Sagebrush Natural Range of Variation Sierra Nevada and South Cascades

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INTRODUCTION

Physical setting and geographic distribution

Sagebrush can be found from 490-3500 m (1,600-11,500 ft) on a wide variety of soils, and covers about 50-100 million ha (124-247 million acres) in the western US (Blaisdell et al. 1982, Brown and Smith 2000, 2012). Sagebrush-dominant systems extend over about 1.6 million ha (4 million acres) in the assessment area and occur in all four assessment subregions, but are most extensive in the east and north (Table 1; see map in Introduction).

The genus *Artemisia* contains 22 species in California, including herbaceous taxa, and dwarf and tall shrub species (Baldwin et al. 2012). This analysis focuses on settings where sagebrush is the site potential (i.e. where it is dominant or codominant with other shrubs in the climax state), and where sagebrush is the site potential under the natural fire regime. The latter includes areas that may be currently dominated by wooded shrublands and savannas, but would presumably be absent of trees under the natural fire regime (Romme et al. 2009). Wooded shrublands and savannas differ from persistent woodlands, which are covered in the Pinyon-Juniper chapter.

The primary sagebrush taxa considered here include big sagebrush, low sagebrush, black sagebrush, Rothrock sagebrush, and silver sagebrush (Table 2; *Artemisia tridentata*, *A. arbuscula*, *A. nova*, *A. rothrockii*, *A. cana*, respectively). Big sagebrush is the most extensive taxon in the assessment area, and has been studied more intensively than the others. The subspecies of big sagebrush differ ecologically, and so are considered separately where information exists; distinction between them is imperative when implementing land management practices. Three other sagebrush shrub species occur within the assessment area (*A. bigelovii*, *A. spinescens, A. spiciformis*), but generally occur in small stands or in low densities, and, to our knowledge, have not been comprehensively mapped. The term sagebrush is used throughout this analysis to refer to woody species of the genus in general.

Sagebrush is associated with the climate regime of the Great Basin, which is characterized by cold nights, warm to cool days, and most precipitation occurring in the winter and early spring months (Bureau of Land Management 2002, Davis 1982). The distributions of different taxa are strongly correlated to temperature and precipitation regimes. Throughout the assessment area, big sagebrush and black sagebrush are restricted to mesic and frigid soils, with low sagebrush occurring on some cryic soils. Beatley (1975) demonstrated that sagebrush communities in southern Nevada can be differentiated from desert shrub communities dominated by saltbush (*Atriplex* spp.) or creosote (*Larrea tridentata*), by a combined regime of daytime and nighttime temperatures, plus precipitation characteristic of the Great Basin. If any single variable differs, i.e. if nighttime temperatures are warmer, or more precipitation occurs in the summer, desert shrubs predominate over sagebrush. In some cases, the current distribution of sagebrush is related to past climate conditions, rather than more recent climatic patterns, a topic that will be examined below.

Ecological setting

At the coarsest scale, sagebrush in the assessment area is differentiated from sagebrush systems of the eastern Great Basin and Colorado Plateau primarily by geographic history and proximity to other vegetation types, but also by climate and community composition. Sagebrush in California is bounded to the west by high elevations of the Sierra Nevada, and, as a result, has been associated with a different flora and climate regime than sagebrush ecosystems found in most of Nevada, Utah, and Colorado. Syntheses of the ecological setting, including climate, geomorphology, geology, soils, and vegetation patterning, as they vary across the assessment area, can be found in Miles and Goudey (1997) and are summarized in Tables 3-4.

Two main gradients drive the ecological patterns seen in Table 4. First, there is a drop in precipitation from west to east, driven by the Sierra-Cascade crest that receives the abundance of precipitation from prevailing storms coming from the west. Second, there is a north-south gradient that is correlated in part to precipitation seasonality and amount, but also to growing season length, and to vegetative biogeography resulting from Tertiary and Quaternary migrations.

Some structural and compositional similarities exist between sagebrush systems of different regions. Sagebrush often occurs with other shrubs, including saltbush, Mormon tea (*Ephedra* spp.), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus* spp.), or forms an understory to pinyon pine (*Pinus monophylla*), Jeffrey pine (*P. jeffreyi*), Ponderosa pine (*P. ponderosa*), and other conifers (Smith 1994). Although associated conifer species may differ, their role with regard to impacts on sagebrush in ecosystem structure and disturbance regime can be similar. Grasses and forbs are usually present in varying abundance (Blaisdell et al. 1982). Because tree cover has varied within sagebrush ecosystems over the NRV period, dynamics at the sagebrush-forest interface will be discussed.

Characteristic animal species of sagebrush ecosystems in the assessment area include sage sparrow (*Artemisoispiza belli*), sage thrasher (*Oreoscoptes montanus*), and mule deer (*Odocoileus hemionus*). The greater sage grouse (*Centrocercus urophasianus*) is listed by the US Fish and Wildlife Service as a candidate for protection under the Endangered Species Act.

Cultural/socioeconomic setting

The terrain and moderate climates of the sagebrush zone are conducive to diverse human uses. Native American uses have included hunting, seed collection, root and bulb gathering, and, in some cases, irrigation to encourage productivity of desirable species. Although these areas are amongst the least populated in California in modern times, several rural to moderately sized towns occur in sagebrush, particularly in the east and north subregions. These areas are often associated with agriculture, including alfalfa farms and grazing allotments.

Various methods of sagebrush control have been used, especially during the mid to late 1900s, such as prescribed fire, chaining, and herbicide, to reduce sagebrush cover and encourage herbaceous productivity (Bristow 2010). These methods have been relatively restricted within the assessment area, with about 1500 acres of known impacts on the Inyo National Forest (Inyo NF; Slaton et al. 2012). Mining and oil and gas production have also impacted many areas. Several major highways occur within the sagebrush zone, as do thousands of minor routes that provide recreational services, and access to rivers, lakes, allotments, mines, and inholdings. Motorized trails and dirt roads provide opportunities for 4WD and off-highway vehicle recreation. Large game and game bird hunting are common practices in sagebrush ecosystems. In recognition of the ecosystem services provided by the sagebrush zone, many ecological restoration projects have been initiated over the last decade, with the goal of maintaining seral stage diversity and ecosystem resilience (Olson 2012).

METHODS

Broad-scale geographic trends could be tracked through pollen records, generally obtained from lake deposit cores, which allowed estimates of sagebrush distribution and provided some community composition information. Charcoal deposits also provided information regarding past fire frequencies. In sagebrush, some of the most valuable information came from packrat (*Neotoma* spp.) middens, which are abundant in dry, rocky terrain where sagebrush often occurs (e.g. Woolfenden 1996). The plant macrofossils in middens provide good spatial resolution for past plant assemblages, but provide information mainly regarding community composition, rather than structure or function. Finally, tree ring chronologies allowed climate reconstructions, and fire scars on trees in and near sagebrush systems provided information about fire frequencies. Some data were examined from sagebrush without current grazing, and far enough away from roads and residential areas to have been more likely to have escaped alterations to the fire regime over the last century.

We acknowledge a large data gap in sagebrush ecosystem data compared to forested lands; socio-economic factors have emphasized forest data collection over the last century, with the need for shrubland data becoming apparent only recently. Furthermore, most sagebrush work to date has been based upon studies conducted outside the assessment area, including southern Oregon and Idaho, northern Nevada, and the Colorado Plateau. Therefore, we used local historical accounts and photos to help judge the relevance of published studies to the assessment area.

The primary source for vegetation mapping of the current distribution of sagebrush shrublands was the R5 Existing Vegetation map, which uses the CALVEG system for classifying vegetation types (Table 2). Sagebrush shrublands with more than 10% cover of trees were generally mapped as forested vegetation types by that methodology, even though the pre-settlement fire regime may have maintained them as sagebrush shrublands (see Pinyon-Juniper chapter). In the development of this assessment, it has become clear that there is a strong need for improved mapping of sagebrush taxa, plus a classification which incorporates the herbaceous component, because both are factors that drive ecosystem function, and particularly fire regime.

NRV DESCRIPTIONS

Function

NRV

Grazing

The primary event marking the transition from the NRV period to the current time period in sagebrush ecosystems was the influx of livestock, including cattle and sheep, during the mid-1800s, and their continued presence for the last century. During the NRV period, deer, elk, and pronghorn antelope grazed sagebrush systems, but bison, which may have impacted rangelands in a similar way to modern livestock, were only known from Surprise Valley and Lower Klamath Lake in the northeastern portion of the assessment area, from 1330-5640 ybp (Grayson 2006). Compared to modern practices, grazing by native species during the NRV period was characterized by differences in foraging pattern, diet, preference for slope and riparian areas, time spent in a single area, and soil trampling (e.g. Currie et al. 1977, Osmond et al. 2007).

Succession

Some patterns of succession during the NRV period could be inferred based on climatic gradients and prevalent disturbances in the assessment area (Table 5). Succession generally occurs more rapidly in warmer and wetter environments, and so we can infer that succession during the NRV period was most rapid at moderate elevations, where temperature and precipitation would have been most conducive to sagebrush germination and seedling survival. During the NRV period, flooding/landslide and fire were the primary disturbances in sagebrush, resulting in greater successional turn-over in steeper terrain, or on alluvial fans, and in areas with greater productivity, and cover and continuity of fuels, as compared to other areas.

During the NRV period, when native herbivores such as deer and elk spent less time in any single location as compared to modern livestock, we can conclude successional pathways would have been characterized by greater herbaceous cover in early seral stages, and, thus delayed establishment of shrubs, due to greater competition (Meyer 1994). A secondary impact of grazing which was not present during the NRV period is disturbance of soil crusts, which are characteristic of late succession, and can facilitate water infiltration into soils, reduce erosion, and create resistance to annual plant invasions (Belnap et al. 2001).

Eisenhart (2004) observed that succession at the sagebrush-pinyon interface in Colorado has shifted between shrub and tree site potential during the Holocene, as the climate has shifted and vegetation responses have lagged, resulting in non-linear successional pathways. Although the study was conducted outside the assessment area, the observation that multiple trajectories of succession exist at the sagebrush-conifer interface is critical to evaluating the cause of current trends, and appropriate management techniques for maintaining resilient ecosystems.

Migration

Sagebrush had its greatest geographic extent in the assessment area at the beginning of the Holocene, when it dominated most lands over 1495 m (4900 ft.), and occurred on both the east and west slopes of the Sierra Nevada (Table 6). Black, big, and low sagebrush were all present in the assessment area in the early Holocene. Betancourt (1986) reported that big sagebrush is the only known vegetation zone that has overlapped from the Pleistocene period to present, and that migrational equilibrium at the interface of sagebrush and pinyon-juniper has not yet been reached. Sagebrush pollen peaked during the cooler and wetter early Holocene, when treelines were much depressed, and the current upper sagebrush belt was more extensive. A subsequent peak in pollen occurred during warm period of the Xerothermic, which is interpreted as a conversion to drier, more open forests, with greater sagebrush cover, and perhaps a more extensive lower sagebrush belt (Anderson 1990; Table 6). Because later periods coincided with more extensive conifer cover, sagebrush ecosystems themselves were not more extensive; instead, sagebrush cover increased in the understory of conifer-dominated stands.

