

Historic Range of Variability for Meadows in the Sierra Nevada and South Cascades

Shana Gross, Ecologist, Lake Tahoe Basin Management Unit
Michelle Coppoletta, Ecologist, Sierra Cascade Province

U.S. Department of Agriculture, Forest Service,
Pacific Southwest Region, Ecology Program



April 2013

Table of Contents

SUMMARY OF NRV DEVIATIONS	1
INTRODUCTION	2
Physical setting and geographic distribution	2
Historical development	5
Ecological Setting	7
Cultural/Socioeconomic setting.....	8
Pre-Historic (prior to 1849 and extensive European-American influence)	8
European-American Settlement and National Forest Administration (after 1849)	9
METHODS	11
Analysis of NRV.....	14
Analysis of Current Conditions and Comparison with the NRV.....	14
Analysis of Future Conditions	14
KEY INDICATORS OF NATURAL RANGE OF VARIATION.....	15
Function	15
Fire	15
Grazing.....	24
Hydrologic Regime.....	27
Structure.....	33
Upland Species Invasion.....	33
Distribution and size of meadows – Meadow Hectares Natural Range of Variation	38
Productivity – Herbaceous biomass.....	43
Composition.....	44
Functional Group Physiognomy – Life Form.....	44
Functional Group Physiognomy – Wetland Indicator	47
Species Diversity	49
ACKNOWLEDGEMENTS.....	53
LITERATURE CITED.....	53

SUMMARY OF NRV DEVIATIONS

In general, there is very little information on the Natural Range of Variation (NRV) for meadows. However, based on the literature, contemporary studies, and historic accounts, we were able to make some inferences about the NRV for a subset of indicator variables. Seventy percent of the determinations presented in this document were made with low confidence (or no confidence for unknown variables). Determinations for the following five variables were made with high confidence: grazing intensity, grazing utilization, number of dams, hectares of meadow, and number of non-native species. Of the 20 indicator variables assessed for meadows, four are considered to be within the NRV (20%), 13 are outside of the NRV (65%), and a determination could not be made for the remaining three (15%). The following summarizes the main findings of this assessment:

- The processes that are controlling the variability within meadows have been altered.
 - Due to fire suppression activities, the fire return interval is longer than the NRV. The fire season has been extended due to human caused ignitions; however, fire severity is still within the NRV because fuel loading in meadows has not significantly changed.
 - The intensity and utilization of meadows by grazing animals increased with the introduction of livestock.
 - While large floods are still within the NRV, the frequency of smaller annual flooding of meadows is likely outside of the NRV; this is due to the frequency of incised streams, dams, and gully formation being outside of the NRV.
- These altered processes have changed meadow structure and composition.
 - The total area of meadows within the assessment area has decreased due to anthropogenic impacts on ecological processes. Meadow area has also decreased with the increasing abundance of conifers, which has moved outside of the NRV due to grazing and fire suppression coupled with increases in temperature.
 - Disruptions to the hydrologic regime, in combination with changes in climate compared to the principal reference period, has likely decreased the abundance of wetland plant species; however, the abundance of species is likely within the NRV for the entire Holocene.
 - While the overall biomass in meadows is within the NRV, species diversity of plants and animals is outside of the NRV due to current rates of extinctions and the introduction of non-native invasive plant species.
- Future changes in climate (i.e., increasing temperatures) combined with a change from a snow-dominated to a rain-dominated system will impact meadows due to changes in the hydrologic regime. Total meadow area may decline, and wet meadows may shift to dry meadows, especially small irregularly shaped meadows at low to mid elevations.

INTRODUCTION

Meadows are classified based on multiple environmental factors that include hydrology, vegetation, soil characteristics, geomorphology, physiography, altitude, and range type (Klikoff 1965, Benedict and Major 1982, Ratliff 1982, Ratliff 1985, Weixelman et al. 2011). For this assessment, meadows were broadly defined as groundwater-dependent ecosystems composed of one or more herbaceous plant communities, where woody vegetation is often present, but not dominant (Weixelman et al. 2011). Meadows in the assessment area include wetland areas; however not all meadows are wetlands (Weixelman et al. 2011). Meadows fall along a hydrologic gradient of wet to dry. Peatlands are at the wettest end of this hydrologic spectrum, occurring primarily as fens in the assessment area. Peatlands are wet meadows that are characterized by organic soils (histosols) that develop at a greater rate than they can decompose, forming “peat”. Dry meadows occur in the most arid topographic positions (Klikoff 1965) and are primarily precipitation-dependent (Weixelman et al. 2011). In general, wet meadows tend to have lower amounts of bare soil compared to dry meadows that have a wider spacing of vegetation and more exposed soil (Klikoff 1965).

Physical setting and geographic distribution

Meadows are groundwater-dependent ecosystems that are found throughout the Sierra Nevada bioregion, Modoc Plateau, and Great Basin (Figure 1). They occur across a wide range of latitudes, elevations and topographic positions and are interspersed throughout almost every dominant vegetation type. Within the assessment area, meadows generally occur between 280 and 3,935 meters (918-12,910 feet) in elevation and range in size from more than a thousand hectares to just a few square meters (Table 1) (Allen 1987, Fryjoff-Hung and Viers 2012). Meadows in the Sierra Nevada are found in areas with impermeable bedrock, where recessional or lateral moraines have formed dams, in sloped areas with seeps or springs, at the base of alluvial fans or low points in valleys, and along stream channels or lake shores (Benedict and Major 1982, Weixelman et al. 2011).

Meadows develop in areas where there is a shallow water table and an accumulation of fine-textured soils, often with rich organic layers that are needed to draw water to shallow rooted meadow plants by capillary rise (Wood 1975, Ratliff 1985, Weixelman et al. 2011). Meadows are often found at the contact between different geologic units causing meadow sediments to be derived from multiple parent materials. Colluvium, alluvium, and glacial drift (Quaternary sediments) form the basin fill material that provides the meadow substrate and overlays bedrock. The dominant underlying geologic material found within the assessment area is plutonic, which includes granitic rock (Table 2). In general, soil derived from plutonic rock has coarser grains, leading to a lower infiltration rate and lower water holding capacity compared to finer grained soils derived from volcanic rock (Viers et al. 2013). Quaternary sediments, sedimentary, and metamorphic derived soils all have variable water holding capacity; in general, the quaternary sediments derived from plutonic and/or volcanic rocks tend to have more nutrients present compared to older sedimentary rocks. Topography and surface-water hydrology

determine whether or not fine-grained soils are deposited and retained in stream valleys. Stream gradient, upstream drainage area, and to some extent the width of the valley floor, determine flow. Once a graded surface is formed it is the shallow groundwater system that determines whether or not a meadow can develop (Wood 1975).



Figure 1. Distribution and extent of contemporary meadows in the Sierra Nevada and Southern Cascade Range based on Fryjoff-Hung and Viers (2012).

Table 1. Contemporary meadow area in hectares (ha) in the assessment area (Figure 1); summary statistics provided for sub-regions as well as across the entire assessment area (AA). Data is based on Fryjoff-Hung and Viers (2012). Nineteen of the polygons overlap two sub-regions causing individual hectares to total 902 ha more than the total for the entire AA.

Meadow Summary Statistics (ha)	Entire AA	North AA	Central AA	South AA	East AA
Minimum	0.4	0.4	0.4	0.4	0.4
Maximum	1865.8	1434.6	533.0	1865.8	1378.4
Mean	4.6	8.6	4.1	3.6	15.1
Median	1.3	1.7	1.3	1.1	2.5
Sum – Total Area	77658.9	17428.2	27577.9	29582.1	3967.5
Number of polygons	17039	2015	6665	8115	263

Table 2. Dominant underlying geologic material in the assessment area (Figure 1); area (hectares) provided for sub-regions as well as across the entire assessment area (AA). Data is based on Fryjoff-Hung and Viers (2012). Twenty-seven rock types were lumped into the six broad categories presented, water was identified as undetermined because the scale of the geology layer used was larger than the 1-acre cutoff used for the meadow layer, therefore water might not be a true representation of what underlies the meadows. The primary rock type found in plutonic was granitic. Nineteen of the polygons overlap two sub-regions causing individual hectares to total 902 ha more than the total for the entire AA.

Dominant Underlying Geologic Material	Entire AA	North AA	Central AA	South AA	East AA
Igneous – Plutonic	47860	9057	19773	19212	283
Quaternary Sediments	21665	7093	5227	6741	2986
Igneous - Volcanic	3475	328	748	2007	434
Metamorphic	2597	263	1757	590	0
Undetermined (water)	1762	480	69	952	260
Sedimentary	297	207	7	79	5

Sierra Nevada meadows are groundwater-dependent ecosystems that rely on the persistence of a shallow water table, generally at a depth of less than one meter, throughout the growing season (Wood 1975, Ratliff 1985, Lowry et al. 2011, Weixelman et al. 2011). In addition to groundwater, other important sources of water for meadows include surface flow, springs, seeps, and precipitation (Weixelman et al. 2011). The geomorphology of a site controls where the water comes from and when it leaves a meadow (Weixelman et al. 2011). Groundwater recharge occurs at both the landscape scale (e.g., fed from the surrounding watershed snowmelt) and local scale (e.g., when a stream is present the stream recharges the meadow) (Loheide et al. 2009). The amount, source, and duration of water influence the composition and structure of meadow vegetation.

The assessment area is characterized by a Mediterranean climate with warm, dry summers and cool, wet winters. Meadows along the western slopes are windward receiving greater precipitation compared to leeward eastern and Modoc Plateau meadows (Viers et al. 2013). The exception is the Modoc Plateau which is considerably drier than the other northern sections of the assessment area. High elevation (greater than 3000 meters) and mid-elevation (between 2000-3000 m) meadows receive the majority of precipitation as snow, while low elevation meadows (less than 2000 m) receive the majority of precipitation as rain (Loheide et al. 2009, Viers et al. 2013).

Historical development

Throughout the Holocene, meadows in the assessment area have developed, disappeared, and redeveloped in the same location (Wood 1975, Anderson and Smith 1994, Koehler and Anderson 1994). While some meadows in the Sierra Nevada have developed through typical successional patterns (i.e., from lake to marsh to meadow), it is widely believed that many contemporary meadows developed abruptly as a result of hydrologic changes brought about by major climatic variation, including deglaciation (Wood 1975) or aggradation of the land surface and lifting of the water table (Ratliff 1985). In the Great Basin most wet meadows are found upstream of alluvial fans that cross the valley floors (Miller et al. 2001). Climate influences meadows directly through modification of water tables and indirectly through encouragement or deterrence of episodic tree invasion (Bartolome et al. 1990, Fites-Kaufman et al. 2007).

Evidence of meadow formation first appears in the sediment and pollen record of contemporary meadows between 12,500 and 8,000 years before present (YBP) (Figure 2) (Wood 1975, Bartolome et al. 1990, Koehler and Anderson 1994, Edlund and Byrne 1991 in Woolfenden 1996) This time period marked the transition from cooler and wetter conditions in the Sierra Nevada to a predominantly warmer and drier climate (Koehler and Anderson 1994, Kinney 1996, Parker 2002). Warming temperatures, beginning ca. 10,000 YBP, resulted in decreases in effective moisture; as a result, ecosystems across the Sierra Nevada began to change rapidly (Woolfenden 1996). Reconstructions of meadow vegetation during this time period suggest that some wet meadows in the Sierra Nevada were invaded by conifers as the depth of the water table dropped and meadows became drier (Figure 2) (Wood 1975, Koehler and Anderson 1994).

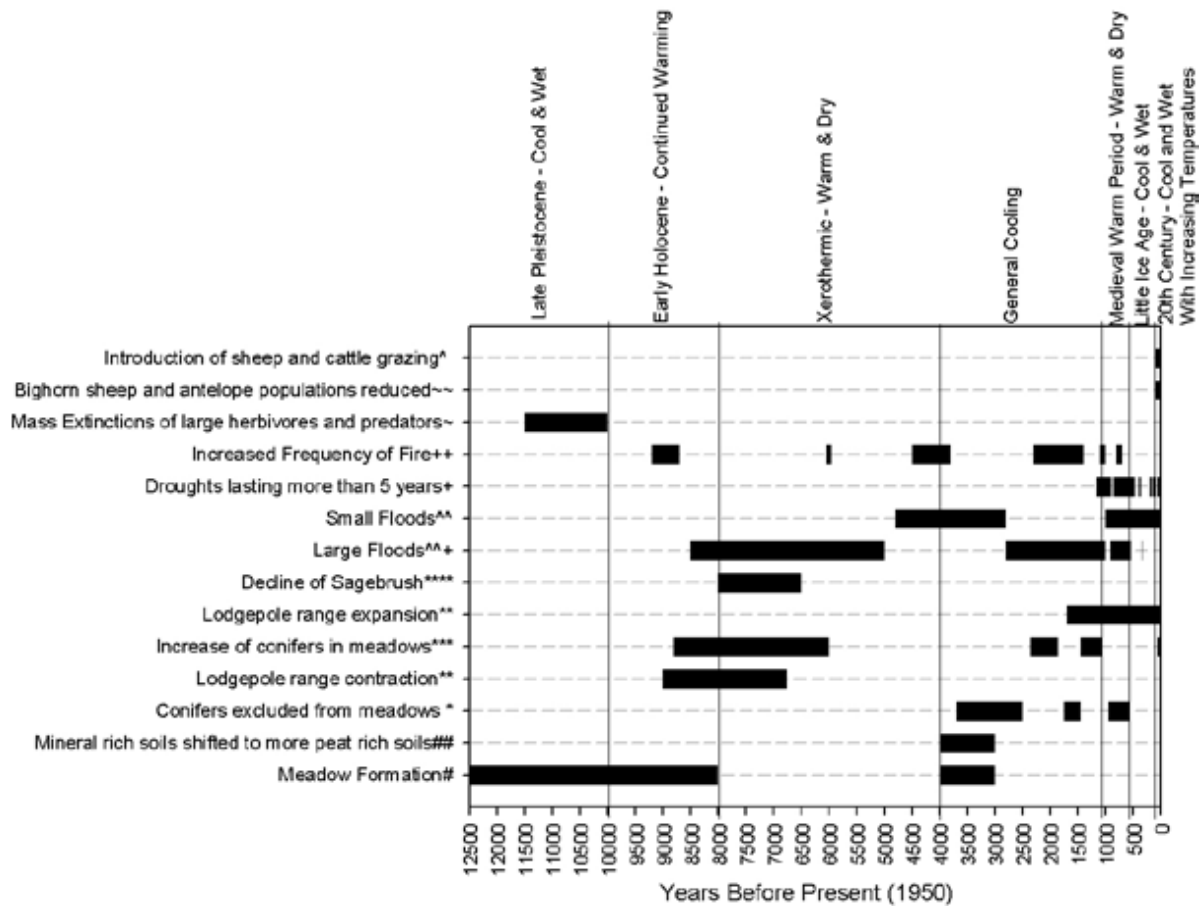


Figure 2. Timeline of meadow development and disturbance. All dates have been adjusted to years before present so that they can be displayed on the same timeline; dates are approximate values based on published dates and do not necessarily correspond to carbon 14 dates: #Wood 1975, Bartolome et al. 1990, Koehler and Anderson 1994, Edlund and Byrne 1991 in Woolfenden 1996, Parker 2002; ##Wood 1975, Anderson and Smith 1994; *Anderson 1987, Anderson and Smith 1994, Parker 2002, Llyod and Graumlich; **Anderson 1996; ***Wood 1975, Koehler and Anderson 1994, Vankat and Major 1978, Lloyd and Graumlich 1997, Millar and Woolfenden 1999, Norman and Taylor 2005; ****Anderson 1987; ^^+Carson et al. 2007, Austin 2012; ^^Carson et al. 2007;+Graumlich 1993, Austin 2012; ++Anderson and Smith 1997;~Wagner 1989, Edwards 1992; ~-Buechner 1960, Edwards 1992, Dull 1999;^Allen-Diaz 1991, McKelvey and Johnston 1992.

