecone Pine Forest	Tree	X (cf, dvp)				
		jeffreyi	Jeffrey pine	Yellow Pine Forest, Red Fir Forest	Tree					
		longaeva	Great Basin bristlecone pine	Subalpine Forest, Bristlecone Pine Forest	Tree	X (cf, dvp)				
		*monophylla**	Singleleaf piñon	Oneneedle piñon pine, nut pine, single leaf piñon, single leaf piñon pine	Tree	X (cf, dvp)				

		monticola	Little sugar pine	Red Fir Forest, Lodgepole Forest, Subalpine Forest	Tree					
		ponderosa	Ponderosa pine	Yellow Pine Forest	Tree					
Polygonaceae	***Eriogonum***						X	X	X	No
		amullaceum	Mono buckwheat	Sagebrush Scrub	Annual herb					
		angulosum	Angled stem buckwheat	Valley Grassland, Foothill Woodland, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	X (cf)				
		apliculatum	San Jacinto buckwheat	Joshua Tree Woodland, Piñon-Juniper Woodland, Yellow Pine Forest	Annual herb					
		baileyi	Bailey Buckwheat	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland, Yellow Pine Forest	Annual herb					
		bifurcatum	Pahrump Valley buckwheat	Shadscale Scrub	Annual herb					
		brachyanthum	Yellow Buckwheat	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	X (cf)				
		brachypodum	Parry's buckwheat	Creosote Bush Scrub, Piñon-Juniper Woodland	Annual herb	X (cf)				
		caespitosum	Clumping buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Yellow Pine Forest	Annual herb					
		contiguum	Reveai's buckwheat	Creosote Bush Scrub	Annual herb	X (cf)				
		davidsonii	Davidson Buckwheat	Chaparral, Piñon-Juniper Woodland, Joshua Tree Woodland, Yellow Pine Forest	Annual herb	X (cf)				
		deflexum	Skeleton Weed	Creosote Bush Scrub, Piñon-Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Annual herb	X (cf, dvp)				
		deserticola	Colorado Desert buckwheat	Creosote Bush Scrub	Shrub					

elatum	Tall buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Yellow Pine Forest	Perennial herb	
eremicola	Telescope Peak buckwheat	Yellow Pine Forest, Piñon-Juniper Woodland	Annual herb	X (cf)
esmeraldense	Esmeralda buckwheat	Piñon-Juniper Woodland	Annual herb	
fasciculatum	California buckwheat	Coastal Sage Scrub, Valley Grassland, Sagebrush Scrub, Piñon-Juniper Woodland, Creosote Bush Scrub	Shrub	X (cf)
gilmanii	Gilman's buckwheat	Creosote Bush Scrub	Perennial herb	X (cf)
glandulosum	Acorn buckwheat	Sagebrush Scrub, Piñon-Juniper Woodland	Annual herb	X (cf)
heermannii	Heerman Buckwheat	Piñon-Juniper Woodland, Foothill Woodland, Joshua Tree Woodland	Shrub	X (cf, dvp)
heracleoides	Parsnipflower buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Yellow Pine Forest	Perennial herb	
hoffmannii	Hoffmann's buckwheat	Piñon-Juniper Woodland, Creosote Bush Scrub	Annual herb	X (cf)
hookeri	Hooker's buckwheat	Piñon-Juniper Woodland	Annual herb	
inflatum	Desert trumpet	Creosote Bush Scrub, Joshua Tree Woodland, Sagebrush Scrub, Piñon-Juniper Woodland	Perennial herb	X (cf, dvp)
intrafractum	Jointed buckwheat	Creosote Bush Scrub	Perennial herb	X (cf, dvp)
kennedyi	Kennedy's buckwheat	Yellow Pine Forest, Alpine Fellfields, Sagebrush Scrub, Piñon-Juniper Woodland	Perennial herb	
maculatum	Angle stemed Buckwheat	Creosote Bush Scrub, Joshua Tree Woodland, Sagebrush Scrub, Piñon-Juniper Woodland	Annual herb	X (cf)