Pinyon pine and juniper species began migrations from further south and from lower elevations around the beginning of the Holocene and were present in the assessment area at elevations below 1220 m (4000 ft.) by that time (Betancourt 1986). Around 8000 ybp, Utah juniper (*Juniperus osteosperma*) began to dominate some higher elevations in the southeast portion of the assessment area that were previously dominated by sagebrush. Pinyon and juniper continued to encroach northward and upward in elevation through the mid Holocene. As they did so, desert species populated behind them, and, in some areas, where sagebrush receded at a slower rate relative to pinyon-juniper, a new belt of sagebrush and mixed desert shrubs formed below the pinyon-juniper belt (Table 6). In other areas, such as the Alabama Hills in Inyo County, CA, the lower sagebrush belt was entirely eliminated. These 'rear edge' populations have different structure and function from the leading, or more recently established populations, though they have been understudied (Hampe and Petit 2005).

The mid Holocene was characterized by numerous expansions and contractions of sagebrush and associated conifers as the climate fluctuated. By the height of the Xerothermic period, regional scale distribution of desert species, sagebrush, and the pinyon-juniper belt were similar to those seen today (Table 6). Warm, dry periods were characterized by elevated treelines and encroachment of desert species into sagebrush, and cool, moist periods by treeline depression, retreat of desert species, and increased herbaceous cover in sagebrush.

Patterns of juniper encroachment into sagebrush were described further by Miller and Wigand (1994), who provided a potential explanation for apparent inconsistencies between juniper expansion and climate trends in the Mid vs. Late Holocene. During the Xerothermic period, juniper was at its peak of expansion northward and to higher elevations. The wetter and cooler periods to follow were marked by some downward expansion, and infilling of open habitats. Johnson and Miller (2008) concluded recent increased juniper density in southern Oregon is most likely due to migrational tracking of climate.

A combination of factors may explain current migration patterns, in which expansion is again occurring during a dry time. Expansion into xeric sites may be explained by grazing, which reduces herbaceous cover and competition for tree seedlings, which have roots at the same soil depth as herbs. Alternatively, concurrent expansion into mesic sites may be explained by climatic warming which increases tree establishment in meadows, drainages, and on north aspects. On a landscape to regional scale, these complex patterns indicate that the current process of migration may not be strongly departed from those of the NRV period (Betancourt 1986).

Nutrient cycling

Conifer encroachment into sagebrush results in changes to the nutrient cycle. Conifer litter decomposes at a slower rate than sagebrush litter, resulting in a greater proportion of immobilized nutrients in the litter and duff layer where conifers are present. Organic matter, phosphorus, sulfur, and potassium were all found to be greater below a *Pinus edulis* canopy, as compared to sagebrush, although no acidifying effects of conifers were detected (Barth 1980). In contrast, nitrogen fixation in soils of shrub interspaces between juniper was found to be 10-fold greater than that beneath the conifer canopy, resulting in an increase in a more readily available form of nitrogen for plant uptake (Warren et al. 2008). As a result, we can infer that variation in nutrient cycling during the NRV had some correlation to community and landscape scale proportions of shrubs to trees.

Disturbances

Fire. Spatial and temporal variability in the role of fire in sagebrush ecosystems over the Holocene have resulted in wide debate over this topic. Evidence from the Sierra Nevada and from northern California indicates that charcoal accumulation in the Early Holocene was low, suggesting a low intensity fire regime (Brunelle and Anderson 2003, Daniels et al. 2005). Fires were most frequent during the Xerothermic period and during the Medieval warm period, when higher temperatures and drought occurred (Table 6). For example, modern fire behavior modeling shows that fire intensity and rate of spread can be 2-3 times higher when sagebrush foliage is cured (Brown and Smith 2000); as a result, we inferred that during times of drought, fire intensity and rate of spread would have increased in sagebrush. However, most information from the Early to Mid Holocene is based upon lake charcoal records, and pertains to coarse trends in fire regime across the assessment area, and so provides limited detail for sagebrush systems.

There is no direct evidence regarding the extent or pattern of the fire mosaic in sagebrush prior to Euro-American settlement. However, studies have interpreted fire scars on trees in or near sagebrush; major results are summarized in Table 7, with a comprehensive review of further work given by Van de Water and Safford (2011). Among the controversial issues debated in the applications of these studies is the frequency with which forest fires spread into shrublands. Baker (2006) pointed out that only a single study demonstrated that a sagebrush fire initiated in forest, and, even there, the sagebrush was a new component in a former grassland (Miller and Rose 1999). Miller et al. (2001) argued that similar age structure of conifers in forest and adjacent shrubland support the assumption that fires do not stop in the ecotone. However, other explanations, such as precipitation patterns could also explain a correlation in age structure. Other issues when interpreting tree fire scars in shrublands include limited sample size, absence of cross-dating, and targeted sampling, where, for logistical reasons, data are collected where fire evidence is most abundant.

Baker (2006, 2011) introduced the concept of a correction factor to account for the ignition ratio (lightning strikes per fire) in forests vs. shrublands, and summarized fire frequency data from other authors, in addition to his corrected estimates (Table 7). According to these findings, the fire return interval (FRI) during the pre-settlement period was 150-300 years in mountain big sagebrush, 200-350 years in Wyoming sagebrush, >200 years in low and black sagebrush, and 40-230 years in mountain grasslands containing patches of mountain big sagebrush.

Miller and Heyerdahl (2008) acknowledged the wide range of fire intervals presented for big sagebrush. They proposed that fire was spatially complex, affected by topography and soils, and, thus the wide range may in fact be an accurate representation of sagebrush fires. For example, proximity to pine has a large impact on fire frequency in sagebrush, as a result of fine fuel accumulation.

Observations of the modern ecology and species traits of sagebrush enable some inferences about the fire regime for sagebrush during the NRV period. For example, because low and black sagebrush are smaller in stature, less productive, and more widely spaced than big sagebrush, the former have a lower FRI (Young and Evans 1981, Miller and Rose 1999, Baker 2006). That difference was likely also true during the NRV period.

Similarly, recent evidence indicates that fires in sagebrush are stand-replacing or mixed severity (Welch and McArthur 1986, Connelly et al. 2000, Baker 2006), and do not act to thin sagebrush crowns, as has been previously implied (e.g.Winward 1991, West and Young 2000). The latter interpretation has been used to argue that fire can act to maintain low cover in a manner similar to that in forested systems, such as yellow pine. It is more accurate to describe fire in sagebrush as mixed severity, on either fine or coarse spatial scales, with little survivorship among individual plants touched by fire. Sagebrush stems are easily killed by fire and sagebrush generally does not resprout, with the exception of *A. cana* and *A. spiciformis*. Although modern changes to annual grass cover have resulted in changes to the fire frequency (see Herbaceous Invasions section), there is no reason to believe that the mixed severity nature of sagebrush fires was different during the NRV period.

Finally, an additional line of evidence for fire frequency comes from the rate that sagebrush returns following fire; fire frequency cannot be shorter than the time it takes for sagebrush systems to achieve a fuel structure that will carry fire (Wright and Bailey 1982, Kitchen and McArthur 2007). This reasoning holds if changes in community composition do not alter the fire frequency. Studies in northeastern CA and southern ID show that mountain big sagebrush recovered to pre-burn cover and composition conditions in 35-100 years (Baker 2006). However, it should be noted that the chronosequence used to draw the conclusions is limited by the absence of trajectory data at any single site over that time period.

Photo retakes on the Inyo NF in mountain big sagebrush provide further information. Photos taken nine years following the Birch Fire illustrate that sagebrush cover was approximately one-tenth that seen in adjacent unburned plots. Photos from a 1972 fire in the Crowley Basin also show that 33 years post-fire, community composition was still weighted toward rabbitbrush, with low sagebrush cover, but that an additional five years resulted in a change from 1 to 10% cover of sagebrush (Slaton 2011). These studies suggest that sagebrush ecosystems still differ from pre-burn conditions 10 years following a burn, and 35 years or more may be required to return to pre-burn conditions. The time required to reach a certain percent cover depends upon pre- and post-disturbance weather, size and severity of disturbance, degree of competition from herbaceous plants, all of which are influenced by disturbance severity and grazing management (Kitchen and McArthur 2007).

We found no direct evidence that allows reconstruction of NRV for fire season. However, the recent introduction of cheatgrass (*Bromus tectorum*), combined with dry winters and/or early springs, and thus, accumulation of fine fuels early in the season, has resulted in a shifting of the fire season from late summer to early spring in some parts of the assessment area. Native American influences on fire season are discussed below.

Native American use and management. The extent of Native American influences on the landscape during the Holocene has been debated, and estimates range from localized (Skinner and Chang 1996) to widespread (Anderson and Moratto 1996). Most information about burning by Native Americans comes from the west slope of the Sierra Nevada, where the practice was used to reduce shrub growth, encourage herbaceous productivity, including tobacco, and control pests (Wickstrom 1987). Relatively concentrated use in sagebrush probably occurred at meadow borders, where burning or tilling were used to encourage geophytic growth (Anderson 1997). Where fire was used, it may have resulted in a change to the seasonality of fire, in comparison to lightning ignitions; historic accounts indicate that burning was conducted in the spring or fall, rather than summer (Wickstrom 1987, Frost 1998). Anderson (1997) quoted a report from the Paiute in Surprise Valley in NE California in the 1930s that root gathering had declined, apparently because of new land use practices by Euro-American settlers, including livestock grazing. Seeds of bunchgrasses within the sagebrush zone were also collected by Native Americans (Simpson 1876, as cited by Vale 1975).

Wind. Wind is a disturbance that has impacted sagebrush systems during the Holocene in two indirect ways. First, at the periphery of post-glacial Great Basin lakebeds, windblown sediments have formed dunes in some areas of sagebrush, resulting in lower sagebrush productivity and altered community composition. This type of activity was probably most prevalent during the Xerothermic and Medieval warm periods (Davis 1982). Recent observations of this phenomenon in the Mono Lake and Adobe Lake Valleys of the Inyo NF suggest that this disturbance has played a more recent role within the assessment area. The second indirect impact of wind is that dust settling on snow causes a reduction in albedo, and subsequent faster snowmelt. During warm, dry periods associated with greater airborne dust, it can be expected that loss of snow was exacerbated by this factor (Davis 1982).

Extreme climate events. Multiple droughts have been documented during the Holocene, and it has been estimated that multi-year droughts have occurred once or twice a century (Graumlich 1987). These events may have had impacts to distribution and composition of sagebrush systems equal or greater than those caused by gradual climatic events. Nelson and Tiernan (1983) reported extensive sagebrush mortality caused by winter injury during drought years in the 1970s, when plants were not covered by snow. This phenomenon occurred in eastern California in 1976-77, and again on the Inyo NF in 2011-12, and we expect that a similar periodicity may have occurred during warmer periods of the Holocene (Table 6).

Extreme climate events may be large enough to result in changes to community composition. For example, low juniper (*Juniperus* spp.) pollen values in Oregon over the last 500 years have coincided with drought (Mehringer and Wigand 1990), indicating that these events may have been an important factor in reducing tree invasion into sagebrush.