The development of most contemporary meadows in the Sierra Nevada coincided with the onset of the Neoglacial period, which occurred between ca. 4,000 and 3,000 YBP and was characterized by cooler and wetter climatic conditions (Figure 2) (Parker 2002). During this time period, some meadow sites exhibited a shift from predominantly mineral sediments to peat-rich biogenic soils (Figure 2) (Wood 1975, Anderson and Smith 1994). This transition to peat is suggestive of widespread changes in the hydrologic regime, with increased effective precipitation resulting in greater soil moisture and higher ground-water tables in meadows (Wood 1975, Anderson and Smith 1994, Kinney 1996, Parker 2002). Higher ground-water tables could have excluded upland woody species from meadows, resulting in a shift from forest to meadow vegetation (Wood 1975, Anderson and Smith 1994). Cooler temperatures and increased available moisture have been linked with increases in meadow vegetation during this time period (Anderson and Smith 1994, Koehler and Anderson 1994).

Ecological Setting

While meadows cover less than one percent of the Sierra Nevada, these ecosystems are of great ecological importance (Fryjoff-Hung and Viers 2012). The ecological significance of meadows is closely tied to the individual meadow setting and hydrologic controls (e.g., more groundwater present in wet versus dry meadows). Meadow ecosystems store high amounts of soil carbon and nitrogen relative to other terrestrial ecosystems (Norton et al. 2011). They can help mitigate the effects of anthropogenic nitrogen deposition (Norton et al. 2011), reduce peak water flow after storms and during runoff, recharge groundwater, protect stream banks and lake shores, filter sediments, reduce sedimentation in lakes, provide forage and offer numerous recreational opportunities (Ratliff 1982, Weixelman et al. 2011). Meadows are important refugia for aquatic invertebrates, fish, amphibians, mammals, birds, and plants. Animals use meadows for water, food, and cooler temperatures during hot dry summer months (Knopf and Samson 1994, Kattelman and Embury 1996).

Local hydrology is the most important factor influencing vegetation patterns within meadows (Allen-Diaz 1991, Kim and Rejmankova 2001, Loheide et al. 2009). Sediment heterogeneity and meadow stratigraphy influence local site groundwater patterns, which in turn influence plant communities (Loheide and Gorelick 2007). In the Sierra Nevada peatlands can develop as a result of springs, the location and/or volume of which can shift due to seismic activity (Bartolome et al. 1990). In addition to local hydrology, a range of other environmental factors control the distribution of vegetation within meadows, including soil moisture, soil texture (Dodd et al. 2002), soil pH (Chytrý et al. 2003), redox conditions (Howes et al. 1981), nutrients (Tilman 1987), and elevation (Loheide et al. 2009).

Water table depth is a primary determinant of the vegetation community; a shallower water table regime supports wet meadow vegetation, and a deeper water table supports xeric vegetation (Allen-Diaz 1991, Dwire et al. 2006, Lowry et al. 2011). Loheide et al. (2009) found that the minimum water table depth and the number of days that the water table is within 30 cm of the surface were the strongest hydrologic correlates for the vegetation community within a meadow. Meadow species are controlled by early

growing season wetness, which is not suitable for upland species because of waterlogged anaerobic conditions; these conditions provide sufficient moisture later in the growing season to support growth and reproduction of wet meadow species (Loheide et al. 2009), which have evolved to thrive in shallow water table conditions.

Cultural/Socioeconomic setting

The biological diversity and richness of meadows in the assessment area has attracted humans for thousands of years. In order to understand the composition, structure, and function of meadow ecosystems at a specific time in history, it is necessary to distinguish the effects of past human use from the effects of the physical environment, climate, and natural processes (Anderson and Moratto 1996).

Pre-Historic (prior to 1849 and extensive European-American influence)

Humans have inhabited the Sierra Nevada bioregion for the past 10,000 years (Anderson and Moratto 1996). Over this time period, human population sizes have fluctuated in response to climatically induced changes in available food and water supplies. As a result, land-use and resource-management activities have also varied with periods of intense activity interspersed with periods of lower populations and reduced land use (Parker 2002).

At the time of European-American contact, indigenous people of the Sierra Nevada were organized into numerous, distinct populations that ranged in geographic distribution from the low elevation foothills to the high Sierra (Parker 2002). Permanent settlements supported dozens to hundreds of inhabitants and were generally concentrated at lower elevations on the western slope (Parker 2002) and the eastern slope (Steward 1933). In the warmer months, villages were often abandoned for small, temporary camps at higher elevations (Anderson and Moratto 1996). Both permanent and temporary camps were often situated in close proximity to streams, springs, and meadows.

Native Americans in the Sierra Nevada sustained themselves through hunting, fishing, and gathering, which they augmented by protecting, encouraging, and cultivating wild plants (Anderson and Moratto 1996). Plant material was also gathered for firewood, crafts, and building materials (Anderson and Moratto 1996). To obtain and sustain these resources, Native Americans employed a variety of management practices that included burning, irrigating, pruning, selective harvesting, sowing, and weeding (Anderson and Moratto 1996). One of the most significant and widely employed indigenous management tools was fire (Anderson and Moratto 1996). Native Americans often preferentially burned Sierra Nevada meadows and other riparian areas to clear brush and young trees (Anderson and Carpenter 1991, Anderson and Moratto 1996); maintain patches of bulbs, corms, tubers, and other edible species (Anderson 1994, Anderson and Moratto 1996, Anderson 1997); and improve forage for wildlife (Anderson and Moratto 1996, Norman and Taylor 2005). In some cases, meadow fires were followed up with hand pulling of young trees if burns were not effective (Ernst 1949). The ecological effect of these management practices on Sierra Nevada meadows likely varied in both time and space and was often

dependent upon the tribe and cultural objective.

While it is known that Native Americans used fire to modify Sierra Nevada ecosystems, the spatial extent and ecological importance of this practice is an issue of debate (Skinner and Chang 1996, Parker 2002). Physical evidence of burning by Native Americans is generally rare, particularly in meadow ecosystems where it is difficult to establish an accurate fire history because herbaceous plants generate very little macroscopic charcoal (Skinner and Chang 1996, Parker 2002). There are also very few case studies that have been able to effectively link vegetation shifts to Native American fire management. In one study of Woski Pond in Yosemite Valley, Anderson and Carpenter (1991) were able to link a spike in charcoal accumulation, an indicator of fire occurrence, with the arrival of the Miwok culture around AD 1300; however, they were not able to ascertain whether the source of ignition was human-related, or lightning caused. They conclude that ethnographic evidence, coupled with incongruent responses to climate strongly suggest that the maintenance of more open, herbaceous vegetation in Yosemite Valley was maintained by cultural burning.

The degree to which Native Americans have altered Sierra Nevada ecosystems, and meadows in particular, is largely unknown. Anderson and Moratto (1996) have argued that prior to European-American contact, Sierra Nevada ecosystems had been shaped by thousands of years of management by indigenous populations. However, Parker (2002) states that these impacts would have been highly localized (i.e., around permanent settlements or frequently used camp sites) and argues that there is little evidence to suggest that Native American management practices moved Sierra Nevada vegetation to a condition outside of the historical range of variability. Instead, Parker (2002) suggests that the “natural variability of climate change, the operation of disturbance regimes, and the landscape scale complexity of physical gradients in the Sierra Nevada would be sufficiently broad enough to incorporate most indigenous human influence within the embrace of natural patterns”.

European-American Settlement and National Forest Administration (after 1849)

The meadows of the Sierra Nevada were dramatically altered by European-American settlers in the latter half of the nineteenth century. One of the most ubiquitous impacts was grazing of Sierra Nevada meadows by sheep and cattle (Figure 3) (Ratliff 1985, Kinney 1996). The early 1860s ushered in an era of intensive livestock use in Sierra Nevada meadows (Figure 2) (Allen-Diaz 1991, McKelvey and Johnston 1992). Increasing human populations, combined with wide scale drought in the 1860s and 1870s, resulted in summer grazing of montane meadows where livestock could take advantage of abundant forage and water (Kosco and Bartolome 1981, Ratliff 1985). Meadows at all elevations, including those in remote locations, were impacted as cattle and sheep were driven virtually everywhere that forage was available (McKelvey and Johnston 1992, Kinney 1996, Menke et al. 1996). Between 1860 and the early 1900s, the number of sheep using meadows in the Sierra Nevada was estimated in the millions (Douglass and Bilbao 1975 in Beesley 1996). In the absence of adequate management controls, livestock overgrazed many of the meadows in the Sierra Nevada (Gruell 2001). Descriptions of grazing

impacts in meadows prior to 1949 are present in much of the historical literature (Vankat and Major 1978, McKelvey and Johnston 1992). In a description of his ascent of Mt. Whitney in 1885, T. Magee noted:

“Mountain meadows are abundant, but the shepherd and his flocks have more largely worked their ruin in the Whitney region than anywhere else in the Sierra that I have visited. Each of these meadows is yearly cropped several times by various flocks of sheep, and the result is that, even where there was genuine mountain meadow, there are now only shreds and patches. The sod and the verdure are gone – eaten and trodden out; the gravel is now in the ascendant” (as quoted by Vankat and Major 1978 pg. 379).



Figure 3. Domestic sheep graze in the Sierras – USDA-Forest Service.

Impacts of sheep and cattle on meadow systems in the Sierra Nevada extended beyond the effects of herbivory and erosion. To feed the increased numbers of horses and cattle, some wet meadows in the Sierra Nevada were also used for hay production (McMillin 1950, Momsen 1996). In addition, herders utilized fire to encourage the regrowth of grasses and forbs in meadows and forested habitats of the Sierra Nevada (Vankat 1977, McKelvey and Johnston 1992). Grazing remained unregulated until the 1920s, when regulations helped bring livestock numbers within reasonable bounds (Kosco and Bartolome 1981). Current management practices have drastically reduced the number of allotments and

stocking rates on Forest Service lands. The high intensity of grazing over a period of nearly 40 years, combined with repeated burning by herders, likely had a significant and long-lasting impact on the herbaceous vegetation in the Sierra Nevada (McKelvey and Johnston 1992).

Additional impacts to meadows during this period include removal of trees during the gold rush; drainage for railway and road placement; construction of homes; introduction of non-native plant and animal species; surface and groundwater diversions; agricultural conversion; fire suppression; and recreation (Kattelman and Embury 1996). Meadows are often situated in close proximity to recreational facilities such as roads, vacation cabins, campgrounds, and trails (Kattelman and Embury 1996). In the Great Basin, roads have been identified as the most significant anthropogenic factor of stream incision within riparian areas (Chambers and Miller 2011). In combination, these historical impacts have interacted to produce complex effects on meadow function, composition, and structure.

METHODS

The biggest challenge with describing the Natural Range of Variation (NRV) for meadow systems is the lack of quantitative data. There are relatively few studies of meadows compared to forested ecosystems and the dominance of herbaceous vegetation makes some historical analyses (e.g., fire histories based on dendrochronology or charcoal analyses) unfeasible. Historical reconstructions that have been conducted in meadows are often limited in both scope and scale, making landscape-level inferences of NRV difficult. Another large challenge with determining the NRV for meadows is the lack of contemporary reference sites. Almost all of the meadows in the assessment area experienced high levels of historic grazing by livestock, which makes it difficult to determine whether contemporary meadows have returned to their pre-grazing condition (Kondolf et al. 1996). Although not as ubiquitous as grazing, current conditions in some meadows were also influenced by other impacts such as logging, road building, mining, urbanization, water diversions, and fire suppression (Kattelman 1996). This long legacy of land use in meadows limits reference sites to those with few human alterations where livestock grazing has been excluded for at least a few decades (Kattelman 1996). The Forest Service has conducted some monitoring of meadow condition, which has allowed for comparisons between grazed meadows and meadows that have been rested and excluded from grazing; these data have provided some insight into the NRV (Weixelman and Zamudio 2001).

This document is structured by ecosystem attribute: function, structure, followed by composition. Within each of these ecosystem attributes we identified nine indicator groups (e.g., fire, productivity, etc.) and 20 indicator variables (e.g., fire return interval, herbaceous biomass, etc.) (Table 3). We then compare the NRV to current conditions based on the 20 indicator variables.

Table 3. Summary of variables related to meadow vegetation in the assessment area relative to their estimated natural range of variability (NRV) and our confidence in the comparison. NRV is presented here as the overall trend across the landscape; however, NRV may vary from site to site with some meadows falling within the NRV and others outside of the NRV. Principle reference period for the NRV is AD 1600-1850 unless noted in the Notes column of the table.

Ecosystem Attribute	Indicator Group	Indicator Variable	Within NRV	Confidence	Notes
Function	Fire	Fire Return Interval	No	Low	FRI has decreased due to fire suppression activities in vegetation surrounding meadows. Therefore, it is likely that the FRI within meadow interiors has decreased as well.
Function	Fire	Fire Severity	Yes	Low	There is limited information on severity of fires within NRV and current conditions. However, since meadows are herbaceous ecosystems, fuel loading is likely not outside of NRV and therefore severity patterns would be within NRV.
Function	Fire	Fire Season	No	Low	Peak fire season is within NRV, however human ignitions have extended fire season outside of NRV.
Function	Grazing	Intensity – Number	No	High	The intensity of grazing increased with the introduction of livestock and decline of native ungulates; however, un-grazed livestock meadows may still be within NRV.
Function	Grazing	Utilization – Native vs. domestic use	No	High	Where livestock grazing occurs, utilization is higher than the NRV. Livestock tend to congregate in a single area compared to the more dispersed grazing pattern of deer.
Function	Hydrologic Regime	Flood magnitude	Yes	Low	Due to the length of time between mega-floods it is difficult to determine if this attribute is within NRV. It likely is within NRV, but may be trending towards a decrease, due to climate rather than management.
Function	Hydrologic Regime	Flood frequency	No	Low	Annual meadow overland flood frequency may have decreased due to increased stream incision and construction of dams.
Function	Hydrologic Regime	Stream Incision	No	Low	Anthropogenic impacts have caused an increase in the rate of stream incision that is likely outside the NRV.
Function	Hydrologic Regime	Erosion – Gully formation	No	Low	Anthropogenic impacts have caused an increase in gully erosion that is linked to channel incision and is likely outside the NRV.
Function	Hydrologic Regime	Erosion – Hillslope aggradation	Yes	Low	Large scale aggradation from surrounding hillslopes is likely within NRV.
Function	Hydrologic Regime	Number of dams	No	High	Manmade dams have increased the number to outside the NRV

Ecosystem Attribute	Indicator Group	Indicator Variable	Within NRV	Confidence	Pages in discussion	Notes
Structure	Upland Species Invasion	Conifer Abundance	No	Low	20-24	Although forests and meadows have formed a shifting mosaic over centuries, recent encroachment appears more extensive and rapid than what may have occurred during most of the Holocene, potentially from increased grazing and fire suppression.
Structure	Upland Species Invasion	Sagebrush Abundance	?		20-24	Similar to notes under conifer density, however there is less information available for shrubs, therefore a determination could not be made
Structure	Distribution and size of meadows	Meadow Hectares	No	High	24-26	Anthropogenic impacts have contributed to the decline of meadow hectares.
Structure	Productivity	Herbaceous biomass	Yes	Low	26	Photographic interpretation from Yosemite does not show change in biomass (although early photographs are post livestock grazing)
Composition	Physiognomy	Graminoid/ Forb Ratio	?		26-29	There has likely been an increase of forbs and a decrease of graminoids in livestock grazed meadows, however there is not sufficient data to identify if this change is within NRV.
Composition	Physiognomy	Herbaceous height	?		26-29	There has likely been a decrease in height of herbaceous species height; however, there is not sufficient data to identify if this change is within NRV.
Composition	Physiognomy	Wetland Species Abundance	No	Low	26, 29-31	Based on contemporary studies, current climate likely does not support the abundance of wetland species seen during the principal reference period which was cooler and wetter than current conditions. However, the current abundance of wetland species ratio may be similar to the early Holocene and Medieval Warm Period. In addition, anthropogenic disturbance to the hydrologic regime has likely decreased the abundance of wetland species and increased the abundance of upland species.
Composition	Diversity	Species Richness	No	Moderate	31-35	Due to the current rate of extinctions, we are likely not within the NRV – species richness is likely lower than under NRV.
Composition	Diversity	Number of non-native species	No	High	31-35	Non-native invasive species are by definition outside of the NRV – we have therefore seen an increase in the number compared to NRV

Analysis of NRV

Our reference period varied for each variable based on the available data; however, in general the reference period begins at the start of the Holocene, about 12,000 years before present (YBP), and extends to about AD 1850 when European-American settlement began. The principal reference period is from AD 1600-1850, because it is the closest temporal comparison to pre-European settlement. Reconstructions of meadow conditions prior to the 1800s are generally based on analyses of sediment stratigraphy, pollen cores, macrofossils, and charcoal deposits (Wood 1975, Anderson and Smith 1994, Koehler and Anderson 1994). These data provide limited information on the historic extent and formation of meadows, and to a lesser degree meadow species composition. In several instances contemporary conditions were used in place of the principal reference period to determine if current conditions are within NRV; specifics are identified in the text. The limited amount of historic meadow information necessitated the use of contemporary studies of meadow vegetation and hydrology, channel recovery, and succession following fire and other disturbance, to provide inferences into the NRV.