mohavense	Western Mojave buckwheat	Creosote Bush Scrub, Piñon-Juniper Woodland	Annual herb	X (dvp)
nidularium	Whisk Broom	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	X (cf, dvp)
nudum	Naked buckwheat	Coastal Strand, Southern Oak Woodland, Yellow Pine Forest, Foothill Woodland, Chaparral, Valley Grassland, Joshua Tree Woodland, Piñon-Juniper Woodland	Shrub	X (cf, dvp)
nummulare	Money buckwheat	Sagebrush Scrub, Piñon-Juniper Woodland	Shrub	
nutans	Dugway buckwheat	Sagebrush Scrub, Northern Juniper Woodland	Annual herb	X (cf)
ochrocephalum	White woolly buckwheat	Piñon-Juniper Woodland	Perennial herb	
ordii	Fort Mojave buckwheat	Foothill Woodland, Creosote Bush Scrub, Piñon-Juniper Woodland	Annual herb	
ovalifolium	Cushion buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Piñon-Juniper Woodland, Red Fir Forest, Lodgepole Forest, Subalpine Forest, Alpine Fellfields	Perennial herb	X (dvp)
palmerianum	Palmer's buckwheat	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	
panamintense	Panamint Mountain buckwheat	Yellow Pine Forest, Piñon-Juniper Woodland	Perennial herb or shrub	X (cf, dvp)
parishii	Parish's buckwheat	Piñon-Juniper Woodland, Yellow Pine Forest, Lodgepole Forest	Annual herb	
pusillum	Yellow Turban	Creosote Bush Scrub, Joshua Tree Woodland, Piñon-Juniper Woodland	Annual herb	X (cf)
reniforme	Kidney leaf buckwheat	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf)

		rixfordii	Rixford's buckwheat	Creosote Bush Scrub, Piñon-Juniper Woodland	Annual herb	X (cf)				
		shockleyi	Shockley's buckwheat	Piñon-Juniper Woodland	Perennial herb	X (cf)				
		strictum	Blue Mountain buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Yellow Pine Forest	Perennial herb					
		thomasii	Thomas' buckwheat	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf)				
		trichopes	Little Trumpet	Creosote Bush Scrub, Joshua Tree Woodland	Annual herb	X (cf)				
		umbellatum	Sulphur buckwheat	Sagebrush Scrub, Northern Juniper Woodland, Yellow Pine Forest, Subalpine Forest, Alpine Fellfields, Piñon-Juniper Woodland, Lodgepole Forest, Red Fir Forest, Foothill Woodland	Perennial herb	X (cf, dvp)				
		wrightii	Bastardsage	Piñon-Juniper Woodland, Foothill Woodland, Yellow Pine Forest, Chaparral, Joshua Tree Woodland, Creosote Bush Scrub, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Perennial herb or shrub	X (cf)				
Rosaceae	***Cercocarpus***	*ledifolius*	Curl leaf mountain mahogany	Sagebrush Scrub, Piñon-Juniper Woodland, Yellow Pine Forest, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Tree, Shrub	X (dvp)	X	X	X	No
	Purshia						X	X	X	No
		*mexicana**	Mexican cliffrose	Joshua Tree Woodland, Piñon-Juniper Woodland	Shrub	X (cf, dvp)				
		*tridentata**	Antelope Bush	Chaparral, Joshua Tree Woodland, Piñon-Juniper Woodland. Sagebrush Scrub, Yellow Pine Forest, Northern Juniper Woodland, Red Fir Forest, Lodgepole Forest, Subalpine Forest	Shrub	X (cf, dvp)				
Zygophyllaceae	***Larrea***	*tridentata*	Creosote bush	Creosote Bush Scrub	Shrub	X (cf, dvp)		X	(trace)	TiC 1, TiC 8a top 2, TiC 15b, TiC take 2d, TiC 16, TiC 21a, TiC 23a, TiC 24

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