Variation in climate has also been associated with changing frequencies of floods and debris flows (Table 6). Lake water levels rose and fell during moist and dry periods of the Holocene. Over the last 3800 years, the water line of Mono Lake has fluctuated by 40 m, with thousands of acres of current sagebrush-bitterbrush inundated during the Neoglacial period (Stine 1990). An analysis of the Oak Creek alluvial fan in the Owens Valley revealed recurrence intervals of several hundred years for debris flows over the late Holocene, with some correlation to fire events and increased frequency of summer cloudbursts during the Medieval warm period. Thus, the 2008 flood in Oak Creek was not outside the NRV, despite the fact it caused extensive damage to infrastructure and residences within the sagebrush zone (Wagner et al. 2012).

Stratigraphic data for the Great Basin illustrate the complex relationships during the rapidly shifting climates from the Mid to Late Holocene, when cycles of warm/dry and then wet/cool conditions followed the Neoglacial period (Miller et al. 2004; Table 6). During this time, the dry periods were associated with greater runoff and sedimentation that resulted from vegetation loss on hillslopes, which reduced stability. These periods of high sedimentation were accompanied by charcoal deposits that indicate higher fire frequencies, which would have further accelerated erosional processes. Another significant driver of sagebrush ecosystem structure and composition during warm periods is the drop in lake and groundwater levels, and associated increase in alkalinity or salinity of some soils, and deposition of mineral- or nutrient-rich layers at lakebed perimeters (Table 6). These altered soils were not conducive to sagebrush regeneration, and instead encouraged reproduction of saltbush, greasewood (*Sarcobatus vermiculatus*), winterfat (*Krascheninnikovia lanata*) and other salt-tolerant species during the Xerothermic and Medieval Warm periods.

The decrease in sedimentation that followed warm intervals was due in part to the reduction in erodible materials on hillslopes, and is thus difficult to correlate with direct climatic influences. The increased moisture during these time periods may have acted instead to incise certain channels, or lead to greater vegetation productivity and soil development. In any case, there was high variability between Great Basin watersheds, and further study is needed to apply information from these time periods to modern conditions.

Volcanism & earthquake. Sagebrush systems in the assessment area occur within volcanically and tectonically active zones. Bedrock geology is largely comprised of Tertiary basalt and andesite in portions of the eastern and northern subregions of the assessment area, including the Inyo and Modoc National Forests. Volcanic activity during the Holocene in Lava Beds National Monument of northern California, and the Mono Basin of the Inyo NF created cones and flows, and deposited ash and dust that impacted ecosystem function (Davis 1982, Davis 1982, Donnelly-Nolan 1990). The significance of tectonic activity to sagebrush systems has not been studied, although the predominance of disturbance-tolerant species, such as manzanita (*Arctostaphylos* spp.) and ceanothus (*Ceanothus* spp.), along an approximate 10 m band in sagebrush that occurs on fault-lines of the Eastern Slopes, where earth was displaced by a meter in the 1980-90s, indicates that earth-shaking has affected the composition and patterning of these systems.

Insects & Disease. There is very little information regarding the NRV of insects and disease within the sagebrush system. We assume that modern observations of insect galls, primarily formed by members of Lepidoptera and Coleoptera, and occurring on all woody sagebrush species, have been present in variable numbers throughout the Holocene (Fronk et al. 1964), as have a variety of leaf-feeding insects, and bark-feeding voles (Bureau of Land Management 2002).

Sagebrush is also prone to infestation by snowmolds during high snow years, when the foliage remains buried by snow for extended periods (Nelson and Sturges 1986).

Current

Grazing

Livestock grazing, which began in widespread manner in the 1850s is the primary disturbance which distinguishes the NRV and post-NRV periods. The influx of Euro-American settlers to California in the 1800s, with hundreds of thousands of sheep and cattle, created a significant impact on the landscape, through alterations to herbaceous cover, soil erosion, and streambanks (Rowley 1985). Approximately 1.6 million acres, or 41% of sagebrush in the assessment area in California, occurs within national forest and BLM grazing allotments, some of which are no longer active.

Grazing removes herbaceous plant cover, thereby influencing fine fuels and the fire regime. The introduction of grazing in the northern subregion, where perennial grass cover was especially high during the NRV period, has probably resulted in stronger changes to community structure and function as compared to other subregions.

There is support in the range management literature that properly managed grazing with respect to utilization level, season of use, and type of animal does not degrade ecosystem functioning (Holochek et al. 2006, Davies et al. 2011). However, recent increased fire frequency in sagebrush, coupled with the increased extent and cover of cheatgrass has led to the need for special consideration of grazing practices following fire. Grazing too soon after burning can promote cheatgrass (Eiswerth and Shonkwiler 2005, Condon et al. 2011), while protection of burns from grazing can promote recovery of perennial grasses (Hosten and West 1994). A number of other studies and reviews support the need for rest from grazing before and after reintroducing fire, if native plant restoration is the goal (Beck and Mitchell 2000, Baker 2011, Knick et al. 2011, Pyke 2011).

Succession

McIver (2010) used state and transition modeling to illustrate that grazing, fire, tree encroachment, and presence of invasive herbs are primary factors that may permanently alter the successional pathway in sagebrush. This occurs by successive changes in ratios of woody to herbaceous cover and perennial to annual cover, and in erosion and nutrient loss. Davies et al. (2012) drew similar conclusions for sagebrush in south-central Washington, and showed that repeated fire caused subsequent changes in successional pathways that were longer-lasting, and differed in trajectory (i.e. composition and rate of return of different growth forms), as compared to single disturbances.

Migration and Woody Invasions

Selection of appropriate management methods in sagebrush, with regard to fire, grazing, and control of invasions, depends strongly upon interpretation of the migrational status of major species, especially trees. Migration of pinyon-juniper is continuing today within the current envelope that supports sagebrush. Evidence from the past suggests that Utah juniper migration is not linear, but is characterized by long distance colonization, then expansion, and then backfilling into open habitats (Lyford et al. 2003). Whereas initial dispersal may be controlled by animals or humans responding to changes in climate, later expansion can be a direct vegetation response to climate, or the result of establishment of a seed bank. Evidence for the latter also comes from observations that once juniper is established, there is no temporal reversal in migration, i.e. it is persistent (Lyford et al. 2003). Current observations of pinyon-juniper expansion down slopes, and infilling into clearings are probably due at least in part to these mechanisms.

The increase in tree cover within sagebrush systems over the last century has been well documented in numerous studies (e.g. Gruell 2001, Johnson and Miller 2008), and is often considered to be an invasion phenomenon. The change in tree distribution and cover has been linked to grazing, climate, fire regime, and long-term demographic expansion, or migration (Table 6). Estimates for the extent of recent conifer encroachment into sagebrush are not available. However, if we assume that all 1.4 million acres of pinyon-juniper in the assessment area has displaced sagebrush over the Holocene, which currently covers 3.9 million acres, there has been potentially a 26% decline in sagebrush. This is probably an overestimate; rough estimates from visual inspection of vegetation maps and imagery indicate a possible 5-10% reduction in sagebrush in the assessment area over the last century, due to conifer encroachment.

Pinyon-juniper invasions over the last century have usually been noted to be greatest on valley floors and on deeper soils, as opposed to ridges and upper slopes (Bauer and Weisberg 2009). These topographic positions reflect different grazing and fire histories, as well as biophysical differences. The combined effects of grazing, road construction, and fire suppression may have reduced fire frequency and allowed for conifer invasion (Burkhardt and Tisdale 1976). Bauer and Weisberg (2009) observed that fires were more frequent on valley floors than on adjacent slopes during the NRV period, and thus interpret fire as a plausible mechanism for excluding conifers from those areas in the past.

A climatic explanation for conifer invasion comes from correlations between cover and precipitation over the last century. First, it has been noted in southwest Idaho that initial invasions occurred in the mid-1800s, prior to extensive livestock grazing, which did not occur until the late 1800s (Johnson and Miller 2008). The expansion did coincide with the end of the Little Ice Age, and continued migration of juniper species northward in the western US has been linked to warming during the Holocene (Lyford et al. 2003). Studies from Oregon, Nevada, and California have correlated conifer expansion to increased precipitation and mild winters in the 1870s-1880s, which was followed by a reduction in invasion after about 1915, when drought characterized climate for an extended period (Young and Evans 1981). Based on these studies, it can be concluded that climate plays a major role in woodland expansion into sagebrush. However, each of these studies has acknowledged that both grazing and fire also play important roles, though perhaps more variable across the landscape.

Throughout the assessment area, sagebrush can occur in association with meadows, which may include linear riparian features, but are characterized by dry to wet areas dominated by graminoids, and may be 100s to 1000s of acres in extent. Silver sagebrush and Rothrock sagebrush are often associated with these meadows, with recent encroachment of sagebrush into meadows documented with rephotography (see Meadow chapter; e.g. Gruell 2001). On the Kern Plateau, encroachment was shown to be correlated to soil exposure, reduced herbaceous biomass, and proximity to sagebrush seed sources, but not to increasing aridity that may be climate or grazing related (Berlow et al. 2002). Other evidence indicates that dry meadows and sagebrush are alternative states that are dependent upon depth to water table (Chambers and Linnerooth 2001, Wright and Chambers 2002).

Herbaceous invasions

Johnson et al. (2006) reviewed invasion information for sagebrush and found that no herbaceous invasions were documented prior to the 1800s. They provided a long list of modern invasives, plus a list of native annuals that may have been displaced by non-native, annual grasses. Robertson and Kennedy (1954) summarized changes in Nevada rangelands 50 years following photographs and descriptions from 1903, including the establishment and significant increases in cover of cheatgrass and halogeton (*Halogeton glomeratus*).

As discussed above, cheatgrass has the potential to alter significantly the fire regime in sagebrush. This annual grass grows rapidly, and, upon senescence in the late spring to early summer, creates a continuous cover of dry fuels that ignite easily and can create large fires. Cheatgrass is also less desirable forage for wildlife and livestock, as compared to native bunchgrasses (Knapp 1996). Halogeton, another invasive annual plant in sagebrush ecosystems, is poisonous to livestock, displaces native biodiversity, and leads to an increase in soil salinity.

The initial establishment of invasive annuals in the 1850s has been linked to the introduction of livestock and their feed, both of which carried non-native seed stock (Chambers et al. 2007). Once invasive annuals are established, grazing can have variable effects on the relative proportion of natives to non-natives, and has interactive effects with both fire and precipitation (Johnson et al. 2006). The removal of native herbaceous cover by livestock reduces aboveground competition for non-natives, and also results in an increase in shrub cover, which partition more resources deeper in the soil, leading to the potential for annual invasion. Removal of sagebrush has also been shown to result in greater cheatgrass cover (Prevey et al. 2010). In general, multiple years of drought can reduce cheatgrass, even when fire and/or grazing have been introduced. Greater precipitation levels, especially in the spring and summer have been linked to increased cheatgrass cover (Concilio et al. 2013). In the absence of grazing, there is some evidence that cheatgrass is less likely to invade burned areas, but it is difficult in these studies to separate grazing exclusion from topographic gradients that may explain variability. Cold winter temperatures are also known to limit cheatgrass distribution (Chambers et al. 2007).

Nutrient cycling

Soil crusts are an important component of the nutrient cycle in sagebrush systems because they include nitrogen-fixing microbiota, sequester many nutrients, including phosphorus and potassium, and increase soil carbon storage. Livestock grazing disturbs soil crusts, and recovery rates are very slow (Belnap et al. 2001). As a result, modern nutrient cycling in sagebrush systems is probably significantly different from that in the NRV period, with greater leaching of nutrients from current systems.