In most cases, inferences about the NRV were based on information specific to meadows and/or riparian ecosystems in the Sierra Nevada, Southern Cascade Range, and a small portion of the Great Basin; however, there were exceptions. For example, inferences about flood magnitudes during the Holocene were based on meadow studies from the Uinta Mountains in northeastern Utah. This study was utilized because, like the assessment area, flood regimes in the Uinta Mountains are influenced by snowpack and spring snowmelt and meadows are underlain by glacial outwash or bedrock (Carson et al. 2007).

Analysis of Current Conditions and Comparison with the NRV

For this analysis, current conditions were defined as those within the last decade, except for those instances where conditions were outside of the NRV due to anthropogenic impacts; for example, if a meadow had a long history of grazing, historical data may have been used as a proxy for current condition. Data on current conditions was limited to information identified during the literature review for the NRV and the professional experience of the authors and is therefore not likely exhaustive. In some instances, current condition data was summarized and is presented (e.g., number of meadow fires between 1908 and 2012). In these cases, the NRV is compared to the current conditions and an inference made as to whether it is within or outside of the NRV. As data on these variables are extremely limited, some of the discussion in this assessment is hypothetical and our conclusions tentative. A level of confidence has been assigned to each statement made in the summary based on the data that was used to derive the NRV; confidence levels assigned include low, moderate, and high (Table 3).

Analysis of Future Conditions

Discussion of future trends in the NRV section is based on future climate predictions and current

conditions; changes in management may also influence future trends, however these were not incorporated into this document. While most climate model projections show increasing temperatures, future precipitation trends are still not resolved (For example: Hayhoe et al. 2004). Although the total amount of future precipitation is unclear, there is general agreement that increasing temperatures will result in more precipitation falling as rain rather than snow. Snowpack is important for meadows in the assessment area because it provides a constant source of ground-water recharge during periods of snowmelt (Viers et al. 2013). The response of individual meadows will depend on the hydrogeomorphology of the meadow and the landscape setting; therefore, our discussion of future condition is generalized across the assessment area.

KEY INDICATORS OF NATURAL RANGE OF VARIATION

Function

Fire

Dendrochronology and stratigraphy are methods commonly used to develop fire histories; however, these methods are not reliable in meadow ecosystems where trees have low, or no cover and herbaceous plants generate very little macroscopic charcoal. As a consequence, the data we do have likely underestimates fire events. Additionally, grazing, which reduces fuel, may confound interpretation of the role of fire in meadows, potentially causing an underestimation of frequency and effect (Fites-Kaufman et al. 2007).

Natural Range of Variation

Fire Return Interval

Fire is a natural occurrence in the vegetation surrounding meadows and although relatively infrequent can also burn within meadow boundaries. Meadows in the assessment area are surrounded by multiple vegetation types; conifer forests are the most common surrounding vegetation type followed by riparian forest (Fryjoff-Hung and Viers 2012). Analysis of the fire return interval (FRI) of these surrounding vegetation types provides some insight into the frequency of fire within meadows. Lodgepole pine (*Pinus contorta* ssp. *murrayana*) is the most common species found in the meadow-forest ecotone and the most common meadow invader (Wood 1975). Lodgepole pine forests have a mean FRI of 37 years, a median of 36 years, a mean minimum of 15 years, and a mean maximum of 290 years (Table 4) (Van de Water and Safford 2011). This varies geographically due to differences in moisture, with longer FRIs in the northern portions of the assessment area compared to the southern areas (Table 5) (Van de Water and Safford 2011).

Table 4. Fire return interval (FRI) for meadows and vegetation types surrounding meadows within the assessment area.

Vegetation Type	Subregion	Mean FRI	Median FRI	Min. FRI	Max. FRI	Years Sampled	Sample Type ¹	Reference
Lodgepole pine forest	Entire AA	37	36	15	290	-	-	(Van de Water and Safford 2011)
Meadow forest ecotone	Northern	-	14	5	28.5	1750-1849	Point	(Norman and Taylor 2005)
Meadow forest ecotone	Northern	10.8	10.5	1	27	1750-1849	Comp.	(Norman and Taylor 2005)
Meadow forest ecotone	Northern	21.4	12	7	49	1680-1849	Comp.	(Norman and Taylor 2003)
Meadow	Central	250-300	-	-	-	1200 YBP*	-	(Wood 1975, Chang 1996)

¹ Refers to whether estimates were derived from a single tree (point) or composite (comp.) sample.

*Fires noted in 1779, 1803, 1842, and 1901

Table 5. Environmental variables associated with riparian areas and their relationship to fire frequency.

Variable	Frequency of Fire	Citation
Stream Size*	Decreases	(Pettit and Naiman 2007)
Soil Moisture*	Decreases	(Pettit and Naiman 2007)
Fuel Moisture*	Decreases	(Pettit and Naiman 2007)
Riparian area surrounded by pine forest	Increases	(Van de Water and North 2010)
Eastside forests [^]	Increases	(Van de Water and North 2010)
Drought*	Increases	(Pettit and Naiman 2007)
Northern California ⁺	Decreases	(Van de Water and Safford 2011)

* Compares fire frequency to increases in these variables.

[^] Compared to west-side forests.

⁺ Compared to Southern California.

During a 100-year period (1750 to 1849) on the Lassen National Forest, individual trees along the meadow edge had a grand median point fire return interval (PFRI) of 9-18 (14) years, with a minimum PFRI of 5 years and a maximum of 29 years (Table 4) (Norman and Taylor 2005). When the individual tree records were combined within a 1-3 ha area, the grand median composite fire return interval (CFRI) was calculated at 10.5 years with a range of 5-16 years (Table 4) (Norman and Taylor 2005). Norman and Taylor (2003) found that on the Lassen National Forest, in the

north-eastern portion of the assessment area fires burned every 7-49 years (1700-1850) along the meadow-forest boundary (Table 4). FRI varied based on a combination of drought, Pacific Decadal Oscillation (PDO), and El Nino Southern Oscillation (ENSO); fires burned following wet-cool years in years that were drier and warmer than normal (Norman and Taylor 2003).

While the FRI of the adjacent upland vegetation provides some information on meadow FRI, riparian areas (which often include meadows) provide additional insight into how meadow fire regimes may differ from surrounding forests. Riparian areas and meadows differ from uplands in their moisture regime, disturbance regime, topography, micro-climate, and vegetation (Pettit and Naiman 2007). In riparian areas, the frequency of fires decreases with increased stream size and increased soil and fuel moisture compared to uplands (Table 5) (Pettit and Naiman 2007). These heterogeneous ecosystems can act as a fire break or as a corridor for fire spread, depending on the conditions (Dwire and Kauffman 2003, Pettit and Naiman 2007). When the surrounding forest is dense with high amounts of fuel, the riparian areas may no longer serve as a natural fuel break (Dwire and Kauffman 2003). In wetter regions the FRI in riparian areas is longer than the surrounding uplands, but in drier forests the FRI is often comparable in riparian and upland forests (Dwire and Kauffman 2003) or more frequent in arid systems (Pettit and Naiman 2007). Fire might occur more frequently in riparian areas surrounded by pine forests in eastside forests where conditions are drier (Van de Water and North 2010), or during periods of drought when decreases in vegetation moisture begin to parallel upland fire regimes (Table 5) (Pettit and Naiman 2007).

It has been suggested that fires were less common in meadows compared to the surrounding forests and where they did occur, they were localized within the meadow (DeBenedetti and Parsons 1979, Millar 1996, Dull 1999). Stratigraphic records from meadows in the assessment area contain some indication of past fires. Repeated evidence of charcoal peaks in meadows in the southern Sierra Nevada represent a pattern indicative of climatic cause (Anderson and Smith 1997, Dull 1999) (Figure 2, Figure 4). The frequency of fires within meadows is expected to be linked to the hydrologic regime where dry meadows burn more frequently compared to wet meadows. In Yosemite and Sequoia National Parks, charcoal layering indicates that meadows burned at least once every 250-300 years (Wood 1975, Chang 1996). It takes a severe fire and wind to deposit significant amounts of charcoal in a meadow from an adjoining forest, therefore charcoal layers may not have captured less severe fires, so these meadows likely burned at a greater frequency (Chang 1996). Historically, burning occurred even in very wet meadows. Bartolome et al. (1990) found the presence of charcoal in a northern Sierra Nevada fen, which indicates at least one major fire about 1190 YBP either in or around the fen. Wood (1975) recognized five major fire episodes in the charcoal stratigraphy of East Meadow in the western Sierra Nevada. All events occurred within the past 1200 years; all seem to indicate forest fires not, in situ burning of the meadow vegetation and peat. Dull (1999) found a charcoal horizon in Monache Meadows (Kern River Plateau) that dates to approximately 370 YBP, which likely represents one or more major forest fire events in the upland areas surrounding the meadow, but there is little evidence that the fire(s) burned the meadow surface.

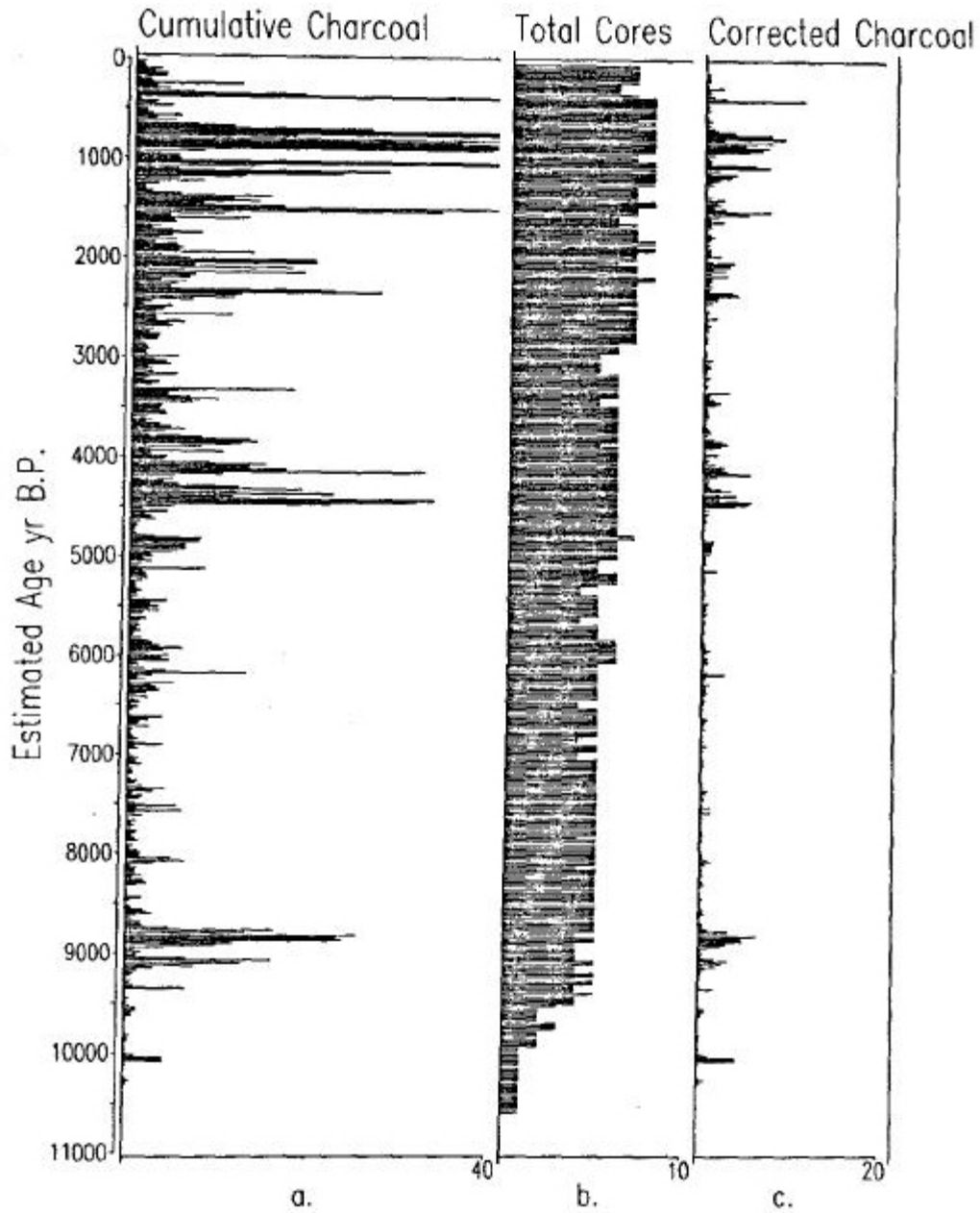


Figure 4. Composite charcoal records from seven meadows in the Sierra Nevada. The northern-most meadow was located in Yosemite National Park and the southernmost meadow was located in Mt. Home State Forest. A) Composite records were developed by summing the 25-year value for each core; b) number of cores that had data for the 25-year period; and c) value of 4a divided by equivalent value of 4b. (Taken from Anderson and Smith (1997) with author's permission)

Fire Severity and Fuel Loading

High fuel moisture content and high soil moisture reduce fire intensity and slow spread (Dwire and Kauffman 2003). Meadows are often dominated by grasses and sedges, which produce a high biomass of fine fuels (Dwire and Kauffman 2003); these are more likely to burn at a lower intensity

compared to woody fuels (Pyke et al. 2010). In meadow valleys protected by slopes, wind speeds may be lower than in surrounding areas, decreasing the fire severity by decreasing the rate of spread, flame length, and intensity (Dwire and Kauffman 2003). Rate of spread is also influenced by the patchiness and density of vegetation and the soil and plant moisture content (Pettit and Naiman 2007). Meadows often contain heterogeneous stands of vegetation, which can contribute to patchy burning (Dwire and Kauffman 2003). All of these factors suggest that interior meadow fires were more commonly of low severity, while the meadow-forest ecotone would have been of higher severity due to higher amounts of woody biomass.

Fire severity studies within meadows are extremely limited. In one study of a 1977 Kings Canyon lightning-caused meadow fire, Debenedetti and Parsons (1984) found that the fire mostly smoldered, with limited areas of high fire severity, and spread at a rate of 0.5 cm/min.

Fire Season

During drier years, meadow fuels dry out making them more susceptible to burning, either by lightning or intentional lighting (Gruell 2001). The timing of fires may have been earlier in surrounding uplands compared to riparian areas and meadows where mesic conditions are maintained into the early summer (Van de Water and North 2010). Meadows may serve as fire breaks until late in the season, with wetter meadows providing fire breaks later in the season than dry meadows (Dwire and Kauffman 2003). Under the NRV, meadow fires occurred predominately during the dormant season after fuels dried out and vegetation senesced. In the northern portion of the assessment area (Lassen National Forest), Norman and Taylor (2003) found that between 1700 and 1849, 57 percent of the fires occurred during the dormant period (late summer/early fall at the end of the dry season), 32 percent occurred in earlywood (spring), and 11 percent occurred in latewood (summer) along the meadow's edge (Figure 5). Between 1750 and 1849 meadow-forest boundary fires on the Lassen National Forest occurred 40 percent in the earlywood, 12 percent in the latewood, and 48 percent in the dormant period (Norman and Taylor 2005). In addition to lightning fires, Native Americans may have ignited fire during fall hunting (Debenedetti and Parsons 1979).