Land conversion

Large lakes and rivers that occur within the sagebrush zone have resulted in opportunity for land conversion, including agricultural development. Gruell (2001) documented the loss of sagebrush shrublands to a golf course in the Mammoth Lakes area, and thousands of acres of sagebrush in the Owens Valley were converted to agriculture in the late 1800s to 1900s. However, most of the latter were abandoned or again converted to less productive rangeland following the Los Angeles aqueduct construction and subsequent water diversion (Baugh 1937). Land conversion for agriculture has also been extensive in the northern subregion.

Disturbances

We give a brief summary here of current conditions for those disturbances with some evidence of change since the NRV period. Large debris flows and flooding have been seen recently on the Inyo NF (Wagner et al. 2012). The R5 fire history layer has delineated 1,696 prescribed burns that cover 14,154 acres in sagebrush in the assessment area, dating back to 1900, and 40,060 wildfires covering 633,075 acres since 1910. A recent trend of increased fire frequency in sagebrush is probably correlated to invasion of annual grasses. Although only 1,130 acres of invasive annual grasses have been documented in sagebrush ecosystems of the assessment area in the R5 NRIS dataset, field observations indicate that this is at least a 100-fold underestimate.

Comparison of NRV to Current Conditions

Departure between current conditions and trends from those during the NRV are summarized in Table 5. Among the most evident departures are recent herbaceous invasion, grazing, and land conversion (Brown and Smith 2000). Other departures are seen when comparing current conditions to the pre-settlement period (1800-1860), but are not evident when looking across the NRV for the entire Holocene. For example, tree density and cover, growth form ratios, and extreme climate events, are currently departed from conditions during the 1800s. However, their indicators are within ranges that were seen during the Hypsithermal period (5000 ybp) or during the Medieval Warm period (1000-1200 AD). We did not find any evidence of differences in wind, volcanism/earthquake, or insect/disease in sagebrush ecosystems between the pre- and post-NRV periods.

Our conclusions also vary based upon the spatial extent at which each indicator is considered. For example, methodologies employed for looking at the fossil record allow us to conclude that species richness and diversity has remained somewhat stable at the regional/landscape scale; however, spatial resolution is not available to make a conclusion at the community or stand scale. Similarly, determination of whether FRI is within the NRV is dependent upon the sagebrush taxa considered. Low and black sagebrush are probably not strongly departed from pre-settlement or overall Holocene conditions, as a result of lower productivity, sparser fuels, fewer invasives, and lower levels of recent grazing (McIver et al. 2001). Alternatively, some areas of big sagebrush may be strongly departed, where fires have been suppressed or where grazing has reduced the herbaceous cover. Other areas of big sagebrush which are infested with non-native annual grasses may be departed from NRV conditions because they have been burning too frequently in recent decades. These changes in function have resulted in the need for careful management of early seral sagebrush, which is now under-represented in comparison to the NRV period (Forbis et al. 2007). This is an especially difficult challenge given projections for invasions, and the possibility of sagebrush ecosystem conversion to persistent annual grasslands.

Future

Finch (2012) predicted that drought, megafires, pests, and non-native invasions will increase over the next century in arid shrublands of the assessment area. Cheatgrass, in particular, is expected to continue to move northward and upward in elevation, and bring significant changes to areas where it is currently absent or sparse. Woodland expansion, invasion by non-native annual grasses, and land conversion have been identified as major stressors to sagebrush ecosystems (Wisdom and Chambers 2009, Davies et al. 2011).

Extreme events, such as major drought, even if short-term or semi-annual, are expected to bring significant changes (Anderson and Inouye 2001). Combined influences of disturbances may become amplified. For example, fire is more likely to be followed by cheatgrass invasion if perennial herbs are first removed by grazing (Chambers et al. 2007). Heavy grazing during drought years can increase soil erosion and result in long-term loss of perennial grass cover.

The influences of most current stressors in sagebrush systems are greatest at lower elevations, where cheatgrass, grazing, increased fire size and frequency, and encroachment of both trees and desert species have been observed (Brooks and Chambers 2011). As discussed above, tree encroachment has occurred during both cool and warm periods during the Holocene; the projected downward encroachment during a warming period, when coupled with upward desert species expansion, may result in a reduction in the extent and size of the lower sagebrush belt in particular.

The complexity of these rapid changes points to the importance of understanding cause prior to engaging in restoration efforts, to ensure that goals have the potential to be met (Hobbs and Norton 1996).

Structure

NRV

During the early Holocene, sagebrush was the predominant vegetation over 1495 m (4900 ft), or 54% of the assessment area. Modern proportions are probably most similar to those during the late Holocene, such as the Medieval warm period, given that not only are the climate regimes of the time periods similar, but the necessary length of time for sagebrush and conifers to migrate had gone by, in contrast to previous warm periods (Table 6). Accounts from Shaw in the mid-1800s from Nevada state that the territory between the Rocky and Sierra Nevada Mountains was "at least nine-tenths sage" (Vale 1975). The proportion of different sagebrush taxa during the NRV period can be inferred from modern correlations to climate; cooler, wetter periods were probably characterized by a greater proportion of low sagebrush, and warmer, drier conditions by more black and Wyoming sagebrush.

A few major trends emerge from an overview of changes in climate and landscape scale vegetation during the Holocene (Table 6). First, there has been an overall decline in the dominance of sagebrush as an ecosystem type since the early Holocene. However, its geographic extent has not changed as much, in comparison to changes in tree cover and composition that have given sagebrush a status as an understory component.

The general pattern of pinyon-juniper migration northward and upward over the entire Holocene is overlaid with temperature and precipitation fluctuations. Warming trends were correlated to increased cover of desert shrubs in sagebrush, and cooling was correlated with depressed treelines. The recent encroachment of pinyon-juniper into sagebrush is occurring during a warming trend. Recent encroachment appears to have been initiated at least in part to the period of high precipitation in the early 1900s in the eastern subregion (Miller and Wigand 1994). We conclude that the trend since then has been jointly influenced by grazing and changed fire regimes, but also by migrational 'infilling' of open habitats, given that the conifer seedbank has continuously been built up over this time.

Very little is known about community scale structure in sagebrush during the NRV period; these attributes are not reflected in the fossil record, which only records presence/absence or relative abundance. Miller et al. (2001) concluded that shrub cover was as much as 10% lower during NRV period in sagebrush systems, by using the reasoning that the FRI was lower at that time, and so shrubs did not have the time to reach full maturity. Because of the number of assumptions used in this conclusion, the confidence about differences in structure between pre- and post-NRV is relatively low. Historic accounts note that "sagebrush was not dense as to block the way" (Ogle 1997). Shrub heights were also given as 0.3-2.1 m (1-7 ft; Brown and Smith 2000).

Hall (2007) conducted a 27 year study in a low sagebrush grazing exclusion in Oregon, and found 2.4-fold annual variability in herbaceous productivity and seedhead production. Similarly, both grass and shrub cover increased after 25 years of grazing exclusion in southern Idaho (Anderson and Holte 1981). From this, we infer that herbaceous cover and reproduction was greater prior to the introduction of large number of livestock to the assessment area in the 1850s, but that annual variation was also high (Table 5).

Modern differences in community structure between taxa were probably similar to the NRV period, because genetic differences in growth rates and stature have presumably remained relatively stable over this time period. A ranking of the growth rates of the major taxa, in descending order is: basin big sagebrush, mountain big sagebrush, Wyoming sagebrush (Welch and McArthur 1986). Black sagebrush could also be included at the lower end. Soils do have an important influence on sagebrush productivity; for example, shrubs on carbonate soils are smaller in stature and more widely spaced, and this characteristic would have been similar during the NRV period.

Correlations between sagebrush density and recent climate trends provide information about the probable variability of sagebrush structure during the NRV period. For example, sagebrush density is generally higher during wet periods ((Anderson and Inouye 2001, Lommasson 1948, Maier et al. 2001, Welch and Criddle 2003, as cited by Baker 2006). A rephotography study in northern Nevada from 1903 to 1953, at numerous locations, indicates a general trend of increased density of sagebrush (Robertson and Kennedy 1954). This has occurred during a warming trend over the last century, but may also be a remnant of wetter conditions that occurred in the early 1900s, or may be more strongly related to livestock grazing and fire suppression than to climatic causes.

Physiognomy

All processes discussed above, including migration, invasion, and disturbances have driven the community physiognomy in sagebrush systems through the NRV period. The variables for which some prehistoric and historic evidence exists include the proportion of perennials vs. annuals and herbs vs. shrubs. During the NRV period, there were few, if any, annuals in most sagebrush systems, and annuals that were present were native (Johnson et al. 2006) . Sagebrush at the interface of deserts to the south, where native annuals are abundant currently, may have had greater annual cover during the NRV period.

The low spatial resolution for grass pollen evidence makes it difficult to determine if variability in the grass:shrub ratio over the Holocene reflects a change in the proportion of sagebrush to meadow ecosystems at the landscape scale, or a change in the grass:shrub ratios within sagebrush communities. It is likely that the proportions at both scales were correlated. The general conclusion from Miller and Wigand (1994) in eastern Oregon that the grass:shrub ratio increased during wetter periods, and decreased during warmer periods, probably is generally true for the assessment area (Table 6).

Based upon a number of historic accounts, Vale (1975) concluded that grass was not abundant in sagebrush shrublands in the mid-1850s, except for on moist valley bottoms, mesic slopes, and some areas east of the Cascades in OR. Therefore, modern variability in grass:sagebrush ratios were probably present during the NRV period (Table 5). Anderson and Inouye (2001) found that perennial grass cover in sagebrush varied by 13-fold in under 20 years in southern Idaho. Grass cover did track precipitation levels following a major drought, but later changes were not well correlated to precipitation, indicating that other factors drive grass:shrub ratios. Miller et al. (2001) concluded that a higher herbaceous component during the NRV period in sagebrush was due to higher fire frequencies, with short intervals that precluded woody growth.

Current

On the Inyo National Forest (Inyo NF), a forest-level dataset was used to conduct an accuracy assessment for the R5 Calveg maps for sagebrush. The acreage and distribution for low sagebrush and for Rothrock sagebrush were similar between the R5 and Inyo NF maps. However, the R5 map overestimated the extent of big sagebrush by around 100,000 acres. This generally occurred in mixed shrub communities, where remote sensing techniques did not differentiate communities dominated by snowberry (*Symphoricarpos* sp.), mountain mahogany (*Cercocarpus ledifolius*), bitterbrush, or ceanothus. However, for analysis at the assessment area scale, the R5 maps provide a reasonably accurate range of current sagebrush extent.

Populations with intermediate characteristics of sagebrush taxa are currently common in the assessment area, and some may be stable hybrid populations (Tart 2004). In some cases, these unique populations may express new disturbance regimes. For example, a hybrid form of big sagebrush-black sagebrush has been documented in the Crowley Basin of the Inyo NF. This population exhibits the relatively tall stature of big sagebrush, but the persistent, dry inflorescences of black sagebrush. This difference in structure appears to have altered the fuels profile, and may result in higher fire frequencies than expected in pure stands of either taxon (Slaton 2005).

A current dataset for the south and east subregions of the assessment area provided some information on current structural attributes in sagebrush, in areas that mostly have some livestock grazing influence (Table 8). Mean sagebrush height is less than 0.5 m for black and low sagebrushes, and ranges from 0.5-1.5 m (1.6-4.9 ft) for big sagebrush. Sagebrush cover is generally between 10-20%, with higher values for silver and basin big sagebrush, and lower values for black and low sagebrush. Graminoid cover is greatest in silver sagebrush and lowest in black sagebrush. Ground surface cover is often dominated by gravel, with higher amounts of fine litter present in areas where bitterbrush is codominant.

Comparison of NRV to Current Conditions

Brown and Smith (2000) contrasted sagebrush and herbaceous cover between the pre- and post-NRV periods. They concluded that native perennial grass and forb cover is currently lower than during the presettlement period, and that sagebrush cover is currently lower, due to degradation caused by grazing, erosion, and increased fire frequency. Comparisons between current conditions and the variability represented over the entire Holocene indicate that sagebrush cover and ecosystem physiognomy seen now probably occurred at certain times in past (Table 5). However, the overall geographic extent of sagebrush is much less than what was seen during the early Holocene.

Future

Bradley (2010) developed a robust model of risk to sagebrush systems in Nevada due to climate change, land cover change, and species invasion, using climate envelopes under future scenarios. Results indicated that sagebrush is most likely to be impacted at its range limits, such as southern Nevada. This technique is limited by the assumption that sagebrush is in climatic equilibrium, but it is in agreement with findings during the NRV period that sagebrush was subject to relatively rapid change at its interface with more arid desert shrublands. A number of authors have predicted that sagebrush will move northward and upward over the upcoming decades (Finch 2012). Miller et al. (2011) estimated that approximately 12% of the current distribution of sagebrush will be replaced by other woody vegetation for each 1 deg. C increase in temperature.

Composition

NRV

Unlike structural characteristics, composition data from the NRV period is readily available from the packrat midden fossil record, though at somewhat coarse resolution. Landscape/regional level composition has remained relatively stable over time within the sagebrush zone, with modern taxa associated with sagebrush present throughout the Holocene, in the southeastern bioregion, including *Eriogonum*, *Chrysothamnus*, *Ephedra*, *Ribes*, *Symphoricarpos*, *Tetradymia*, *Opuntia*, *Castilleja*, *Stephanomeria*, *Elymus*, and *Lomatium* (Jennings and Elliott-Fisk, 1993). Composition at specific sites has varied more widely. For example, the current plant species assemblage in the Alabama Hills, in the Owens Valley, at the current lower limit of sagebrush, is similar to that of the mid Holocene, with the exception of *Purshia,* which is now absent, and cottontop cactus (*Echinocactus polycephalus*), which appeared after 2830 ybp (Woolfenden 1996). A general pattern does emerge, where the sagebrush zone that dominated over 1495 m (4900 ft) during the early Holocene gained an increasing proportion of desert taxa into the Mid Holocene. The upward movement of conifers through the sagebrush zone also changed community composition.

Given that composition of modern species assemblages is generally not transferable to historic periods, one exception may be areas of low productivity, where structural shifts have been observed in response to climate, but composition can remain relatively stable (Briles et al. 2011). The stability is emphasized in systems with infrequent fire (Dobrowski et al. 2011), and so we can infer that composition in less productive sagebrush systems, such as Wyoming or black sagebrush, may be highly similar in composition between modern times and the NRV period.

Several Tertiary and glacial relicts currently occur within the sagebrush zone of the southeastern portion of the assessment area (e.g. *Dedeckera eurekensis, Fraxinus anomola, Philadelphus microphylla*), which have presumably contributed to landscape scale diversity, and expanded periodically during favorable climate regimes during the NRV period (Stewart and Lister 2001). These species are generally restricted to mesic or cool sites. Similarly, some peripheral populations of sagebrush within deserts of the assessment area are probably relicts themselves.

Modern correlations between climate and diversity may have some transferability to earlier Holocene periods. For example, in a 45 year study in Idaho, in a location with similar species composition to eastern California, increased precipitation was correlated to higher cover of rabbitbrush and big sagebrush, and less horsebrush (*Tetradymia* spp.), an indicator of sagebrush-desert ecotones. Thus, moister periods during the Holocene probably had a smaller component of desert shrub species (Anderson and Inouye 2001). Increases in numbers of aquatic macroflora and fauna in the sagebrush zone were also observed during moister periods of the Holocene (Wigand 1987). Finally, disturbance-tolerant species and resprouters, such as rabbitbrush, horsebrush, and ceanothus often increase with fire (Martin and Johnson 1979); therefore, warmer periods with greater fire frequencies, such as the Xerothermic and Medieval warm periods, may have been characterized by greater proportions of those species.

Ogle (1997) described historical accounts that mention the presence of rabbitbrush, currant (*Ribes* spp.), Mormon tea, bitterbrush, and snowberry within sagebrush systems in the 1850s, and all those species are common associates in sagebrush today. Robertson and Kennedy (1954) provided an important account of change in sagebrush systems from 1903-1953. They found that desirable browse species, such as fourwing saltbush (*Atriplex canescens*), bitterbrush, budsage (*Artemisia spinescens*), and shadscale (*Atriplex confertifolia*) decreased during that time period, which is consistent with increased livestock use.

Packrat middens indicate that there have been changes in species assemblages over time, but not an overall increase or decrease in diversity (Woolfenden 1996). Highest diversity in sagebrush systems is currently found in the transition area between sagebrush and desert shrublands on the Inyo NF (Slaton et al. 2012); based on this, we can infer that warmer periods, especially those without severe drought, may have been associated with higher diversity in the NRV period.

Current

A current dataset for sagebrush ecosystems in eastern and southern California provided species richness information, showing 11-22 total species and 1-8 shrub species per 0.04 ha (0.1 acre) plot (Table 8). Numerous historic accounts give us high confidence that few or no non-native species occurred in sagebrush prior to the mid-1800s (Johnson et al. 2006). This is in contrast to the 63 invasive plant species reported within sagebrush areas of the assessment area by 2013, according to the R5 NRIS Invasives dataset.

There is an ongoing dispute over whether grazing causes increased diversity (Laycock 1991); Anderson and Inouye (2001) concluded that in semi-arid systems without historic native grazing, that grazing increases shrub cover at the expense of herbaceous diversity. These authors also found that the impact of non-natives on native cover did not translate to a similar reduction in native richness. A major caveat of using grazing exclusion studies to infer conditions for areas never grazed is represented by Anderson and Holte (1981). Even after a 25 year grazing exclusion in Idaho, these authors found that composition did not return to ungrazed levels; alterations to the seed bank and soil may have exceeded a threshold, and resulted in a new steady state for these systems.

Comparison of NRV to Current Conditions

Evidence indicates that composition in sagebrush is not strongly departed from conditions during the NRV period, especially from warm and dry periods, including the Hypsithermal and Medieval Warm period. The primary exception is the establishment of non-native species (Table 5).

Future

Using the Hypsithermal and Medieval Warm periods and proxies, we expect that desert shrub species will increase in proportion relative to sagebrush in current sagebrush ecosystems. Recent observations on the Inyo NF indicate that saltbush is currently expanding upward into the sagebrush zone.

Some of the Tertiary and glacial relict shrub species in the sagebrush zone will probably decline, because they are best adapted to moister and cooler conditions than are predicted, thereby leading to a loss of compositional diversity (Hampe and Petit 2005, Finch 2012, Wiens and Slaton 2012). These species often have low reproductive rates, which limits their dispersal capacity and ability to migrate; in combination with changes to climate and the fire regime, these species are at high risk (Clark et al. 2001).

The complexity of terrain in which sagebrush occurs is expected to be an important factor in its long-term structural and compositional stability in the assessment area. Proximity of different habitats to one another in steep terrain and with strong climatic gradients is linked to long-term persistence of populations (Lancaster and Kay 2013). Sagebrush may be most at risk in areas of uniform terrain, where variation in microclimates does not occur, or where no terrain breaks serve to constrain fires or invasions.

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LITERATURE CITED

Anderson, J. E. and K. E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of Rangeland Management 34:25-29.

Anderson, J. E. and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531-556.

Anderson, M. K. 1997. From tillage to table: The indigenous cultivation of geophytes for food in California. Journal of Ethnobiology 17:149-169.

Anderson, M. K. and M. J. Moratto. 1996. Native American Land-Use Practices and Ecological Impacts. Pages 187-206 Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options., University of California, Davis: Centers for Water and Wildland Resources.

Anderson, R. S. 1990. Holocene forest development and paleoclimates within the central Sierra Nevada, California. The Journal of Ecology:470-489.

Anderson, R. S. 2004. Response of Sierra Nevada Vegetation and Fire Regimes to Past Climate Changes. Pages 47-50 in D. D. Murphy and P. A. Stine, editors. Proceedings of the Sierra Nevada Science Symposium, PSW-GTR-193. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Antevs, E. 1938. Rainfall and tree growth in the Great Basin. Carnegie Institution of Washington

American Geographical Society of New York, Baltimore.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177-185.

Baker, W. L. 2011. Pre-Euro-American and recent fire in sagebrush ecosystems.in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in avian biology (Vol 38). University of California, Berkeley, CA.

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, editors. 2012. The Jepson manual: vascular plants of California. 2nd edition. University of California Press, Berkeley, CA.

Barger, N. N., H. D. Adams, C. Woodhouse, J. C. Neff, and G. P. Asner. 2009. Influence of Livestock Grazing and Climate on Pinyon Pine (Pins edulis) Dynamics. Rangeland Ecology & Management 62:531-539.

Barth, R. C. 1980. Influence of pinyon pine trees on soil chemical and physical properties. Soil Science Society of America Journal 44:112-114.

Bauer, J. M. and P. J. Weisberg. 2009. Fire history of a central Nevada pinyon-juniper woodland. Canadian Journal of Forest Research 39:1589-1599.

Baugh, R. E. 1937. Land use changes in the Bishop area of Owens Valley, California. Economic Geography.

Beatley, J. C. 1975. Climates and vegetation pattern across Mojave Great Basin desert transition of southern Nevada. American Midland Naturalist 93:53-70.

Beck, J. L. and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:993-1002.

Belnap, J., J. H. Kaltenecker, R. Rosentreter, J. Williams, S. Leonard, and D. Eldridge. 2001. Biological soil crusts: ecology and management. USDI Bureau of Land Management, Denver, CO.

Berlow, E. L., C. M. D'Antonio, and S. A. Reynolds. 2002. Shrub expansion in montane meadows: The interaction of local-scale disturbance and site aridity. Ecological Applications 12:1103-1118.

Betancourt, J. L. 1986. Paleoecology of pinyon-juniper woodlands: summary. Pages 129-139 in R. L. Everett, editor. Proceedings of the Pinyon-juniper conference, GTR-INT-215. USDA Forest Service, Intermountain Research Station, Ogden, UT.

Blaisdell, J. P., R. B. Murray, and E. D. McArthur. 1982. Managing intermountain rangelands-sagebrush-grass ranges, GTR-INT-134. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Bradley, B. A. 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198-208.

Briles, C. E., C. Whitlock, C. N. Skinner, and J. Mohr. 2011. Holocene forest development and maintenance on different substrates in the Klamath Mountains, northern California, USA. Pages 590-601. Ecology.

Bristow, N. A. 2010. Long-term vegetation response to treatments of prescribed fire and chaining in Great Basin pinyon-juniper woodlands. University of Nevada, Reno.