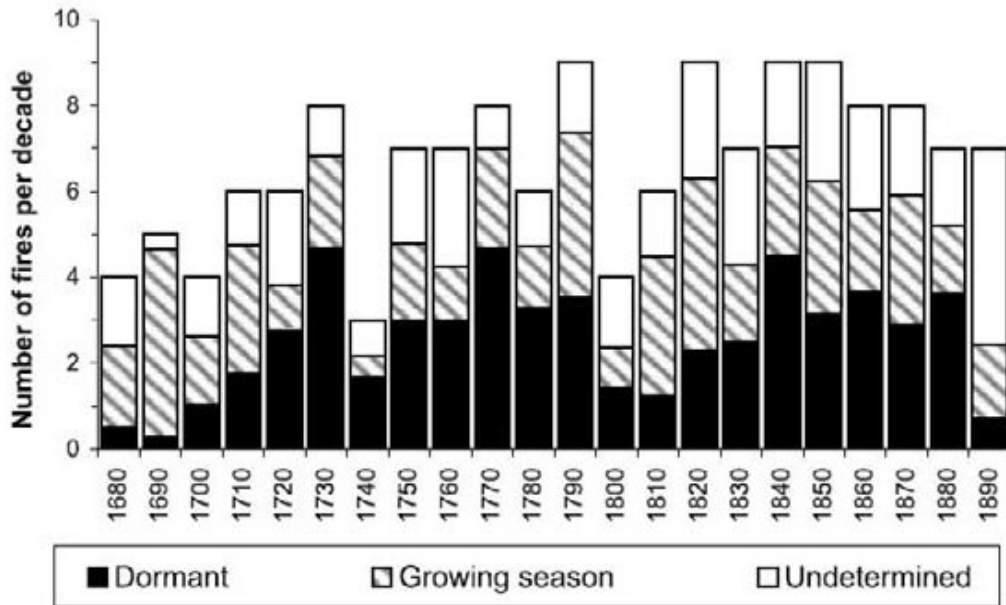


Figure 5. Number of fires by decade (1680-1890) and by season that occurred along the meadow edge in north-eastern California, in the southern Cascade Mountains. (Taken from Norman and Taylor (2003) with author's permission).

Meadows with high productivity and biomass are most likely to carry fire during prolonged drought (Debenedetti and Parsons 1979, Vale 1987, Chang 1996). Anderson and Smith (1997) saw an increase in fire after 4500 YBP within meadows in the southern portion of the assessment area; this period coincided with the transition from warm and dry conditions to cooler and wetter conditions. The authors suggest that meadow fires occurred when conditions allowed for enough biomass to carry the fire, following increases in winter storms. On the Lassen National Forest, in the northern portion of the assessment area, Norman and Taylor (2003) put forward a similar hypothesis that wet/cool conditions are needed to increase the fine fuel biomass so that fire can carry within and alongside meadows during subsequent drought.

Current Conditions

Fire Return Interval

In the assessment area, fire frequency has decreased compared to presettlement times, with the greatest departure occurring in lower montane, montane, and woodland forest types (Safford and Van de Water 2013). Lodgepole pine stands have experienced moderate departure from presettlement conditions. In the Great Basin, big sagebrush (*Artemisia tridentata*) has also experienced moderate departure (Safford and Van de Water 2013). This departure from presettlement fire frequency generally decreases as elevation and precipitation increase, due to increased snowfall and decreased temperatures (Safford and Van de Water 2013).

From 1908 to 2012 there have been a total of 371 human ignitions that burned a mean of 54 (with a standard error of ± 11.6) ha of meadow annually and 273 lightning ignitions that burned a mean of 41 (with a standard error of ± 10.3) ha of meadow annually meadows (Figure 6, Figure 7). A total of 7,687 ha of meadow have burned between 1908 and 2012, 4868 ha which were due to human ignitions.

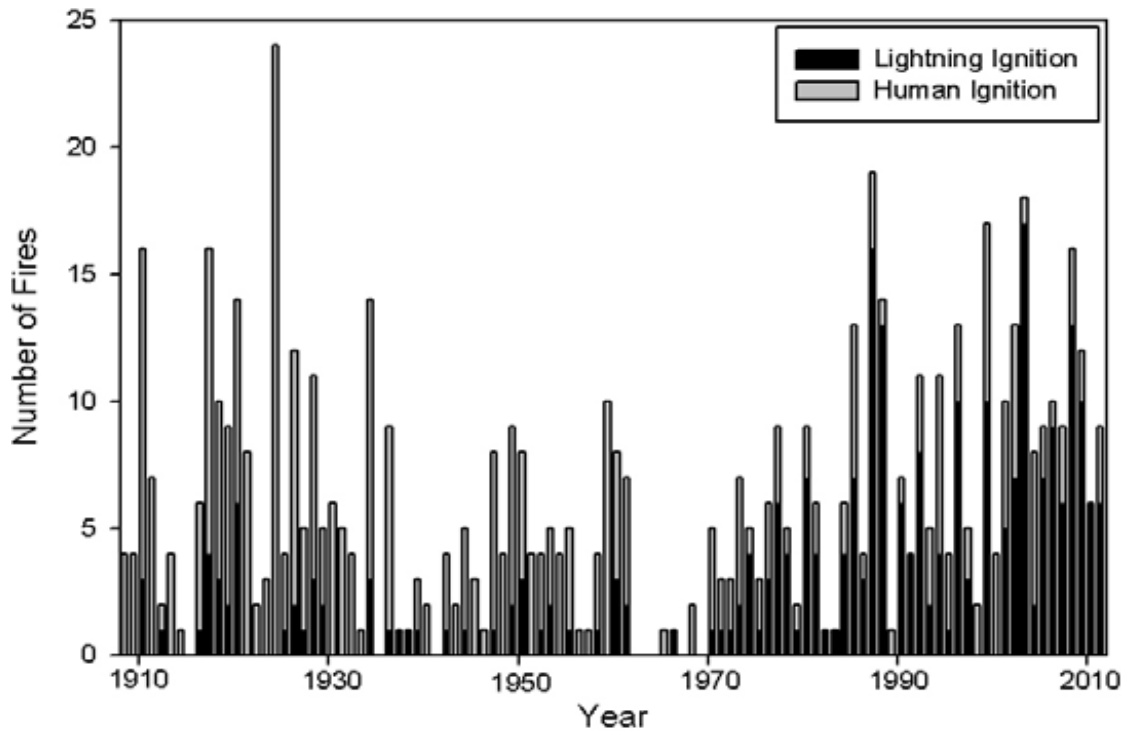


Figure 6. Total number of fires that burned within meadows in the assessment area. Number of fires was identified in ArcMap 10 using the Identity tool in ArcTool box based on the Sierra Nevada meadow layer (Fryjoff-Hung and Viers 2012) and the 2012 wildfire-fire perimeter dataset (CAL-Fire 2012).

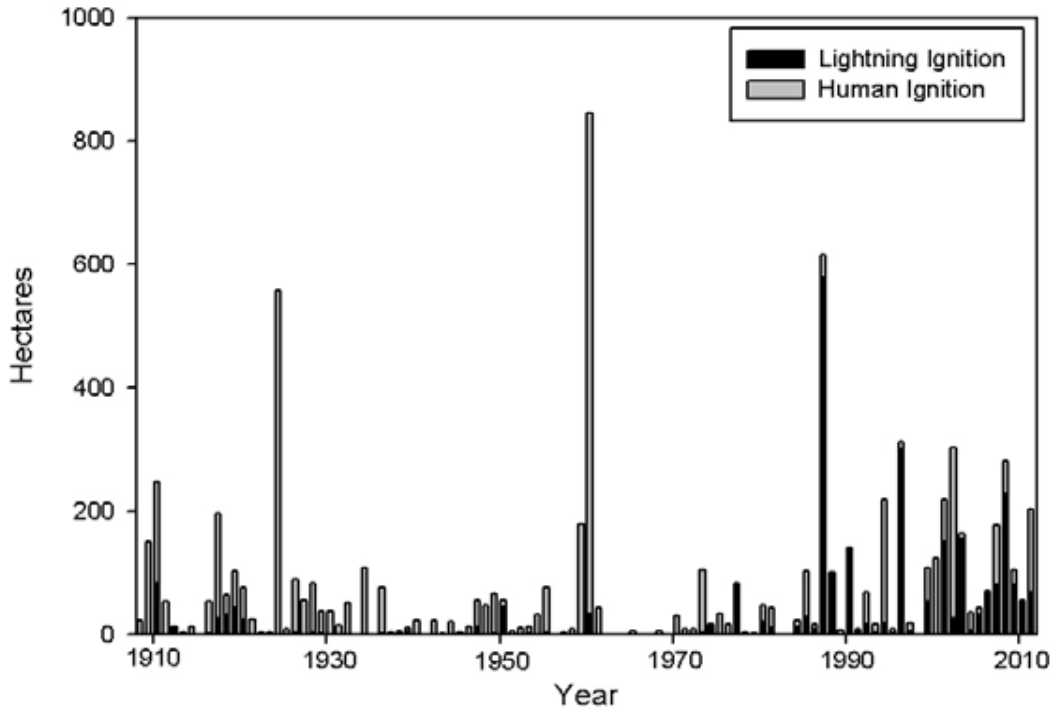


Figure 7. Total meadow hectares burned in the assessment area by year. Hectares of fire was identified in ArcMap 10 using the Identity tool in ArcTool box based on the Sierra Nevada meadow layer (Fryjoff-Hung and Viers 2012) and the 2012 wildfire-fire perimeter dataset (CAL-Fire 2012).

Fire Season

During the end of the 19th century cattlemen and sheepherders utilized fire to promote specific plant species and open the forest (Vankat 1977). While sheepherders set large fires every fall between 1880 to 1910 (SNEP 1996), these fires may not have spread throughout the meadow since heavy grazing and trampling would have left little fuel in meadows (Gruell 2001).

Some of the highest contemporary lightning strike densities in California occur in the Sierra Nevada on eastern and higher elevation western slopes with average lightning strike densities ranging from 0.3 to 0.55 strikes/km²/year (Safford and Van de Water 2013). In Kings Canyon National Park, several meadows burned in 1977 during a severe two-year drought until fall thunderstorms extinguished the fire (Debenedetti and Parsons 1984). On the Lassen National Forest, lightning ignitions over a recent period of 31 years occurred primarily in late summer; 31 percent of the fires occurred in August, 19 percent in July, and 11 percent in June (Norman and Taylor 2003). Based on CAL-Fire (2012) wildfire perimeter data, most fires that have burned into meadows have occurred between July and September (Figure 8). However, human ignitions have extended the fire season (Figure 8).

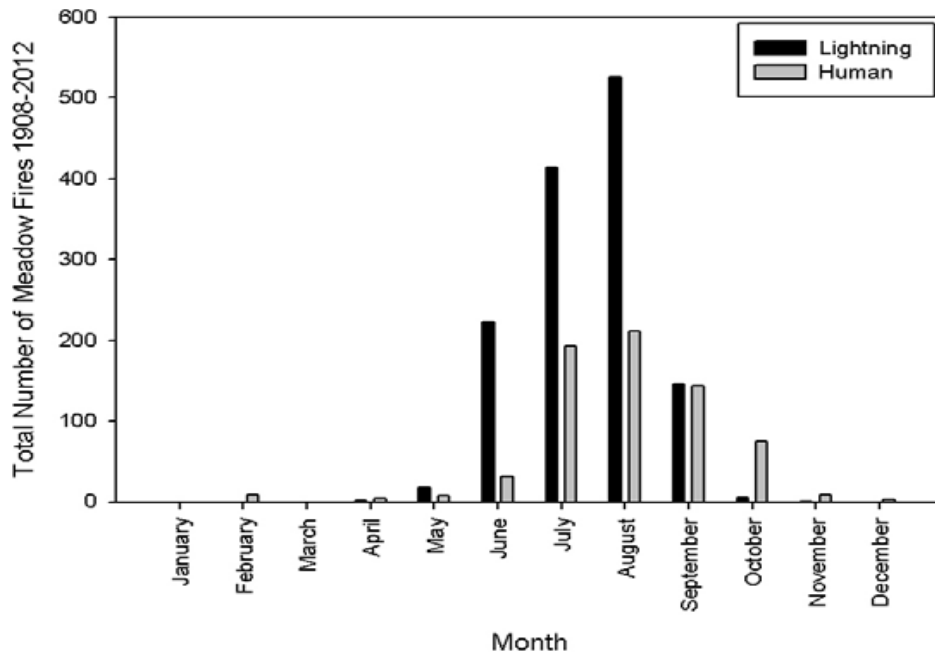


Figure 8. Total number of fires within meadows between 1908 and 2012 by month. Fires without a known month of ignition are not included (812 human caused fires and 126 lightning fires). Fires were identified in ArcMap 10 using the Identity tool in ArcTool box based on the Sierra Nevada meadow layer (Fryjoff-Hung and Viers 2012) and the 2012 wildfire perimeter dataset (CAL-Fire 2012).

Comparison of Current Conditions to NRV

The limited fire history data available from meadows makes it challenging to identify if current burn patterns are within NRV. Data supports frequent low severity fires occurring within meadows and higher severity fires occurring about every 250-300 years. The fire perimeter data from 1908 through 2012 demonstrates that fire continues to occur within meadows. Because the fire return interval has decreased in lower montane, montane, and woodland forest types, including lodgepole and sagebrush vegetation types, it is likely that the fire return interval has also decreased for meadows. Meadows in drier portions of the assessment area (east slope, southern sub-region, and Modoc Plateau) may have had a more frequent fire regime and thus may be further from the NRV than wetter regions within the assessment area. The fuel loading has not changed significantly in meadows, because meadows are by definition herbaceous dominated systems and therefore fire severity is expected to be within NRV. Peak fire season is within NRV, although human ignitions have increased the length of the fire season, which is outside of the NRV.

Potential Effects from Future Climate

Fire will be more frequent under future climatic regimes (Table 8). Increased fire will occur in meadows, especially as the number of drought years increases. However, an increase in the number of drought years will also cause a decrease in biomass, which could decrease fire spread within meadows. Projections of future fire probability and frequency are expected to more than double over 8,000 feet in the Southern Sierras by the end of the century (Figure 9, Moritz et al. 2013).

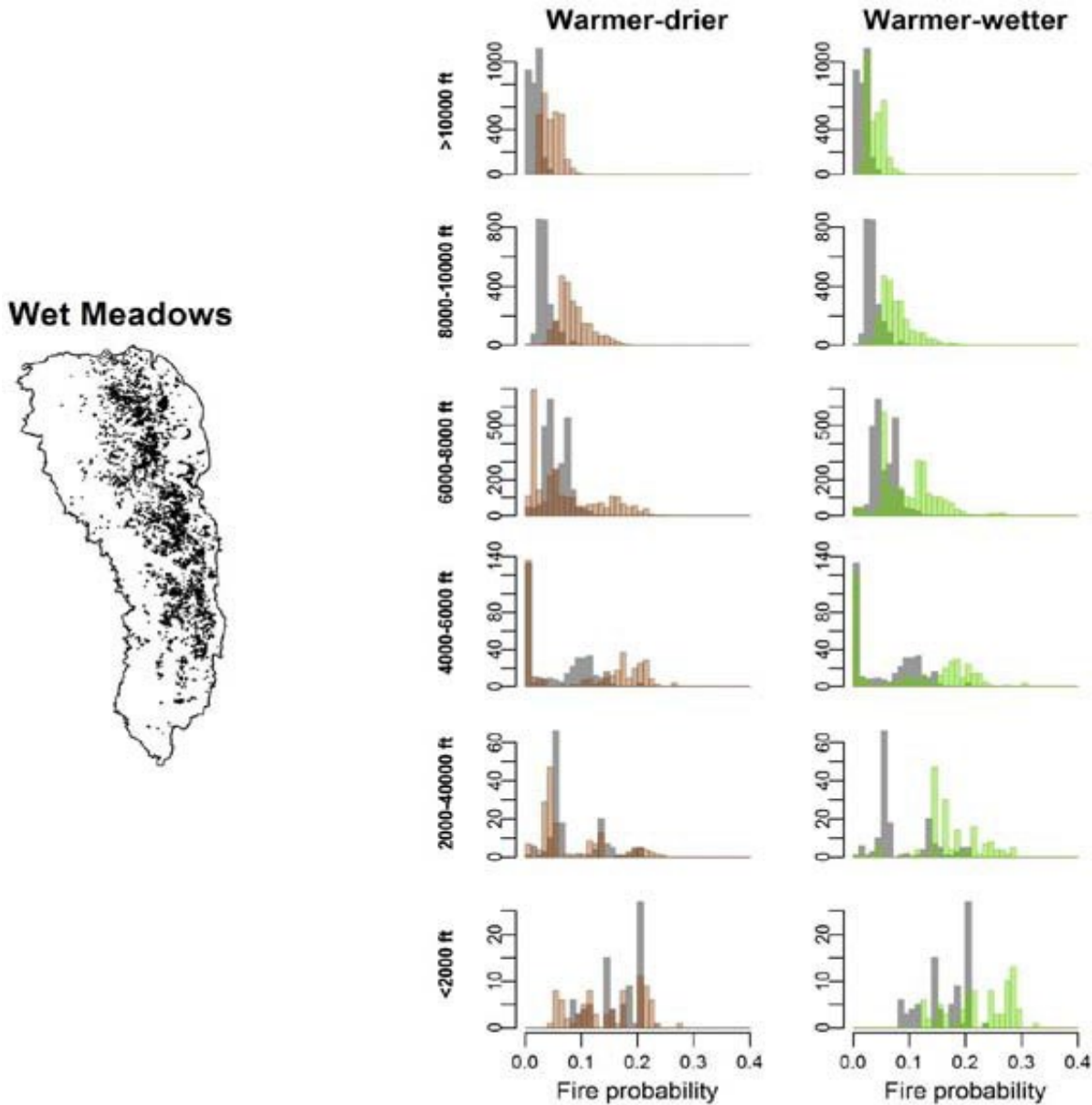


Figure 9. Projected increase in fire probability for subalpine forests in the southern Sierra Nevada under the GFDL (warmer-drier) and PCM (warmer-wetter) climate models by the end of century (2070–2099). Frequency distributions represents future projected (red, green) and current (gray) climate conditions. Y-axis represents the number of model simulations. Model projections based exclusively on the wet meadow CalVeg type. Graphics courtesy of Moritz et al. (2013).