Brooks, M. L. and J. C. Chambers. 2011. Resistance to Invasion and Resilience to Fire in Desert Shrublands of North America. Rangeland Ecology & Management 64:431-438.

Brown, J. K. and J. K. Smith. 2000. Wildland fire in ecosystems: effects of fire on flora. Page 257. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Brunelle, A. and R. S. Anderson. 2003. Sedimentary charcoal as an indicator of late-Holocene drought in the Sierra Nevada, California, and its relevance to the future. Holocene 13:21-28.

Burkhardt, J. W. and E. W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472-484.

Chambers, J. C. 2008. Climate change and the Great Basin. Pages 29-32 in J. C. Chambers, N. Devoe, and A. Evenden, editors. Collaborate management and research in the Great Basin - examining the issues and developing a framework for action, RMRS-GTR-204. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Chambers, J. C. and A. R. Linnerooth. 2001. Restoring riparian meadows currently dominated by Artemisia using alternative state concepts - the establishment component. Applied Vegetation Science 4:157-166.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? Ecological Monographs 77:117-145.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. American Naturalist 157:537-554.

Concilio, A. L., M. E. Loik, and J. Belnap. 2013. Global change effects on Bromus tectorum L. (Poaceae) at its high-elevation range margin. Global Change Biology 19:161-172.

Connelly, J. W., K. P. Reese, R. A. Fischer, and W. L. Wakkinen. 2000. Response of a sage grouse breeding population to fire in southeastern Idaho. Wildlife Society Bulletin 28:90-96.

Currie, P. O., D. W. Reichert, J. C. Malechek, and O. C. Wallmo. 1977. Forage selection comparisons for mule deer and cattle under managed Ponderosa Pine. Journal of Range Management 30:352-356.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology doi: 10.1002/joc.1688.

Daniels, M. L., R. S. Anderson, and C. Whitlock. 2005. Vegetation and fire history since the Late Pleistocene from the Trinity Mountains, northwestern California, USA. Holocene 15:1062-1071.

Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22:1562-1577.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573-2584.

Davis, J. O. 1982. Bits and pieces: the last 35,000 years in the Lahontan area. Pages 53-75 in D. B. Madsen and J. F. O'Connell, editors. Man and Environment in the Great Basin. Society for American Archeology SAA Papers No. 2.

Dobrowski, S. Z., J. H. Thorne, J. A. Greenberg, H. D. Safford, A. R. Mynsberge, S. M. Crimmins, and A. K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. Ecological Monographs 81:241-257.

Donnelly-Nolan, J. M. 1990. Geology of Medicine Lake volcano, northern California Cascade Range. Geothermal Resources Council Transactions 14:1395-1396.

Eisenhart, K. S. 2004. Historic range of variability and stand development in pinon-juniper woodlands of western Colorado. University of Colorado.

Finch, D. M., editor. 2012. Climate change in grasslands, shrublands, and deserts of the interior American west: A review and needs assessment. US Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Forbis, T. A., L. Provencher, L. Turner, G. Medlyn, J. Thompson, and G. Jones. 2007. A method for landscape-scale vegetation assessment: application to Great Basin rangeland ecosystems. Rangeland Ecology Management 60:209-217.

Fronk, W. D., A. A. Beete, and D. G. Fullerton. 1964. Dipterous galls on Artemisia tridentata complex and insects associated with them. Annals of the Entomological Society of America 57:575-577.

Frost, C. C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Pages 70-81 in T. L. Pruden and L. A. Brennan, editors. 20th Tall Timbers Fire Ecology Conference: Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Research, Inc., Boise, ID.

Graumlich, L. T. 1987. Precipitation variation in the Pacific Northwest (1675-1975) as reconstructed from tree rings. Pages 19-29. Ann. Assoc. Amer. Geogr.

Grayson, D. K. 2006. Holocene bison in the Great Basin, western USA. Holocene 16:913-925.

Gruell, G. E. 2001. Fire in Sierra Nevada forests : a photographic interpretation of ecological change since 1849. Mountain Press Pub. Co., Missoula, Mont.

Hall, F. C. 2007. Variation in shrub and herb cover and production on ungrazed pine and sagebrush sites in eastern Oregon : a 27-year photomonitoring study, GTR-704. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Hampe, A. and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461-467.

Harvey, A., P. Wigand, and S. Wells. 1999. Response of alluvial fan systems to the late Pleistocene to Holocene climatic transition: contrasts between the margins of pluvial Lakes Lahontan and Mojave, Nevada and California, USA. Catena 366:255-281.

Hobbs, R. J. and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93-110.

Holochek, J. L., T. T. Baker, J. C. Boren, and D. Galt. 2006. Grazing impacts on rangeland vegetation: what we have learned. Rangelands 28:7-13.

Johnson, D. D. and R. F. Miller. 2008. Intermountain presettlement juniper: distribution, abundance, and influence on postsettlement expansion. Rangeland Ecology and Management 61:82-92.

Johnson, M., L. J. Rew, B. D. Maxwell, and S. Sutherland. 2006. The role of wildfire in the establishment and range expansion of nonnative plant species into natural areas. Center for Invasive Plant Management, Montana State University, MT.

Kitchen, S. G. and E. D. McArthur. 2007. Big and black sagebrush landscapes. Pages 73-95 in S. M. Hood and M. Miller, editors. Fire ecology and management of the major ecosystems of southern Utah. Gen. Tech. Rep. RMRS-GTR-202. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Knapp, P. A. 1996. Cheatgrass (Bromus tectorum L) dominance in the Great Basin Desert - History, persistence, and influences to human activities. Global Environmental Change-Human and Policy Dimensions 6:37-52.

Knick, S. T., S. E. Hanser, R. F. Miller, D. A. Pyke, M. J. Wisdom, S. P. Finn, E. T. Rinkes, and C. J. Henny. 2011. Ecological influence and pathways of land use in sagebrush. Pages 203-251 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Pres, Berkeley, CA.

Lancaster, L. T. and K. M. Kay. 2013. Origin and diversification of the California flora: re-examining classic hypotheses with molecular phylogenies. Evolution.

Laycock, W. A. 1991. STABLE STATES AND THRESHOLDS OF RANGE CONDITION ON NORTH-AMERICAN RANGELANDS - A VIEWPOINT. Journal of Range Management 44:427-433.

Lyford, M. E., S. T. Jackson, J. L. Betancourt, and S. T. Gray. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73:567-583.

Management, B. o. L. 2002. Management considerations for sagebrush (Artemisia) in the Western United States: a selective summary of current information about the ecology and biology of woody North American sagebrush taxa. USDI, Washington DC.

Martin, R. E. and A. H. Johnson. 1979. Fire management of Lava Beds National Monument.in R. M. Linn, editor. First Conference on Scientific Research in the National Parks. US Deptartment of the Interior, New Orleans, Louisiana.

McIver, J. D. 2010. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP) : a test of state-and-transition theory, GTR-237. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Mehringer, P. J. and P. E. Wigand. 1990. Comparison of Late Holocene environments from woodrat middens and pollen, Diamond Craters, Oregon.in P. S. Martin, J. Betancourt, and T. R. Van Devender, editors. Fossil Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, AZ.

Mensing, S., S. Livingston, and P. Barker. 2006. Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. Western North American Naturalist 66:64-77.

Meyer, S. E. 1994. Germination and establishment ecology of big sagebrush: implications for community restoration. Pages 244–251 in S. B. Monsen and S. G. Kitchen, editors. Ecology, management, and restoration of Intermountain annual rangelands: proceedings; 1992 May 18–22, Boise, ID, Gen. Tech. Rep. INT-GTR-313. USDA Forest Service, Intermountain Research Station, Ogden, UT.

Miles, S. R. and C. Goudey. 1997. Ecological Subregions of Califronia - section and subsection descriptions.in P. S. R. USDA Forest Service, editor., San Francisco, CA.

Miller, J. R., K. House, D. Germanoski, R. J. Tausch, and J. C. Chambers. 2004. Fluvial geomorphic responses to Holocene climate change. Pages 49-87 in J. C. Chambers and J. R. Miller, editors. Great Basin riparian ecosystems. Island Press, Washington.

Miller, R., C. Baisan, J. Rose, and D. Pacioretty. 2001. Pre- and post-settlement fire regimes in mountain big sagebrush steppe and aspen: the northwestern Great Basin. Final Report to the National Interagency Fire Center, Oregon State University, Eastern Oregon Agricultural Research Center.

Miller, R. F. and E. K. Heyerdahl. 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. International Journal of Wildland Fire 17:245-254.

Miller, R. F., S. T. Knick, A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdon, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in avian biology. Berkeley, CA, University of California Press.

Miller, R. F. and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550-559.

Miller, R. F. and P. E. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. Bioscience 44:465-474.

Nelson, D. L. and D. L. Sturges. 1986. A snowmold disease of mountain big sagebrush. Phytopathology 76:946-951.

Nelson, D. L. and C. F. Tiernan. 1983. Winter injury of sagebrush and other wildland shrubs in the western United States. U.S. Dept. of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Ogle, K. 1997. Historical vegetation on national forest lands in the Intermountain Region. USDA Forest Service, Intermountain Region, Ogden, UT.

Olson, S. 2012. Olson, S. An introduction to the Sagebrush Steppe Treatment Evaluation Project (SageSTEP): Fire science research to inform land management decision. The Progressive Reader February:26-27.

Osmond, D. L., D. M. Butler, N. N. Ranells, M. H. Poore, A. Wossink, and J. T. Green. 2007. Grazing practices: a review of the literature, Technical Bulletin 325-W. North Carolina Agricultural Research Service, North Carolina State University, Raleigh, NC.

Prevey, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. Plant Ecology 207:39-51.

Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. Pages 531-548 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38. University of California Press, Berkeley, CA.

Robertson, J. H. and P. Kennedy. 1954. Half-century changes on northern Nevada ranges. Journal of Range Management 7:117-121.

Romme, W. H., C. D. Allen, J. D. Balley, W. L. Baker, B. T. Bestelmeyer, P. M. Brown, K. S. Eisenhart, M. L. Floyd, D. W. Huffman, B. F. Jacobs, R. F. Miller, E. H. Muldavin, T. W. Swetnam, R. J. Tausch, and P. J. Weisberg. 2009. Historical and Modern Disturbance Regimes, Stand Structures, and Landscape Dynamics in Pinon-Juniper Vegetation of the Western United States. Rangeland Ecology & Management 62:203-222.

Rowley, W. D. 1985. U.S. Forest Service grazing and rangelands: a history. Page 270. Texas A&M University Press, College Station.

Shultz, L. 2012. Pocket guide to sagebrush. PRBO Conservation Science, Petaluma, CA.

Skinner, C. N. and C.-R. Chang. 1996. Fire regimes, past and present. Pages 1041-1069 Sierra Nevada Ecosystem Project: Final Report to Congress. University of Caliornia, Centers for Water and Wildland Research, Davis, CA.

Slaton, M. R. 2005. Greater sage grouse habitat analysis and mapping, Lake Crowley Basin, Inyo National Forest.in U. FS, editor., Bishop, CA.

Slaton, M. R. 2011. FY11 Monitoring report for INF ecology plots. Internal Report. Inyo National Forest, Bishop, CA.

Slaton, M. R. 2013. Ecology plots of Eastern California. Inyo National Forest, Bishop, CA.

Slaton, M. R., V. McLean, T. Ellsworth, and C. Clark. 2012. Inyo National Forest Landtype Association Scale Terrestrial Ecological Unit Inventory. Inyo National Forest, USFS Internal Report, Bishop, CA.

Smith, S. 1994. Ecological guide to eastside pine plant associations, R5-ECOL-TP-004. USDA Forest Service, Pacific Southwest Region.

Soule, P. T. and P. A. Knapp. 1999. Western juniper expansion on adjacent disturbed and near-relict sites. Journal of Range Management 52:525-533.

Soule, P. T., P. A. Knapp, and H. D. Grissino-Mayer. 2004. Human agency, environmental drivers, and western juniper establishment during the late holocene. Ecological Applications 14:96-112.

Stewart, J. R. and A. M. Lister. 2001. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology & Evolution 16:608-613.

Stine, S. 1990. Late Holocene fluctuations of Mono Lake, Eastern California. Palaeogeography Palaeoclimatology Palaeoecology 78:333-&.

Tart, D. 2004. Sagebrush taxonomy field trip - Sierras and White Mountains 9/20-23/2004. Field Notes. Inyo National Forest Files, Bishop, CA.

Tausch, R. J., C. L. Nowak, and S. A. Mensing. 2004. Climate change and associated vegetation dynamics during the Holocene: The paleoecological record.in J. C. Chambers and J. R. Miller, editors. Great Basin riparian areas: Ecology, management, and restoration. Island Press, Washington.

Tausch, R. J. and R. S. Nowak. 1999. Fiftly years of ecotone change between shrub and tree dominance in the Jack Spring Pinyon Research Natural Area. Pages 71-77 in E. D. McArthur, W. K. Ostler, and C. L. Wambolt, editors. Proceedings: shrubalnd ecotones. RMRS-P-11. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. Journal of Range Management 28:32-36.

Van de Water, K. M. and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26-58.

Wagner, D. L., J. T. Lancaster, and M. B. DeRose. 2012. The Oak Creek post fire debris and hyperconcentrated flows of July 12, 2008, Inyo County, California: A geologic investigation. California Geologic Survey, California Department of Conservation, Sacramento, CA.

Warren, S. D., L. L. St. Clair, J. R. Johansen, and P. Kugrens. 2008. Effects of prescribed fire on biological soil crusts and their subsequent recovery in a Great Basin juniper woodland, Final Report to the Joint Fire Science Program

Welch, B. L. and E. D. McArthur. 1986. Growth rate of big sagebrush as influenced by accessions, sites, subspecies, and years.in E. D. McArthur and B. L. Welch, editors. Proceedings-symposium on the biology of Artemisia and Chrysothamnus, July 9-13, 1984, GTR-INT-200. USDA, Forest Service, Intermountain Research Station, Ogden, UT.

West, N. E. and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Pages 255-284 in M. G. Barbour and W. D. Billings, editors. North American Terrestrial Vegetation. Cambridge University Press, New York.

Wickstrom, C. K. R. 1987. Issues concerning Native American use of fire: a literature review. Publications in Athropology No. 6. USDI National Park Service, Yosemite Research Center, Yosemite National Park.

Wiens, D. and M. R. Slaton. 2012. The mechanism of background extinction. Biological Journal of the Linnean Society 105:255-268.

Wigand, P. E. 1987. Diamond Pond, Harney County, Oregon - Vegetation history and water table in the eastern Oregon desert. Great Basin Naturalist 47:427-458.

Wigand, P. E., M. L. Hemphill, S. E. Sharpe, and S. Patra. 1995. Great Basin semi-arid woodland dynamics during the late Quaternary.in Climate change in the four corners and adjacent regions: implications for environmental restoration and land-use planning. Workshop Proceedings. Campbell College Center, Mesa State College, Grand Junction, CO.

Winward, A. H. 1991. A renewed commitment to management of sagebrush grasslands.in K. Sanders and J. Durham, editors. Research in rangeland management. Agricultural Experiment Station Special Report 880. Oregon State University, Corvallis, OR.

Wisdom, M. J. and J. C. Chambers. 2009. A Landscape Approach for Ecologically Based Management of Great Basin Shrublands. Restoration Ecology 17:740-749.

Woolfenden, W. B. 1996. Quaternary vegetation history. Pages 47-70 Sierra Nevada Ecosystem Project: Final Report to Congress. University of Caliornia, Centers for Water and Wildland Research, Davis, CA.

Wright, H. A. and A. W. Bailey. 1982. Fire ecology: United States and southern Canada. Wiley, New York.

Wright, J. M. and J. C. Chambers. 2002. Restoring riparian meadows currently dominated by Artemisa using alternative state concepts - above-ground vegetation response. Applied Vegetation Science 5:237-246.

Young, J. A. and R. A. Evans. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34:501-506.

TABLES

Table 1. Summary of sagebrush taxa and climate by subregion. Climate data are from the PRISM data source, 1992-2008, with summer values for March-May, and winter for December-February (Daly et al. 2008). Sagebrush data are from R5 Calveg dataset.

	Central	**East**	**North**	**South**	
Climate					
Mean summer temp (C)	19	20	18	19	
Mean winter temp (C)	3	1	1	3	
Mean summer precip (cm/3 mo)	3	2	4	2	
Mean winter precip (cm/3 mo)	63	14	46	39	
Vegetation types - acres					**Total**
Low sagebrush	25,295	34,802	459,335	15,270	534,702
Big sagebrush*	65,350	1,442,237	907,881	147,582	2,563,050
Sagebrush-bitterbrush	41,594	77,832	71,024	1,066	191,516
Black sagebrush	796	43,544	0	0	44,341
Rothrock sagebrush	10	0	0	6,936	6,946
Basin big sagebrush	12,355	150,453	67,718	214	230,739
Silver sagebrush	0	0	18,639	0	18,639
Mountain big sagebrush	56,137	82,883	135,181	22,475	296,676
Wyoming sagebrush	0	0	225	0	225
Total	201,538	1,831,750	1,660,003	193,542	3,886,834

**A. tridentata* in this category was not mapped to the subspecies level.

Table 2. Woody sagebrush taxa in the assessment area mapped in the R5 Existing Vegetation dataset.

CALVEG Code	**Common Name**	**Scientific name**
BL	Low sagebrush	Artemisia arbuscula
TU	Silver sagebrush	*A. cana* var. *bolanderi*
TN	Black sagebrush	A. nova
TR	Rothrock sagebrush	A. rothrockii
BS	Big sagebrush	A. tridentata
TT	Basin big sagebrush	*A. tridentata* ssp. *tridentata*
TV	Mountain big sagebrush	*A. tridentata* ssp. *vaseyana*
TW	Wyoming sagebrush	*A. tridentata* ssp. *wyomingensis*

Table 3. Summer and winter climate in assessment subregions, from the PRISM data source, 1992-2008, with summer values for March-May, and winter for December-February (Daly et al. 2008).

		Winter				Summer			
		MIN	**MAX**	**MEAN**	**STD**	**MIN**	**MAX**	**MEAN**	**STD**
Precipitation (cm/3 mo)	Central	18	127	63	21	1	6	3	1
	East	5	48	14	7	1	5	2	1
	North	10	165	46	33	2	9	4	1
	South	8	86	39	17	1	5	2	1
Temperature (C)	Central	-6	9	3	4	10	26	19	4
	East	-7	10	1	3	9	32	20	4
	North	-3	9	1	3	13	27	18	2
	South	-10	10	3	5	4	28	19	6

Table 4. Ecological settings for sagebrush systems by subregion.

	Central	East	North	South
Major Ecological Sections with sagebrush (Miles and Goudey 1997)	Sierra Nevada	*Southeast:* Southeastern Great Basin, Mono, Lahontan Basin, Sierra Nevada *Northeast:* Northwestern Basin and Range, Sierra Nevada, Modoc Plateau	Modoc Plateau, Northwestern Basin and Range, Sierra Nevada	Sierra Nevada, Mono
Associated species*	Greenleaf manzanita, bush chinquapin, mountain whitethorn, tobaccobrush, sedges, Ponderosa pine, white fir, lodgepole pine, western juniper, whitebark pine, willow, aspen	Saltbush, greasewood, hopsage, rabbitrush, saltgrass, needlegrass, ricegrass, singleleaf pinyon pine, Utah juniper, limber pine, aspen	Saltbush, greasewood, rabbitbrush, bitterbrush, saltgrass, wheatgrass, ricegrass, western juniper, Ponderosa pine, Jeffrey pine, white fir	Ceanothus, Greenleaf manzanita, canyon live oak, saltbush, singleleaf pinyon pine, Utah juniper (Southeast), Jeffrey pine, white fir
Geomorphology	Block mountain range and accordant crest; large glaciated canyons and valleys	Widely separated ranges and basins; plateaus, alluvial fans, sand dunes; lava flows and cinder cones	Isolated ranges separated by plains; incised canyons and alluvial channels; lava flows and cinder cones	Moderately sloped ridges, isolated ranges, fans, and basins; mass wasting processes dominate
Lithology	Granitic, with some metamorphic, sedimentary, and volcanic rock	Sedimentary, volcanic, granitic rock sources, and alluvium	Alluvium and lacustrine deposits, volcanic rocks	Volcanic rocks and alluvial deposits, with some sedimentary and granitic rock
Growing season	10-200 days	100-275 days	25-150 days	20-200 days
Hydrology	Rapidly flowing streams and rivers	Many water channels terminate in basins; ephemeral channels	Some channels terminating in basins; numerous lakes	Rapidly flowing streams and rivers
Disturbances (non-fire)	Seismic activity with ground shaking; avalanche, wide variation in annual precipitation	Flash floods associated with irregular precipitation; landslide; volcanic and seismic activity	Irregular precipitation, varying lake levels	Seismic and volcanic activity, wide variation in annual precipitation
Land Use	Grazing, mining, recreation	Grazing, motorized recreation, military testing	Grazing, agriculture, forestry	Grazing, mining, recreation

*Species include Greenleaf manzanita (*Arctostaphylos patula*), bush chinquapin (*Chrysolepis sempervirens*), mountain whitethorn (*Ceanothus cordulatus*), tobaccobrush (*Ceanothus velutinus*), sedges (*Carex* spp.), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), western juniper (*Juniperus occidentalis*), whitebark pine (*Pinus albicaulis*), willow (*Salix* spp.), aspen (*Populus tremuloides*), saltgrass (*Distichlis spicata*), needlegrass (*Stipa* spp.), limber pine (*Pinus flexilis*), wheatgrass (*Agropyron* spp.), canyon live oak (*Quercus chrysolepis*). Scientific names for remaining taxa given in the text.