Grazing

Grazing has been a natural disturbance process in Sierra Nevada meadows for over 10,000 years. Grazers influence meadow ecosystems at both the patch and landscape scale by breaking down dead plant material, recycling nutrients, influencing primary production, reducing competition, and altering abiotic disturbance regimes (Hobbs 1996). In combination with climate, grazing animals can play a large role in determining species composition, structure, and ecosystem processes within meadow systems

(Zimov et al. 1995, Hobbs 1996). In response to grazing, many meadow species have evolved adaptations to herbivory that allow for regrowth after browsing; these include low stature, deciduous leaves, rhizomatous growth, high shoot density, below ground nutrient reserves, rapid transpiration, and higher photosynthetic rates (Mack and Thompson 1982, Hobbs 1996, Coughenour 2006).

Natural Range of Variation

Grazing intensity and utilization

Prior to mass extinctions, which occurred ca. 10,000 YBP, ecosystems in the assessment area supported a diverse assemblage of large herbivores and mammalian predators (Figure 2) (Wagner 1989, Edwards 1992). Palaeoecological evidence, such as the abundance of dung fungus (*Sporormiella*) in meadow sediment cores older than 11,000 YBP, suggests that grazing animals were likely abundant in Sierra Nevada meadows until sometime near the end of the Pleistocene (Davis and Moratto 1988, Davis and Shafer 2006). Following the late-Pleistocene megafauna extinctions, meadows in the Sierra Nevada most likely experienced a significant reduction in grazing pressure (Davis and Moratto 1988, Davis and Shafer 2006).

After the late-Pleistocene megafauna extinctions and prior to the historic introduction of livestock to the assessment area, most meadows were grazed at low to moderate intensity by a small suite of native herbivores that included deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and antelope (*Antilocapra americana*) (Ratliff 1985). One of the most important native herbivores in pre-European Holocene meadows was the mule deer (Dull 1999). Mule deer migrate from low elevation winter ranges to higher elevations in spring and rely on the high-quality forage and cover in meadows to nourish and hide fawns (Loomis et al. 1991). Native grazers, such as deer, are less likely to congregate for long periods in specific areas and have a dispersed grazing behavior (Loft et al. 1991, Kie and Boroski 1996). Small herbivorous mammals, such as pocket gophers (*Thomomys* spp.) and meadow mice (*Microtus* spp.) likely also played an important role in Holocene meadows (Ratliff 1985) and may have been particularly important in reducing conifer invasion (Johnson 1986).

Current Conditions

The introduction of domestic sheep and cattle in the mid-1800s significantly increased the number of grazing animals in meadows of the assessment area. In some locations, the abundance of livestock during this historic period has been estimated to equal or exceed the abundance of large herbivores during the late-Pleistocene (Davis and Shafer 2006). During this time period, many small mammal populations also increased in mountain meadows, particularly in areas where livestock substantially reduced vegetative cover (Dull 1999).

In contrast to domestic livestock, utilization of meadows by large native grazers has likely declined. Sierra Nevada populations of bighorn sheep and antelope were significantly reduced in the early 1900s by hunting, disease, and predation (Buechner 1960, Edwards 1992, Dull 1999). Mule deer, which prefer

many of the same meadow types as domestic livestock, have been shown to use a higher proportion of meadow habitats when livestock are absent compared to when livestock grazing levels are moderate or heavy (Loft et al. 1991). Moderate to heavy cattle grazing in Sierra Nevada meadows has been linked to reductions in deer forage and hiding cover in willow stands, particularly in late summer or during years of low precipitation (Loft et al. 1987, Loft et al. 1991, Kie 1996); significant reductions in these variables can result in lower selectivity of meadow-riparian habitats by deer and increased use of habitats avoided by cattle (Loft et al. 1991, Loomis et al. 1991).

Domestic sheep and cattle continue to utilize many of the meadows in the assessment area, although numbers of livestock have been sharply reduced over the past 100 years and fencing has been used in some locations to effectively reduce or eliminate livestock in specific meadows (Figure 10). While contemporary management practices, such as fencing, range improvements, mineral supplementation, and predator control reduce use in some meadows, these practices often result in higher densities and concentrations of livestock in other meadow systems (McNaughton 1993, Kie and Boroski 1996). Higher densities of livestock have been shown to have a negative impact on forage abundance (Westoby 1985, Hobbs 1996). Domestic livestock congregate for long periods of time in specific areas (Loft et al. 1991, Kie and Boroski 1996).

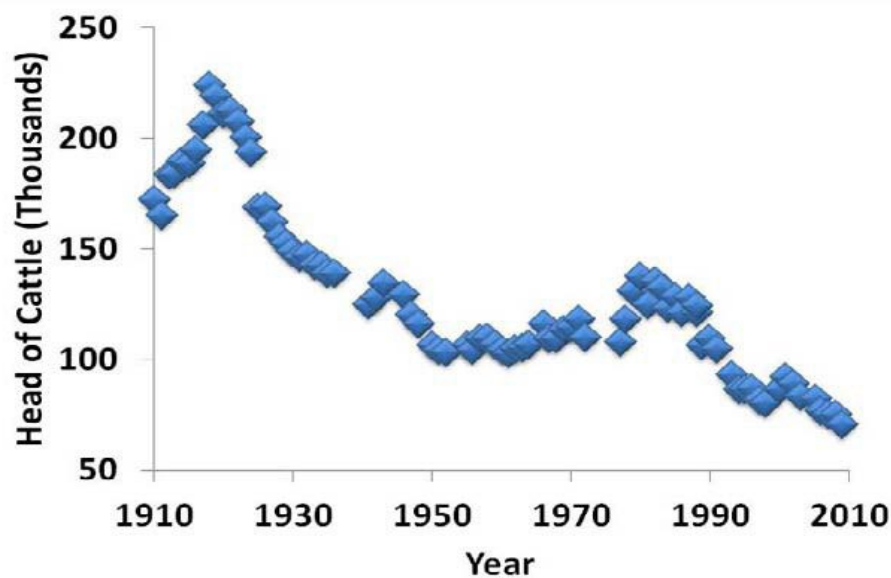


Figure 10. Permitted livestock grazing – the number of permitted head of cattle on Forest Service Lands in California (USDA 2011).

Cattle use in meadows has also been associated with increases in bare soil, an attribute often used as an indicator of significant degradation. Eighty-nine meadows in the assessment area were selected to represent a range of condition classes from reference sites to meadows in poor condition; meadows were categorized based on percent cover of bare soil: high ecological status meadows have $1.9 \pm 3.6\%$ bare soil, meadows of moderate ecological status have $3.6 \pm 5.9\%$ bare soil, and meadows with low ecological status have $7.8 \pm 8.9\%$ bare soil (Weixelman and Zamudio 2001). Analysis of 101 meadows

in the assessment area indicate that 81 percent had less than 10 percent bare ground, while 19 percent have more than 10 percent bare ground (Analysis completed by Dave Weixelman using data from Fryjoff-Hung and Viers 2012).

Comparison of Current Conditions to NRV

The introduction of domestic sheep and cattle to the assessment area in the mid-1800s increased the grazing intensity and utilization of meadows beyond the NRV. Pre-European Holocene meadows were grazed at low to moderate intensity by a small suite of native animals, which differed significantly from domestic livestock in both their foraging and habitat use patterns. Some native grazing animals, such as mule deer, continue to use meadows in the assessment area; however, their foraging patterns have been altered, resulting in decreased utilization of meadows with moderate to high livestock use (Loft et al. 1991, Loomis et al. 1991, Dull 1999). The degree of variation from NRV is very site-specific; some meadows probably experience higher levels of disturbance from native and non-native grazing animals than they did during the pre-European Holocene while others may be within the NRV if domestic grazing has been removed and recovery occurred (Meyer et al. 2005).

Potential Effects from Future Climate

If biomass decreases due to increasing drought, there could be increased grazing pressure on areas that remain productive which may decrease overall biomass further.

Hydrologic Regime

Sierra meadows exhibit a wide range of hydrologic conditions that controls the distribution of meadows along a wet to dry gradient. Both local and watershed scale hydrologic processes influence meadow site conditions (Lowry et al. 2011). Variability in the movement of water within a meadow's contributing watershed has been shown to significantly affect groundwater levels within the meadow (Lowry et al. 2011). Climate change (de Valpine and Harte 2001), changes in channel morphology (Loheide and Gorelick 2007), and cumulative watershed impacts due to land use practices (Patterson and Cooper 2007) all influence meadow hydrology. Historically, changes in water depth may have come about from sediment deposition, erosion, fire, and surface drainage (Wood 1975). Water tables would have risen when sheet erosion of valley fill lowered the meadow ground surface, fire or insect attack caused mortality of the plant community decreasing evapotranspiration rates, or drainage of the meadow surface at a site was dammed by beavers, landslides, log jams, or tree falls (Wood 1975). Water tables would lower when aggradation of meadow valleys increased the thickness of fill above the water table or fill became entrenched below the water table level (Wood 1975).

Climatic variations govern the height of the water table during the growing season; a high-water table results from greater winter snowpack during cool-moist episodes and is maintained by infiltration of sustained meltwater discharge from snowbanks (Wood 1975). Streamflow, snowmelt, precipitation, springs, seeps, hillslope hydrology, groundwater flow processes, and evapotranspiration influence the

dynamic hydrologic regime of meadows (Lowry et al. 2011). Seasonal extremes in meadow hydrology occur during spring snowmelt and late-season drought conditions (Lowry et al. 2011). Increased ground water in meadows during the late Holocene was probably a result of an increased snowpack (Anderson 1987). There was a general warming and drying trend throughout the assessment area during the early Holocene and Medieval Warm periods (Figure 2). California has been exposed to extended and single year droughts during the last several thousand years (Figure 2) (Graumlich 1993, Austin 2012). During these periods of drought, xeric upland species likely increased within meadows.

Natural Range of Variation

Flood Magnitude and Frequency

Frequency, magnitude, and seasonality of flooding in meadows has varied over time, often in response to climate (Carson et al. 2007, Austin 2012). During the late Wisconsin (20,000 YBP) lack of vegetation cover in meadows above timberline probably resulted in high peak flows (Wood 1975). Today, as throughout the Holocene, low magnitude floods, typically in the spring or early summer occur annually throughout the Sierra, whereas winter floods created by rain-on-snow events are relatively rarer and of greater magnitude (Wood 1975). Over the last 1,800 years six mega-floods have occurred in the southern portion of the assessment area approximately every 200 years (Figure 2) (Austin 2012). Data suggests that peak flows during the Holocene on the other hand, were lower, and that the maximum likely flood (65.58 m³/sec/km² (6,000 cfs/mi²)) has not occurred in the last few thousand years on the west slope of the Sierra (Wood 1975).

The depth of the winter snowpack and the rate of spring melt affect the magnitude of floods (Carson et al. 2007). In general, smaller than normal floods occur during warm dry conditions and larger than normal floods occur during cool and wet conditions (Carson et al. 2007); although floods are also common during periods of drought (Austin 2012). One study from meadows in the Uinta Mountains in northeastern Utah, suggests that historically large floods were as much as 10-15 percent larger compared to current conditions and small floods as much as 15-20 percent smaller than contemporary floods (Figure 11) (Carson et al. 2007). Larger floods were found to correspond with two historic time periods. The first was during the early Holocene (8500-5000 YBP) when rapid melting of snowpacks/glaciers may have occurred due to the warmer mean annual temperatures; the second period was during glacial re-advances (2800-1000 YBP) (Carson et al. 2007). Smaller floods were found to correspond with increased fire frequencies (5000-2800 YBP, 1000 YBP to near present) and warming during the Medieval Warm Period (AD 900-1350) (Carson et al. 2007).

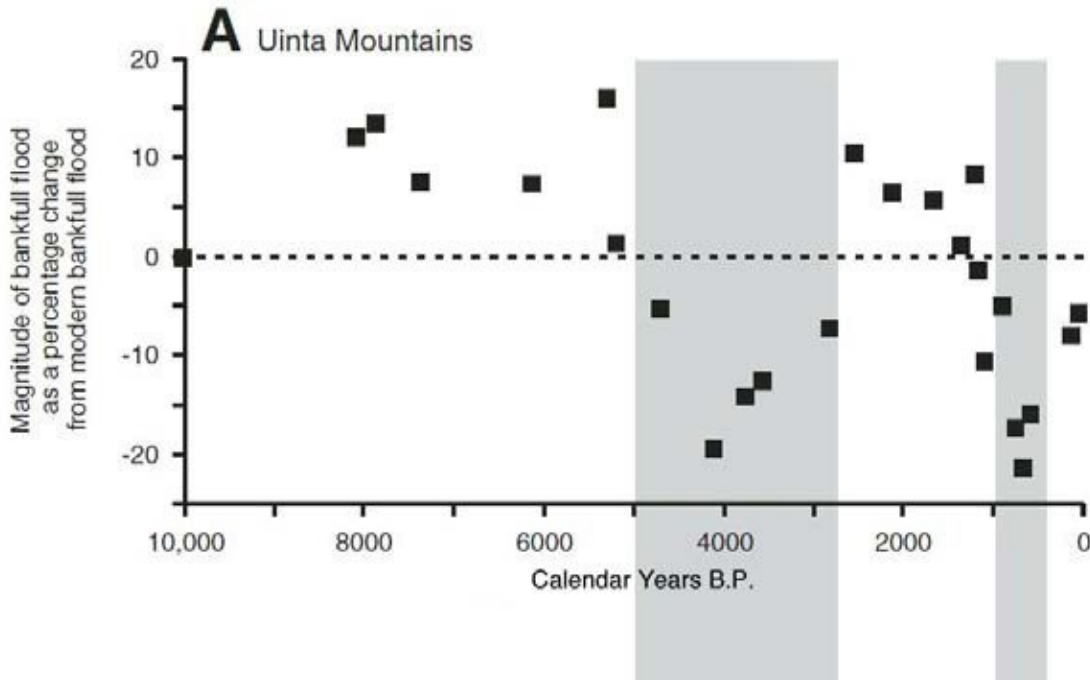


Figure 11. Paleo-flood chronology from meadows in the Uinta Mountains, UT. Smaller flood periods compared to current flood magnitudes are represented by shaded areas. (Taken from: Carson et al. (2007) with author's permission).

Stream Incision

Drainage basin area and meadow slope are primary controls on the presence of stream channels through meadows (Wood 1975). Stream flow and duration of flow are related to the size of the drainage basin and proportion of drainage basin above 3050 meters, where more snow than rain is captured (Hess 2002). As the size of the drainage basin increases there is a greater variation in the timing of flow due to a greater variation in the size of channels and potential for increased sediment yields (Viers et al. 2013). Channels typically form if the drainage basin is greater than 200 hectares (Wood 1975), although channels also form in glaciated headwaters with less drainage area. In general, small, vegetated channels often form when the slope exceeds two percent, but dissipate when the slope becomes shallower; overland flow from surrounding tributaries is common in these meadows (Wood 1975). Sinuosity of the stream channel increases as the drainage area increases, slope decreases, and sediment loads change. Large meandering streams in relatively flat meadows often shift course through time. Sinuous streams undercut topsoil banks annually, but deposit gravel and sand at inner bends only during major floods (Wood 1975).

Stream incision affects meadow hydrology by changing the pattern of water flow from down valley, where the groundwater spreads through the meadow, to flow towards the channel, decreasing the meadow moisture (Loheide and Gorelick 2007). Channel incision lowers groundwater and reduces overland flow frequencies (Micheli and Kirchner 2002a). Evidence of channel incision includes high cut banks, a channel cross-section that exceeds the capacity to carry the mean annual flood (Micheli and Kirchner 2002a), or a widened channel that causes a decrease in duration of runoff (Norton et al. 2011).

Channel incision reduces bank stability by increasing the bank height and encouraging the conversion of wetland vegetation to dry meadow vegetation (Micheli and Kirchner 2002a). Based on extensive Sierra-wide meadow sampling, obligate and facultative wet meadow species (excluding species in peatlands) tend to have deeper root depths than dry meadow facultative upland and upland species that have adapted to utilize precipitation and near surface water (David Weixelman, personal communication, April 10, 2013). Stream banks with mesic species are on average five times stronger than stream banks with xeric species. The root-area ratio for wet meadow banks has been shown to be 50 percent compared to less than 5 percent for dry meadow banks (Micheli and Kirchner 2002b). Wet meadow vegetation increases bank strength by increasing thickness, width, and cohesiveness of the stream bank; the increase in strength is correlated with stem counts, standing biomass, and ratio of root to soil mass (Micheli and Kirchner 2002b).

Riparian vegetation can reinforce bank soils by increasing shear strength up to eightfold (Micheli and Kirchner 2002b). Rushes are better at stabilizing coarse bar surfaces and sedges are better at stabilizing actively eroding banks (Micheli and Kirchner 2002b). Sedges have a large number of randomly oriented fine roots (<2 mm diameter) which help bind sands and gravel together which can be effective at stabilizing vertical cut banks, undercut banks, and banks protected by failed slump blocks (Micheli and Kirchner 2002b).

During the past 1900 years axial channels have alternated between periods of stability and periods of incision in response to channel-bed degradation, (Miller et al. 2004). In the Great Basin, there is evidence of minor channel incisions from 1900 to 1300 YBP; axial channel incision may have occurred during this period following a decrease in hillslope runoff and sediment (Miller et al. 2004). Localized entrenchment in Great Basin streams began about 450 YBP, potentially in response to the Little Ice Age and a shorter growing season, increased precipitation, and change to a snow-dominated regime (Miller et al. 2004). Increased runoff (regardless of the source) often leads to entrenched axial channels in the Great Basin with some of the most susceptible areas being within wet meadow complexes (Miller et al. 2001). Alluvial fans and sediment size influence the local rate of entrenchment through the meadows (Miller et al. 2001, Carson et al. 2007). Incision likely did not occur during the Holocene in meadows with large cobbles and boulders in the outwash but would have primarily meandered laterally across the outwash (Carson et al. 2007).

Erosion – Gully Formation and Hillslope Aggradation

Erosion can alter the depositional surface of meadows; however, the thickness and depth of topsoil and alluvium found in montane meadows suggests that these sites are generally aggrading rather than eroding (Wood 1975). Over the past 5000 years, aggradation has been correlated with short, abrupt climate-related shifts in flood frequency and magnitude (Miller et al. 2004). In general, over the past 10,000 years, drought conditions have coincided with fan and valley floor aggradation in the Great Basin (Miller et al. 2001, Miller et al. 2004). As precipitation decreased, the abundance of upland vegetation would have decreased changing the hillslope hydrology and increasing erosion (Miller et al. 2001, Miller et al. 2004). Soil development and accumulation of organic material occurred around 4200

YBP (Miller et al. 2001). At about 1900 YBP, a shift from moister to drier conditions initiated massive hillslope erosion followed by side-valley fan and valley floor aggradation (Miller et al. 2004).

Dams

In the assessment area, some meadows are found in areas with impermeable bedrock, where recessional or lateral moraines have formed dams (Benedict and Major 1982, Weixelman et al. 2011). Wood (1975) found no evidence of historic damming (by beavers or log jams) in meadow stratigraphic sections. However, other authors have suggested that the removal of beaver in the west may have reduced the saturated area of meadows (thus reducing wet meadows) and extent of riparian vegetation (Naiman et al. 1988). In some localized areas, dams were built by Native Americans for agriculture. For example, the Paiute built temporary annual dams on the eastside of the Sierra to irrigate areas in the Owens Valley (Lawton et al. 1976).

Current Conditions

Contemporary changes to meadow hydrology are a result of direct and indirect human activities. Direct impacts often occur from channelization, stream straightening, drainage, and culvert construction. Indirect impacts are most often associated with grazing, logging, roads, climate change (Loheide et al. 2009), and forest successional dynamics under altered fire regimes. In the Sierra Nevada the most widespread land drainage has occurred in wet meadows (Kondolf et al. 1996). Drainage of meadows in the assessment area began in the mid-1800s. In 1870 a moraine was intentionally dynamited in Yosemite Valley to drain an upstream meadow and indirect drainage occurred due to channel incision (Kondolf et al. 1996). Drainage of wetlands occurred as an accepted practice until the mid-1970s (Kattelman and Embury 1996).

Floods

The severe mega-flood of 1861-1862 in the southern portion of the assessment area was of lower magnitude than previous mega-floods seen over the last 1800 years (Austin 2012). Frequent flooding is common, with the most recent floods occurring in 2011 (Austin 2012).

Stream Incision

Recent channel incision may be due to a combination of changing climate (e.g., channel-bed degradation, which has been driven by moderate to low magnitude floods) and anthropogenic disturbance (e.g., road building, grazing, etc.). A recent analysis of 101 low and middle gradient riparian sites across six National Forests in the assessment area found that approximately 54 percent of channels within meadows were significantly incised (Analysis completed by Dave Weixelman using data from Fryjoff-Hung and Viers 2012). An increase in stream bank height can lead to meadow drying. Micheli and Kirchner (2002a) found that dry meadows along the South Fork of the Kern River in the southern Sierra had stream bank heights greater than one meter; this incision depth generally restricts overland flow to 100-year flood events. In contrast, wet meadows had stream bank heights less than one meter,

which allowed for overland flow during mean annual floods.

Erosion – Gully Formation and Hillslope Aggradation

Wood (1975) examined gully erosion in 23 southern Sierra meadows and determined that all had been initiated after 1900; he found no evidence of pre-20th century gullies (Wood 1975).

Dams

Over the past 150 years, the construction of dams on small streams (e.g., for water diversions) and large rivers (e.g., for hydroelectric) has significantly changed the hydrology of meadows in the assessment area (Beesley 1996). In the mid-1800s, streams were frequently dammed for gold mining activities (Kattelman and Embury 1996). Construction of dams also occurred in broad valleys with wide riparian areas to create reservoirs, leaving large areas of riparian ecosystems under water. It has been estimated that 900 to 1,200 kilometers of riparian corridors in the Sierra Nevada are now under water (Kattelman and Embury 1996). Dam construction changes the hydrologic regime of streams, often reducing peak flows by an order of magnitude (Kattelman and Embury 1996).

Comparison of Current Conditions to NRV

Groundwater fluctuations are a natural occurrence in meadows; however hydrologic function has been significantly altered since the mid-1800s. The frequency of annual meadow floods is likely outside of the NRV due to increased rates of stream incision and an increased number of dams, which are outside of the NRV. Minor channel incision likely alternated with periods of channel stability throughout the Holocene; however, contemporary anthropogenic impacts have increased rates of channel incision outside the NRV. There has also been an increase in gully erosion, which appears to be outside the NRV, although aggradation from the surrounding hillslope likely is within the NRV. The presence of manmade dams has resulted in conditions outside of the NRV.

Potential Effects from Future Climate

Irregularly shaped meadows have a greater ratio of edge to meadow and therefore may be more vulnerable to changes in hydrology than compact meadows (Viers et al. 2013). Increasing temperatures will cause more frequent droughts, which will affect meadow hydrology (Hayhoe et al. 2004). Future climate predictions of increased temperature suggest that snow melt will occur earlier, and flood potential will increase during winter and early spring (Miller et al. 2003). Mid-elevation areas (1500-3000 m) meadows are to be predicted to be more vulnerable to changing climate compared to high elevation meadows that will likely still be snow dominated (Viers et al. 2013). This may lead to a decrease in available water later in the growing season. Sierra Nevada mountain meadows may be further threatened by predicted changes in future water yields, which will potentially result in overall longer periods of low flow conditions (Null et al. 2010).

Changes in precipitation will likely lead to changes in erosion. Effective precipitation amounts between

200 and 500 millimeters/year are correlated with maximum sediment yields (Miller et al. 2004); in general, when precipitation is less than 200 mm there isn't enough force to move sediment and when values are greater than 500 mm vegetative cover is greater. If meadow soil erodes, then surface water will be released more rapidly. When erosion does not occur, surface water will be available for meadow vegetation. The greatest change in flow is expected in the northern portion of the assessment area because these meadows are generally found at lower elevations (Viers et al. 2013). Low flow conditions in the central portion of the assessment area are predicted to last longer and flows in the southern portion of the assessment area will occur earlier (Viers et al. 2013). Changes in flow will lead to flashy runoff events and increased sediment loads which may further increase rates of incision and erosion (Viers et al. 2013).

Structure

Upland Species Invasion

While there has been considerable research investigating successional change in Sierra Nevada meadows, no single variable has emerged to explain why some meadows are invaded by trees and shrubs, and others are not. At higher elevations and latitudes, upland woody plant invasion is hypothesized to be a response to warming temperatures, reduced snowpack, and in some cases, grazing by livestock (Bradley 1911, Ratliff 1985, Dull 1999, Gruell 2001, Veblen et al. 2003, Norman and Taylor 2005). Encroachment into lower elevation meadows, which have a much more complex history of land use, has been correlated with a larger number of factors that include fire, livestock grazing, and climate (Vale 1977, Norman and Taylor 2005). Based on limited available information, wet meadows generally show lower levels of tree and shrub invasion than drier meadows and less episodic patterns of successional change (Wood 1975, Helms 1987, Vale 1987, Bartolome et al. 1990, Gruell 2001). At the patch scale, factors that can influence the expansion of trees and shrubs into meadows include competition, seed or seedling predation, local seed supply, and disturbances or gaps created by burrowing mammals or herbivores (Johnson 1986, Peart 1989, Van Auken and Bush 1997, Berlow et al. 2002). Succession may occur as a "leap and fill" process in which trees first establish in relative isolation and then establish in the spaces between in subsequent years and decades (Norman and Taylor 2005). Trees that establish themselves far from the forest edge may be more responsive to climate-related change than those that infill around already established trees (Norman and Taylor 2005).

Natural Range of Variation

While periods of meadow establishment and tree invasion have occurred in Sierra Nevada meadows over the past 10,000 years, Wood (1975) suggests that invasion of meadows during the Holocene was a relatively infrequent event. Fluctuations in the water table were likely important for preventing invasion of woody species into meadows, with the cyclical establishment, survival, and mortality of trees and shrubs largely dependent on water levels (Wood 1975, Bartolome et al. 1990). This was evident during the Neoglacial cooling period (~4500 to 2000 YBP) when groundwater rose and excluded tree species from the meadow floor, allowing wet meadow species to dominate (Figure 2) (Wood 1975). Flooding

also influenced successional patterns through disturbance, inundation, and channel morphology changes (Kattelman and Embury 1996).

In the southern Sierra Nevada, flooding during peak spring snowmelt may have been frequent enough to kill sagebrush seedlings that colonized between flood events; however, this may have changed in contemporary meadows where stream channels became incised, and the frequency of meadow floods declined (Berlow et al. 2002).

Conifer Abundance

In general, conifers invade meadows during warm dry periods and are excluded from meadows during cool wet periods. Reconstructions of meadow vegetation during the early Holocene (ca. 8,800 and 6,000 YBP) suggest that as the water table dropped and meadows became drier, some wet meadows in the Sierra Nevada were converted to upland forest types (Figure 2) (Wood 1975, Anderson 1990, Koehler and Anderson 1994). During this period of meadow invasion, the range of lodgepole pine contracted by shifting upward in elevation (Figure 2) (Anderson 1996). Meadows may have served as refugia during this warmer-drier climatic period, providing woody species such as lodgepole pine, with additional water; this may explain the increase in conifers in meadows despite a range contraction. In one study of a meadow in Sequoia National Park, Lloyd and Graumlich (1997) found evidence of foxtail pine (*Pinus balfouriana*) invasion between 2150-1850 YBP and 1450-1050 YBP, which coincides with the transition from the Neoglacial period to the Medieval Warm period (Figure 2) (Lloyd and Graumlich 1997). Additional invasion into meadows coincides with the end of the Little Ice Age (ca. 1400-1900 AD) and the beginning of a general warming trend across the Sierra Nevada (Millar and Woolfenden 1999) (Figure 2).

In general tree abundance has been documented to increase during warmer drier conditions, however some species have also been shown to decrease during warmer drier conditions. In their study of a meadow in Sequoia National Park, Lloyd and Graumlich (1997) documented a negative trend in conifer abundance, in mono-specific foxtail pine (*Pinus balfouriana*) stands, between 950-550 YBP, which corresponds to the Medieval Warm period (~1100-650 YBP) when the climate became warmer and drier (Figure 2) (Lloyd and Graumlich 1997). Decline of conifers within meadows during warm-dry periods is challenging to interpret; potential explanations include an interaction of climate, fire, and seed mortality (e.g., due to an increase in small mammal populations). Tree establishment could have increased and decreased during the cool wet period due to an increase of herbaceous biomass sufficient to carry fire. Norman and Taylor (2003) suggest that in open meadow conditions, trees were absent if the meadow provided enough biomass to carry fire (Norman and Taylor 2003).

Sagebrush Abundance

In contrast to the general trend observed for trees, Anderson (1987) documented a widespread decline in sagebrush species (*Artemisia* sp.) during the warm and dry climate ca. 8000 to 6500 YBP, at Balsam and Exchequer Meadows in the southern Sierra Nevada (Figure 2). Before 1850, woody shrubs such as

sagebrush appear to have been restricted to the dry soils at meadow fringes, expanding into the meadows after the onset of intensive grazing. This trend, in addition to contemporary studies of sagebrush establishment, suggests that sagebrush colonization may be more closely tied to disturbance processes than moisture regime. The highest rates of Rothrock sagebrush (*Artemisia rothrockii*) germination and seedling growth occur within moist microhabitats when there is exposed soil (<1 m²) (Berlow et al. 2002). Without disturbance, intact herbaceous meadow vegetation effectively prevents Rothrock sagebrush germination and strongly inhibits growth and survival of sagebrush (Berlow et al. 2002). When adequate soil disturbance is present, sagebrush germination and seedling survival increase in wet years (Bauer 2002). Berlow et al (2002) hypothesizes that factors that reduce competition from herbaceous species, such as disturbance, may be critical for Rothrock sagebrush establishment at intermediate soil moisture; in contrast, at wet sites disturbances such as fire and seedling predation may cause sagebrush mortality, maintaining high herbaceous cover. This concept that biologically stable or intact meadow systems have fewer opportunities for invasion has been proposed by other researchers as well (Benedict and Major 1982).