Table 5. Variables included in NRV analysis for sagebrush, and confidence level for comparison of current conditions to NRV period. Determinations for current conditions as within the NRV (Yes/No) are specifically with reference to pre-settlement conditions (1500-1850 AD). Refer to the notes column and discussion for variability over the entire Holocene. Abbreviation: CC = Current Conditions

Ecosystem attribute	Indicator Group	Indicator	Variable	Within NRV	Notes	Confidence
Function	Succession	successional patterns	qualitative	No	Due to presence of grazing	High
Function	Migration	migration patterns	qualitative	Yes		High
Function	Invasion	invasion patterns	number, cover, and extent of invasives	No	Refers to herbaceous invasions	High
Function	Hydrology	stream incision	length, number	Yes	Stream incision similar to Little Ice Age, but CC with different causes	Moderate
Function	Nutrient cycling	nutrient cycling rates	qualitative	No	Due to grazing	Moderate
Function	Disturbance	fire return interval (FRI)	years	Variable	Depends on type – See text	Moderate
Function	Disturbance	fire severity	categorical	Yes		Moderate
Function	Disturbance	fire season	time of year	No	CC within NRV for Med. Warm Per.	High
Function	Disturbance	grazing utilization	utilization	No		High
Function	Disturbance	wind	extreme events	Yes		Moderate
Function	Disturbance	insects	type, acres	Yes		Moderate
Function	Disturbance	disease	type, acres	Yes		Moderate
Function	Disturbance	flood, debris flows	frequency, acres	No	CC within NRV for Med. Warm Per.	Moderate
Function	Disturbance	extreme climate events	type, frequency	No	CC within NRV for Holocene	Moderate
Function	Disturbance	volcanism	frequency	Yes		High
Function	Disturbance	land conversion/agriculture	type, acres	No		High
Structure	Biogeography	extent of hybrid taxa	acres	?		Low
Structure	Physiognomy	tree density and cover	no. trees per area	No	See text for similarities between CC and Holocene	Moderate
Structure	Physiognomy	growth form ratio (forest:non forest)	proportion	No	See text for similarities between CC and Holocene	High
Structure	Physiognomy	growth form ratio (perennial:annual)	proportion	No		High
Structure	Physiognomy	growth form ratio (woody: herbaceous)	proportion	No	CC within NRV for Med. Warm Per.	Moderate
Structure	Physiognomy	number of invasives	no. of spp.	No		High
Structure	Physiognomy	cover of invasives	% cover	No		High
Composition	Biogeography	geographic distribution of major species	extent, acres	Yes		High
Composition	Species diversity	species richness	no. of spp.	Yes	Yes at landscape scale; unknown at community scale	High
Composition	Species diversity	species diversity	index	Yes	Yes at landscape scale; unknown at community scale	Moderate

Table 6. Changes in climate and hydrology during the Holocene, and associated ecological changes. Refer to the Pinyon-Juniper chapter for further detail on ecological changes in that type. Abbreviations GB = Great Basin; SN = Sierra Nevada; PJ = pinyon-juniper; veg = vegetation.

Time period	Climate and geomorphology	Ecological change/event	References
Early Holocene (10000-6900 ybp)	• Precip mainly in winter; modern lakes higher, often connected (Carson basin, Walker Lake) • Trend is toward drying, but variation in aridity debated • Climate changes through Holocene reflected in alluvial fan development, with more aridity and less vegetation on fans than previous period • Great Basin floodplain aggradation	• Sagebrush pollen peaked in SN at 10K; sagebrush and alpine veg dominated over 1495 m (4900 ft) on E and W side of SN, and sagebrush and other GB shrubs were in central valley • Treeline depressed by 1000 m in SN relative to today at beginning of Holocene – this means the 'upper' sagebrush belt would have been larger, but the 'lower' belt below PJ would have been smaller • Sagebrush, saltbush, mt. mahogany (*Cercocarpus* sp.), bitterbrush, bursage (*Ambrosia* sp.) increase at Mono Lake and Owens Valley • Relative proportion of sagebrush to desert species, such as saltbush, and to PJ decreased • Utah juniper limited to Mojave and southern GB at beginning of Holocene, and appeared in White Mts. around 8000 ybp • White Mts. midden from 8790-7810 ybp similar to current community, now pinyon pine-black sagebrush-bitterbrush-mt. mahogany, except middens lack latter 2 species • As warming progressed, veg moved N and upward in GB; conifers replaced by sagebrush from Owens Valley to Lake Tahoe; formation of 'lower' sagebrush belt takes shape, below the elevation of conifers; Mojave species replace lowermost sagebrush • Alabama Hills – juniper and pine replaced by mt. mahogany, bitterbrush, ephedra, saltbush, ambrosia, and other desert species, e.g. boxthorn (*Lycium* sp.), hopsage (*Grayia* sp).; no lower sagebrush belt	Anderson 1990, 2004 Brunelle & Anderson 2003 Davis 1982 Harvey et al. 1999 Jennings & Elliott-Fisk 1993 Lyford et al. 2003 Mehringer 1985 Miller et al. 2004 Tausch et al. 2004 Woolfenden 1996

Mid Holocene (6900-3200 ybp)	• Early Mid - precip shifts to summer; mudflows frequent, larger; soil horizonation, depositing salt, carbonate • Mid – Xerothermic/ Hypsithermal - drier, warmer; lakes desiccated, Lake Tahoe dropped; eolian processes increased • Late Mid - Neoglacial - wettest Hol. period; more freeze-thaw and colluvium, alluvial fan deposits; more precip in winter	• Western juniper reached NE CA • Xerothermic - Desert shrubs expanded; greasewood and saltbush replaced sageb rush/juniper near Fallon, NV; treelines up to 500 m higher than present; sagebrush increased in mid elevation forests • Decline in Native American activity in GB during Xerothermic droughts • 5640 ybp there was PJ near head of Silver Cyn in Whites, where limber pine-bristlecone pine now occur • Neoglacial – PJ in GB and western juniper in north expanded at low to mid elevations to similar extent seen today • Grass:sagebrush ratios were higher during wetter periods • Increase in herbaceous understory in wetter periods correlated to fire	Anderson 1990, 2004 Antevs 1938 Brunelle & Anderson 2003 Davis 1982 Lyford et al. 2003 Miller & Wigand 1994 Tausch et al. 2004 Wigand 1987 Wigand et al. 1995 Woolfenden 1996
Late Holocene (3200 ybp-present)			
2600 -2000 ybp	• Shift from moist/cool to dry (temp uncertain)	• Climatic fluctuations marked by changes in alluvial fan formation and geographic range of desert species within sagebrush zone	Mensing et al. 2006 Miller et al. 2004
Medieval warm period 1000-800 ybp; 1000-1200 AD	• Steady trend toward warming and drying following Neoglacial, culminates in Medieval warm period • Droughts confirmed by submerged trees in Lake Tahoe; Mono Basin drought; fires followed by debris flows in east subregion • Shift in seasonality of precip with greater proportion in late spring and summer	• Woodlands contracted, including juniper • Desert shrub communities expanded, including saltbush • Coarse:fine charcoal ratio dropped, indicating shift to finer fuels • Grass:sagebrush ratio decreased • Wetlands contracted, water levels and aquatic macrofossils decreased	Davis 1982 Tausch et al. 2004 Wagner et al. 2012 Wigand 1987 Wigand et al. 1995
Little Ice Age 1550-1850 AD	Precip shifted to winter; cooler, moister; glaciers began to reform in SN; higher lake levels; stream incision	• Sagebrush and grass increased; desert shrubs decreased • Treelines depressed, including White Mts. • Utah juniper expanded in NW GB; pinyon pine expanded to lower areas previously dominated by Utah juniper	Bauer & Weisberg 2009 Davis 1982 Lyford et al 2003 Miller et al. 2004 Tausch et al. 2004 Wigand 1987
1850 AD-present	Streamflow in increased in winter and spring, snowpack declined; stream channels widen, more soil erosion; low precip 1870-1904, high 1905-1930, low 1931-1955 in W GB	• PJ expanded into sagebrush, mainly at middle and low elevations • Conifers encroached into upper sagebrush zone • Saltbush expanded in lower sagebrush zone • Grass:sagebrush ratio lower than Little Ice Age • Expansion of western and Utah juniper greatest in early 1900s	Antevs 1938 Burkhardt & Tisdale 1976 Chambers 2008 Johnson & Miller 2008 Robertson & Kennedy 1954 (See text for veg references)

Table 7. Fire return interval (FRI) data (years) for sagebrush from peer-reviewed literature.

Mountain big sage-brush	**Grasslands with patches of mountain big sagebrush***	**Low sagebrush**	**Black sagebrush**	**Wyoming sagebrush**	**Silver sagebrush**	**Reference**
10-40						Arno & Gruell 1983
70-200	35-100	325-450		100-240		Baker 2006
150-300	40-230	>200		200-350		Baker 2009, 2011
30-40						Burkhardt & Tisdale 1976
10-40						Houston 1973
3-54						Miller & Rose 1999
12-25						Miller & Tausch 2001
10-20						Miller et al. 2001
15-85		35-115	35-115		15-65	Van DeWater & Safford 2011
				60-110		Whisenant 1990
40-80 (10-40 for historic grassland)						Wright & Bailey

*Sagebrush intermixes with forest

Table 8. Structural attributes for sagebrush systems based on a southeastern California dataset (Slaton 2013). Cover values are aerial cover for vegetation, and ground surface cover for other attributes. Species richness is number of species per 0.04 ha (0.1 acre) plot.

		% Cover															
Subregion	**Type**	**Bare ground**	**Gravel**	**Rock**	**Fine Litter**	**Coarse woody debris**	**Conifer**	**Shrub**	**Forb**	**Graminoid**	**Sagebrush**	**Sagebrush height**	**% of sagebrush canopy dead**	**Shrub species richness**	**Forb species richness**	**Graminoid richness**	**Total species richness**
East	Low sagebrush	14.4	66.0	5.6	1.8	0.2	0.0	14.2	7.8	4.6	10.2	13.8	15.0	4	10	4	18
East	Silver sagebrush	22.1	20.0	0.0	35.7	0.0	0.0	40.0	5.6	52.9	26.0	41.7	13.2	2	4	5	11
East	Black sagebrush	13.0	61.0	8.2	17.4	0.0	0.0	27.0	2.6	1.4	17.6	43.4	14.2	5	3	3	11
East	Mountain big sagebrush	22.7	36.1	20.6	17.0	0.0	0.2	25.9	5.4	8.1	19.7	55.4	20.2	6	7	3	17
East	Sagebrush-bitterbrush	24.3	28.6	1.8	37.7	0.8	0.1	40.4	10.0	9.9	20.0	60.5	31.2	6	8	3	16
East	Basin big sagebrush	32.1	38.8	0.2	26.6	0.2	0.0	26.1	13.8	11.6	20.4	87.5	30.0	4	6	2	11
South	Low sagebrush	1.0	75.0	0.0	10.0	0.0	0.0	25.0	1.0	4.0	20.0			4	7	4	15
South	Black sagebrush	43.7	36.7	8.3	10.7	0.0	0.0	23.3	5.7	8.3	6.7	25.3	10.0	8	11	4	22
South	Silver sagebrush	21.3	36.7	0.7	18.7	0.0	0.0	17.7	11.3	52.3	17.3	27.0	4.7	1	9	4	15
South	Mountain big sagebrush	19.0	38.4	12.6	27.2	0.1	0.0	40.9	5.1	11.3	11.9	64.6	20.2	7	9	3	19
South	Sagebrush-bitterbrush	15.6	31.8	11.4	37.4	0.1	0.0	45.3	2.7	10.7	16.9	56.2	13.1	6	4	3	13
South	Basin big sagebrush	10.0	47.5	16.5	23.0	0.1	0.0	40.0	1.1	11.0	25.0	128.5	25.0	7	6	4	17