Current Conditions

Conifer Abundance

Heavy sheep grazing, which began in the late 1800s, both impeded and encouraged tree invasion in Sierra Nevada meadows (Ratliff 1985, Chang 1996). Many meadows were invaded by conifers in the early 1900s, which coincided with large reductions in the high concentration of sheep and cattle in the Sierra Nevada (Vankat and Major 1978, Ratliff 1985, Taylor 1990, Gruell 2001). Heavy grazing, particularly by sheep, followed by periods of low to moderate grazing have been linked to conifer and shrub invasion in many Sierra meadows (Bradley 1911, Vankat and Major 1978, Chang 1996, Gruell 2001). In these cases, low to moderate grazing may facilitate invasion because few seedlings are killed by trampling or browsing and past overgrazing has created meadow conditions, such as expanses of bare ground, that are conducive to seedling establishment (Taylor 1990). While the Taylor Grazing Act of 1934 was introduced to provide regulations to grazing, some legacy effects of early grazing practices may still exist in meadows of the assessment area (Norton et al. 2011).

A number of factors can interact with grazing to influence patterns of succession within meadows (Berlow et al. 2002). Heavy grazing of herbaceous meadow plants can disrupt fuel continuity and reduce fire frequency (Dull 1999, Norman and Taylor 2005). Livestock-induced changes in stream and watershed hydrology, which have been hypothesized to include increased runoff, soil erosion, and stream entrenchment, can result in lowered water tables and improved conditions for tree seedling establishment (Vankat and Major 1978). Increased bare mineral soil and reduced competition as a result of heavy grazing may also predispose meadows to invasion (Ratliff 1985). Other factors may include declines in the abundance of native herbivores (Weltzin et al. 1997), changes in climate or the frequency of extreme weather events (Millar and Woolfenden 1999), elevated concentrations of atmospheric carbon dioxide (Polley et al. 1997) and increases in shrub seed dispersal by livestock (Brown and Archer 1999).

While the response to changes in grazing may be difficult to separate from changes in the fire regime (Taylor 1990), small fires have been shown to reduce conifer seedlings (Vankat 1977, Frenzel 2012) and thus may have reduced tree invasion. As fire frequency was reduced in the 20th century, surrounding lodgepole pine forests became denser and meadow invasion increased (Vankat 1977). Altered fire regimes and livestock grazing, combined with a warmer drier climate, appear responsible for the spatial pattern of tree establishment that occurred during the late 19th and 20th century (Taylor 1990, Norman and Taylor 2005). Decline in fire and intense grazing led to successional changes that may have been reinforced by positive feedbacks – early tree establishment could have ameliorated site conditions for subsequent establishment (Norman and Taylor 2005). Post-fire observations in Ellis Meadow in Kings Canyon National Park showed differential mortality of lodgepole pine, indicating that fire can influence the dynamics of the forest-meadow ecotone and in some cases be important in determining the success of lodgepole invasion (DeBenedetti and Parsons 1979). This differential mortality may be linked to tree size (Pyke et al. 2010) and cover of herbaceous vegetation; higher severity fire is needed to kill larger diameter trees and greater herbaceous cover increases fire intensity and spread (Frenzel 2012).

Comparisons of historical and contemporary photographs and descriptive letters of meadows across the Sierra Nevada provide evidence for an increase in tree cover on meadow margins over the past 100 years (Figure 12, Figure 13) (Bradley 1911, Ernst 1949, Vale 1987, Gruell 2001, Wasserman 2008). High rates of tree invasion and establishment in Sierra Nevada meadows have been estimated between 1903 and 1939 in Sequoia, Yosemite, and Lassen National Parks, although the specific years of establishment within this time period can be variable (Wood 1975, Vankat and Major 1978, Norman and Taylor 2005). Tree invasion continues to be documented in the late 20th century. Sixty percent of high elevation meadows in Sequoia and Kings Canyon National Park and more than 42 percent of high elevation meadows in the Lake Tahoe Basin contain seedlings and saplings of lodgepole pine; these saplings occur in a wide range of meadow conditions from dry disturbed soil to relatively undisturbed wet areas (D'Antonio et al. 2004) (Gross et al. 2013). Based on data from Fryjoff-Hung and Viers (Fryjoff-Hung and Viers 2012) 72 percent of 101 meadows on National Forest land found in the assessment area have some degree of conifer encroachment; 40 percent of these have greater than 10 percent cover of conifers (Analysis completed by Dave Weixelman using data from Fryjoff-Hung and Viers 2012).

In their study of meadows on the Lassen National Forest, Norman and Taylor (2005) suggest that the average rate of establishment after 1850 exceeded the maximum tree density of forests that developed over centuries. They hypothesize that a combination of reduced fire frequency and intense grazing has facilitated tree invasion into meadows (Table 6) (Norman and Taylor 2005). Millar and Woolfenden (1999) found that recent vegetation changes are often correlated with the significant warming trend observed since the 1900's (Millar and Woolfenden 1999).



Figure 12. Repeat photograph comparing 1907 conditions to 2008 conditions in Yosemite National Park, CA. Mount Dana in background. Notice the increased abundance of conifers in the meadow. A) Photograph 1907 by G.K. Gilbert, USGS reference 3116; B) Photograph 2008 by Noah Wasserman, 8-V08-US3116 (Wasserman 2008).

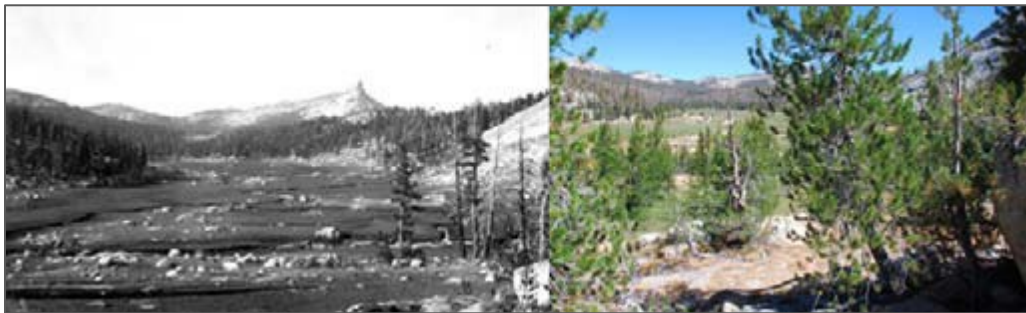


Figure 13. Repeat photograph comparing 1914 conditions to 2008 conditions at Columbia Finger, in Yosemite National Park, CA. Notice the increased abundance of conifers in the meadow. A) Photograph 1907 by F.E. Matthes; B) Photograph 2008 by Noah Wasserman, 94-VBK-66 (Wasserman 2008).

Table 6. Tree establishment rates related to intensity of grazing on the Lassen National Forest in meadows (Norman and Taylor 2005).

Intensity of Grazing	Trees/ha/decade
Heavy grazing (prior to 1905)	22.9
Moderate Grazing	62.6
Reduction in sheep grazing (cattle replace sheep)	40.7

Sagebrush Abundance

The response to changes in grazing may be difficult to separate from changes in climate and fire regime (Taylor 1990). Fire has been documented to kill big sagebrush (*Artemisia tridentata* ssp. *tridentata*), especially in meadows with high water tables (Wright and Chambers 2002). In their study of meadows on the Kern Plateau in the southern Sierra Nevada, Bauer et al (2002) correlated changes in frequency and intensity of El Nino events over the past century with Rothrock sagebrush invasion; once sagebrush is established, continued recruitment is independent of climate.

Comparison of Current Conditions to NRV

Although forests and meadows have formed a shifting mosaic over centuries, recent encroachment of conifers and shrubs into meadows appears more extensive and rapid than what may have occurred during most of the Holocene. Climate-induced successional patterns are likely within the NRV; however, climate in combination with other factors (e.g., fire suppression and grazing) that influence succession of meadows to tree or shrub dominated stands, have resulted in rates of invasion that trend outside of the NRV.

Potential Effects from Future Climate

Irregularly shaped meadows have a greater ratio of edge to meadow and therefore may be more vulnerable to encroachment from upland plant species than compact meadows (Viers et al. 2013). The warmer-drier conditions that occurred during the xerothermic period of the early Holocene (~8,000-5,000 YBP) have been suggested as a possible analogue for future climate in the Sierra Nevada. Based on the limited available data, and often contradictory results, it is difficult to predict what may happen to meadows in relation to conifer and sagebrush invasion. Millar et al. (2004) predict that meadow invasion from lodgepole pine will occur during a combination of negative Pacific Decadal Oscillation (PDO) combined with warmer temperatures, low precipitation, and low inter-annual variability in moisture. Taylor (1990) found that tree establishment in Lassen National Park meadows varied significantly with precipitation; establishment was greater during periods with above normal spring, summer, and annual precipitation, which would suggest a negative PDO phase in the northern portion of the assessment area. Harte and Shaw (1995) found that big sagebrush increased in experimentally heated dry meadow plots in an experiment in the Rocky Mountains. If fire is limited and there is sufficient soil disturbance within the meadow, sagebrush will be able to establish and persist under a warming climate.

Distribution and size of meadows – Meadow Hectares Natural Range of Variation

There is no information describing the distribution and size of meadows prior to European-American settlement of the assessment area. However, there are indications that meadows in the assessment area developed, disappeared, and redeveloped throughout the Holocene (Wood 1975, Ratliff 1985, Kinney 1996).

Current Conditions

Historical accounts from the mid-1900s suggest a decline in meadow area over a relatively short time period. Emil Ernst, a Yosemite Park Forester in the early 1940s, noted that the “area of clear open ground, with abundance of luxuriant native grasses and flowering plants, was at least four times as large [in the mid-1800s] as the present time” (Ernst 1949). In Yosemite National Park, comparisons of maps made by the 1864 California Geologic Survey and Emil Ernst’s 1942-1943 resurvey of the same area suggest that invading conifers reduced meadows from 745 acres to 327 acres over an 80-year period (Gruell 2001). In the southern portion of the assessment area in the Golden Trout wilderness, studies of two meadows suggest that approximately 60-70 percent of the area below the alluvial margins of the meadows would have been occupied by meadow vegetation before grazing (Odion et al. 1988). It has also been suggested that meadow vegetation may have occurred continuously for a relatively long time in some of the locations now occupied by gullies in the southern portion of the assessment area (Odion et al. 1988).

The National Research Council (1992) estimates that only about 9 percent (183,700 ha) of California wetlands remain compared to the area occupied by wetlands in 1780. Based on the dataset of Fryjoff-Hung and Viers (Fryjoff-Hung and Viers 2012), there are 77,659 ha of meadows in the assessment area (Table 1). Contemporary meadows range in size from 0.4 ha to 1866 ha (Table 1). The largest number and area of meadows in the assessment area is found in the southern sub-region, followed by the central, northern, and eastern sub-regions (Table 1). Past and present land management of meadows that fall under different jurisdictions with varying management objectives has had an effect on the distribution and size of meadows. While meadows in the assessment area are predominately managed by the Forest Service, other landowners have also played a role. In the northern and eastern sub-regions there is a greater area of meadows on private land compared to public land (Table 7).

Comparison of Current Conditions to NRV

The size and distribution of meadows in the assessment most likely shifted throughout the Holocene (Wood 1975, Ratliff 1985, Kinney 1996); however historical accounts, survey data, and evidence of anthropogenic impacts (see preceding section on European-American Settlement and National Forest Administration) within meadows suggest that the total area of meadows has declined below the NRV.

Potential Effects from Future Climate

Meadows are groundwater dependent ecosystems that require water at or near the surface, many of which are recharged through snowmelt. Decreases in spring snowpack and an earlier peak snowmelt (Hayhoe et al. 2004) in much of the assessment area may decrease meadow area and result in a shift to upland/xeric dominated ecosystems (Table 8).

Table 7. Land ownership of contemporary meadows in the Sierra Nevada and Southern Cascades in California bioregional assessment area (Figure 1); area (hectares) provided by individual assessment areas (AA) as well as across the entire assessment area. Data is based on Fryjoff-Hung and Viers (2012). Nineteen of the polygons overlap two assessment areas causing individual hectares to total 902 ha more than the total for the entire AA due to duplication.

Land Ownership	Entire AA	North AA	Central AA	South AA	East AA
USFS National Forest	35658	6507	10353	18316	669
Private	21959	10376	8371	2098	1505
National Park and National Monument	16891	453	8546	8185	0
County, City and Regional Lands	1795	0	56	137	1683
Military	844	0	0	844	0
State Lands - State Lands Commission	219	1	217	0	0
Bureau of Land Management	144	52	1	0	91
California Department of Parks and Recreation	62	28	33	0	0
Regional Park	56	0	0	0	0
Bureau of Indian Affairs	25	5	0	0	20
U.S. Fish and Wildlife Service	5	5	0	0	0
California Department of Forestry and Fire Protection	1	0	0	1	0

Table 8. Potential climate change impacts and meadow vegetation response to the climate change impact in the Sierra Nevada.

Potential Climate Change Impact	Indicator	Variable	Potential Impact to Meadow
Increase in annual fire due to warmer-drier conditions	Fire	Fire return interval	Increase in FRI, until biomass decreases, and fire can no longer be carried. An increase in FRI may bring meadows closer to NRV than under current conditions.
	Hydrologic Regime	Flood Frequency	Increased flood potential in winter and early spring.
Early peak snowmelt and a decrease in spring snowpack combined with an increase in peak daily flow	Hydrologic Regime	Stream Incision	Changes in flow will lead to flashy runoff events which will increase the rate of incision
	Hydrologic Regime	Erosion – Gully formation	Changes in flow will lead to flashy runoff events which will increase the rate of erosion.
	Upland Species Invasion	Conifer Abundance	There will most likely be an increase in the abundance of conifers and some meadows may transition to woodland or evergreen forests as it becomes warmer and drier.
Increasing temperature and decreasing water tables due to a change from snow to rain	Upland Species Invasion	Sagebrush Abundance	Sagebrush may increase in meadows if fire is limited and there is sufficient disturbance for establishment.
	Distribution and Size of Meadows	Meadow Hectares	Meadow area may decrease due to encroachment from upland xeric species; irregularly shaped meadows may be more vulnerable to hydrologic changes compared to compact meadows

Potential Climate Change Impact	Indicator	Variable	Potential Impact to Meadow
Increased temperature combined with drier summers	Productivity	Herbaceous biomass	Decrease in biomass due to a decrease in available moisture, decreasing biomass will also result in a decrease in fire spread.
	Physiognomy	Graminoid/Forb ratio	Potential change in life form ratio due to changing water requirements. Some meadow forbs have been documented to decrease during warming experiments.
	Physiognomy	Wetland species abundance	Decrease in wet meadow species and an increase in dry meadow species
	Diversity	Species Richness	Decrease in richness of species dependent on hydric and mesic conditions, especially species with a narrow thermal tolerance.
	Species Diversity	Number of non-native species	Increase of non-native species

Productivity – Herbaceous biomass

Natural Range of Variation

Meadows are considered to be highly productive systems (Weixelman et al. 2011). The dominance of grasses, sedges, and other herbaceous plant species within meadows results in large amounts of biomass (Dwire and Kauffman 2003). In general, there is an increase in biomass during cool-wet periods and a decrease during warm-dry periods. Fire has also been shown to increase biomass; for example, one study of meadows in the Toiyabe Mountain Range of central Nevada showed a three-fold increase in biomass two years following prescribed fires (Wright and Chambers 2002).

Current Conditions

Contemporary measures of vegetative biomass range from 336 kilograms per hectare (kg ha⁻¹) in dry meadows to 4,484 kg ha⁻¹ in moist to wet sites (Ratliff 1985). In the southern portion of the assessment area (Sequoia and Kings Canyon National Park) biomass declined with increasing elevation and was shown to be less in areas grazed by pack stock, except during wet years (Table 9) (Abbott et al. 2003).

Table 9. Biomass measurements in Sequoia-Kings Canyon National Park from 1995-2000 in meadows grazed by pack stock and in un-grazed meadows (Abbott et al. 2003).

Elevation (meters)	Biomass kg/ha grazed	Biomass kg/ha un-grazed
1828-2132	2,146	2461
2133-2437	1,809	2,176
2438-2742	1,030	1690
2743-3047	647	868
3048-3657	615	691

In his comparison of historic (early 1900's) and more recent photographs (1984 and 1985) from Yosemite Valley, Thomas Vale (1987) noted that meadow sod height and thickness had not changed, but herbaceous meadow density may have increased; this increase in biomass may have been due to livestock grazing which occurred during the period when the early photographs were taken. In more a more recent photographic comparison (1907 to 2008) we see similar trends of meadow density looking as if it has increased (Figure 12).

Comparison of Current Conditions to NRV

Photographic interpretation suggests that biomass is within NRV. Contemporary studies suggest that grazing may have decreased herbaceous biomass within meadows; however, this variable is likely still within the NRV.

Potential Effects from Future Climate

Even if precipitation increases, the change from a snow dominated system to a rain dominated system will likely decrease available water during the growing season, which may cause a decrease in herbaceous biomass (Table 8).

Composition

The mosaic of microhabitats found in meadow ecosystems support diverse plant and animal species (Kattelman and Embury 1996). Meadows are composed of different vegetation communities that change over fine and broad spatial and temporal scales in response to hydrologic influences (Fites-Kaufman et al. 2007). Hydrologic changes, and subsequent shifts in species composition over the past 10,000 years, have most likely been in response to climatic changes; this is evident in large-scale vegetation patterns such as the synchronous response of Holocene vegetation on both the east and west sides of the Sierra Nevada during periods of climatic change (Anderson 1987). In addition to climate, post-European settlement caused changes in species composition have been the result of a number of factors that include fire suppression, grazing, non-native plant invasions, and human use.

It has been suggested that meadow borders were well-defined communities of grasses, sedges, and forbs in the beginning of the 20th century; while some cotemporary meadows still have a sharp meadow border, many meadow borders have become more integrated with the surrounding vegetation as trees and shrubs become scattered through the meadow (Bauer 2002, Berlow et al. 2002, Millar et al. 2004). The invasion of woody species into meadows can reduce the amount of open meadow conditions, alter light and moisture availability, and cause shifts in species composition and productivity (Ratliff 1985, Berlow et al. 2002).

Functional Group Physiognomy – Life Form

Natural Range of Variation

While species composition probably varied within individual meadows during the Holocene, studies of contemporary meadow life forms and their ecological requirements may be used to make inferences about the NRV. The four life forms that are prominently represented in contemporary meadows within the assessment area are grasses, sedges, rushes, and forbs (Fites-Kaufman et al. 2007). A recent classification in Yosemite National Park identifies herbaceous vegetation types as those with more than ten percent cover of graminoids and forbs and less than ten percent cover of woody species (Keeler-Wolf et al. 2012). Shrub and woodland meadows

are considered transitional meadows; shrub meadows generally have 10-40 percent cover of clumped shrubs (primarily willow species) up to 5 m in height (Fites-Kaufman et al. 2007, Keeler-Wolf et al. 2012). As open meadows are converted into tree dominated systems, herbaceous cover decreases and tree cover increases. Woodland meadows have sedges, grasses, and forbs with scattered (25-60% cover) lodgepole and/or aspen trees and conifer forests have trees greater than five meters with 60-100 percent

cover (Fites-Kaufman et al. 2007, Keeler-Wolf et al. 2012).

Disturbances such as fire, seedling predation, and high-water tables are key sources of woody plant mortality and important functions for maintaining high herb cover in meadows (Johnson 1986, Berlow et al. 2002). Fire reduces the density of small trees and may indirectly reduce tree seed germination (Table 10) (Frenzel 2012); fire has also been shown to reduce shrubs like big sagebrush (*Artemisia tridentata* var. *tridentata*) which are not fire tolerant (Wright and Chambers 2002).

Contemporary studies of meadow fires can provide some insight into the influence of fire on community composition. Riparian plants have been shown to have a high recovery rate after fire (Pettit and Naiman 2007). Low intensity fires with short duration consume standing herbaceous fuels and patchy litter but may not result in changes in meadow composition or vegetation cover (Frenzel 2012). High severity fire may reduce the total vegetation cover in meadows; in one meadow in Sequoia and Kings Canyon National Park, Debenedetti and Parsons (1984) documented reestablishment of post-fire vegetation cover within five years of a high severity fire (Debenedetti and Parsons 1984).

Species composition post-fire may largely be determined by pre-fire vegetation with will flux from year to year. Propagules of herbaceous annuals and species with underground regeneration structures (bulbs, corms, tubers, or rhizomes) are more likely to survive a fire (Pyke et al. 2010). Riparian grasses and sedges have been shown to recover rapidly following surface fires by regenerating from roots and rhizomes, especially when there is enough soil moisture so that the fire remains on the soil surface (Boyd et al. 1993, Chang 1996, Dwire and Kauffman 2003). Post fire in the Great Basin, there was a shift in life form abundance; wetter meadows had a greater abundance of perennial grasses post-fire while dry meadow recovery was dominated by forbs (Wright and Chambers 2002). One year after a meadow fire in Sequoia and Kings Canyon National Park there was 8.6 percent cover of annual plants and 30.7 percent cover of bryophytes. After four years, the cover of annual plants decreased to one percent. Over the four years following the fire, cover of graminoid and broadleaf species increased, while bryophytes decreased in cover. Bryophyte cover was highest in the two wettest years; this suggests that changing cover of bryophytes may be linked to moisture conditions rather than early seral colonization following fire (Debenedetti and Parsons 1984).

The selection of certain plant species over others by grazing animals can greatly influence the composition of species within meadows (Ratliff 1985, Menke et al. 1996). For example, native deer preferentially graze meadow forbs, leaves, twigs, and woody material (Table 10). In his study of meadows on the Kern Plateau in the southern Sierra Nevada, Dull (1999) found dramatic shifts in plant assemblages since 1850; his analysis of pollen records suggests a decrease in bryophytes (*Riccia* sp.) and riparian shrubs (*Salix* spp.) and an increase in xeric shrubs (*Artemisia* spp.) and grass-like species in the sedge (Cyperaceae) family. Stratigraphic pollen records suggest that stream incision and the resulting lowering of the meadow water table, as well as more direct impacts of livestock on the meadow (i.e., trampling, defoliation), likely caused these community changes (Dull 1999).

Table 10. Relative life form proportion in meadows compared under different disturbance types

Disturbance	Grasses and Grass-Like (Sedges, Rushes)	Forbs	Shrubs	Trees	Bryophytes	Soil Cover
Grazed Meadows – Cattle, Sheep, Bighorn Sheep*	Lower	Higher	Lower	N/A	Lower	N/A
Grazed Meadows – Deer**	Higher	Lower	N/A	N/A	N/A	N/A
Fire***	Higher (rhizomatous spp.)	Lower	Lower	Lower	Higher	Lower

N/A indicates that the literature did not specifically describe a particular life form's response to that disturbance.

* (Hanley and Hanley 1982, Odion et al. 1988, Dull 1999, Fites-Kaufman et al. 2007)

** (Hanley and Hanley 1982)

*** (Debenedetti and Parsons 1984, Chang 1996, Dwire and Kauffman 2003, Fites-Kaufman et al. 2007)

Current Conditions

Cattle and domestic sheep will forage on forbs and woody plants, but generally favor grass-like species (Table 10) (Hanley and Hanley 1982, Ratliff 1985). This pattern is evident in contemporary meadows. Wet meadows that are grazed at high intensities by livestock generally have more forbs and fewer grasses and grass-like species than meadows that are grazed at lower intensities or are ungrazed (Table 10) (Ratliff 1985, Fites-Kaufman et al. 2007). Higher intensity grazing in meadows can also result in a shift from taller plant species to more low-growing species (Ratliff 1985, Fites-Kaufman et al. 2007). Several studies of riparian meadows in the western US, suggest that sedges (*Carex* sp.) are typically much better able to withstand herbivory than willows (Odion et al. 1988, Green and Kauffman 1995, Dull 1999); however, willows (*Salix* sp.) have been shown to re-establish along riparian zones when grazers are removed (Table 10) (Odion et al. 1988, Dull 1999).

The proportion of plants in various functional groups has been used as an indicator of meadow condition (Weixelman and Gross 2013). High functioning sites are dominated by tall (>60 cm) grasses and grass-like species and tall rhizomatous forbs (Weixelman and Gross 2013). Conversely sites in a more degraded condition have a high proportion of annual species and short tap rooted forbs. Currently, more than half of meadows sampled on National Forest land in the assessment area are considered to be of moderate to high condition (Weixelman and Gross 2013) (Table 11). In general, sites selected to represent grazing impacts are similarly functioning to the larger meadow as summarized across Sierra meadows (Table 11), based on the proportion of plants in various plant functional groups. While a large proportion of meadows in the assessment area on Forest Service land still experience active grazing the Lake Tahoe Basin is a region where active grazing was reduced in 2001 and ceased in 2008; therefore, this data may provide insight into the NRV of meadows. Lake Tahoe basin meadows are dominated by forbs with a high frequency of grass-like (sedges and rushes) species; the majority of these meadows are considered in moderate to high functioning condition (Gross et al. 2013).

Table 11. Meadow vegetation condition class on National Forest lands in the Sierra Nevada. Entire meadow represents samples that were taken across the entire meadow, from edge to edge. Selected sites represent smaller sample plots chosen to best represent the impacts from livestock grazing and thus do not represent the entire meadow. Data summarized from (USDA 2012). There are four condition categories represented: low, moderate, upper moderate, and high. Each category represents the proportions of plants in various plant functional groups (Weixelman and Gross 2013), with high condition having a high proportion of late successional plant species. Conversely sites in low condition have a low proportion of late successional plant species.

Condition Class	Entire Meadow	Selected Sites
Low	15%	7%
Moderate	43%	41%
Upper Moderate	28%	35%
High	14%	17%

Comparison of Current Conditions to NRV

It is difficult to determine if current life form ratios are within the NRV. Meadow specific trends in species composition are determined by both history of disturbance and local hydrology and geomorphic controls. Life form response to disturbances, such as fire and grazing, can provide insight into the NRV. Contemporary studies suggest that the NRV for meadows would have a high proportion of rhizomatous grass and grass-like species (graminoids) compared to forbs and shrubs.

The impact of native grazers on meadow structure, species composition, and function was likely altered with the introduction of domestic livestock to Sierra Nevada meadows in the mid-1800s. A shift from predominantly deer grazed meadow systems during the Holocene to domestic livestock grazing after the mid-1800s may have had large impacts on meadow species composition in the Sierra Nevada. Differences in life form preference between native and domestic grazers suggest that livestock grazing may have increased the proportion of forbs and decreased the proportion of grasses, riparian shrubs and bryophytes. However, the introduction of grazing management in the 1920's has initiated recovery in some meadows, as numbers of livestock continue to be reduced (Figure 10).

Potential Effects from Future Climate

Increasing temperature (Dettinger 2005) may change the ratio of life forms within a meadow. During a warming experiment conducted in the Rocky Mountains of Colorado, Harte and Shaw (1995) found that shrub biomass increased in mountain meadows while forb biomass decreased (Table 8). This change in life form abundance could be linked to rooting depth, and therefore depth to water table.

Functional Group Physiognomy – Wetland Indicator

Natural Range of Variation

The abundance of wetland indicator species likely changed throughout the Holocene in response to

variation in climate and subsequent changes in hydrologic regime. Some mesophytic conifer species declined during the beginning of the Holocene, when the climate was warmer and drier, but increased as the climate cooled and became wetter (Kinney 1996). Based on this, the abundance of some mesophytic meadow species may also have been the greatest during periods of cool wet conditions, such as the Neoglacial period and the Little Ice Age.

In groundwater dependent ecosystems, the depth of the water table can be an important predictor of vegetation composition (Loheide and Gorelick 2007); therefore, contemporary studies of meadow hydrology can provide insight into the NRV. In a number of studies, mean growing season water table depth has been shown to explain the greatest variation in meadow composition (Loheide et al. 2009, Lowry et al. 2011). Several studies have identified one meter as the critical water table height to determine the difference between wet and dry meadow vegetation. Loheide and Gorelick (2007) found that in the north portion of the assessment area on the Plumas National Forest water needs to remain within 1 meter of the surface of the meadow during June and July in order to provide sufficient water for wet meadow species during the growing season, when the water is within 0.5 m of the surface xeric species will perish from waterlogging (Micheli and Kirchner 2002a, Loheide and Gorelick 2007). In the southern portion of the assessment area, along the Kern River at Monache Meadow, Micheli and Kirchner (2002a) found that wet meadow vegetation wouldn't colonize an area if the water table was greater than one meter.

Open wet meadows are abundant in obligate and facultative wet rhizomatous or stoloniferous species that may form dense sod (Odion et al. 1988, Fites-Kaufman et al. 2007, Jones 2011) while drier meadows have more facultative and upland species. Peatlands are composed of obligate and facultative wet (Jones 2011) peat forming species, often with a large bryophyte component. Stream channels tend to be dominated by wetland vegetation. While meadow margins tend to be dominated by upland species unless stream incision has changed the flow of water or groundwater is present near the meadow margin, in which case wetland species will be present along the meadow edge. Loheide and Gorelick (2007) found reverse vegetation patterning occurred along incised stream channels (> 2 m) on the Plumas National Forest. Xeric vegetation occurred along the stream margin, where the soil was driest due to lowering of the water table and mesic vegetation mixed at the meadow border with upland species (Loheide and Gorelick 2007).

Current Conditions

The hydrologic regime has been shown to interact with grazing intensity to affect the composition and distribution of meadow vegetation (Ratliff 1985). Variation in the timing and availability of moisture can result in either a negative or positive growth response to grazing, even among plants of the same species (Hobbs 1996). Studies have shown an increase in stream erosion and incision due to livestock grazing (subsequent grazing section), can cause an increase in xeric species along the stream channel (Loheide and Gorelick 2007). Efforts to restore degraded stream channels can increase wetland plant species within meadows. On the Plumas National Forest, in the north portion of the assessment area, restoration of the stream channel was shown to restore meadow vegetation from xeric to mesic within

one growing season (Loheide and Gorelick 2007). The current ratio of wetland species within meadows is limited to meadow data within the Lake Tahoe Basin, a region where grazing has been reduced over the past decade. In the LTB, there is a high proportion of wetland indicator species in meadows (Gross et al. 2013). While the number of wetland indicator species in the LTB is high, drier areas of the assessment area may have a much lower ratio of wetland species and a higher proportion of drier meadow species. The Forest Service in cooperation with UC Davis is analyzing condition and trend data for more than 600 permanently marked meadow sites in the Sierra-wide and results will be forthcoming on condition and trend from those data.

Comparison of Current Conditions to NRV

Based on the limited available data the current climate likely does not support the ratio of wetland indicator species seen during the principal reference period (1600-1850 AD) but may reflect similar ratios to the early Holocene and Medieval Warm Period. While the proportion of wetland indicator species has changed throughout the Holocene, additional disturbance to the hydrologic regime (e.g., stream incision, dams, and erosion – see previous hydrologic regime section under function) may have decreased the abundance of wetland indicator species compared to the NRV. Incision can lead to meadow drying, resulting in a decrease in wetland plant abundance and an increase in xeric species, compared to the NRV.

Potential Effects from Future Climate

Even if precipitation increases, the change from a snow dominated system to a rain dominated system will likely decrease available water during the growing season. Future changes in climate will likely lead to drier growing seasons (Dettinger 2005) within meadows, which would cause a decrease in wet (obligate and facultative-wet) meadow species and an increase in dry (facultative and upland) meadow species (Table 8) (Lowry et al. 2011).

Species Diversity

Natural Range of Variation

Species Richness

Shifts in species composition have occurred throughout the Pleistocene and Holocene, often in response to climatic changes (D'Antonio et al. 2004). One study of pollen and macrofossil data from several meadows (Balsam Meadow and Dinkey Meadow) in the southern Sierra Nevada show that the same species have been present for the last 5000 years; however, a shift in species abundance occurred, as identified by an increase in fir pollen, ca. 3,000-2,000 YBP (Anderson 1987). In the Great Basin, there was a high diversity of plant species during the neoglacial period, decline in plant species occurred by 2500 YBP when there were severe droughts (Miller et al. 2001). In another study of meadows on the Kern Plateau in the southern Sierra Nevada, Dull (1999) found that prior to the introduction of domestic livestock grazing in the early 1900s, grasses (Poaceae), composites (Asteraceae), and *Riccia*, a genus of

liverwort, dominated upper wet meadows and willows (*Salix* sp.) were abundant in meadow-riparian areas. Microphytic or cryptogammic crusts may have been present in broad upper meadow zones before livestock introduction (Table 10).

While meadows cover a small area relative to other vegetation types, they make substantial contributions to species richness which varies depending on hydrologic regimes and landscape patterns (Jones 2011). Species richness has been shown to increase with decreasing elevation (Jones 2011). There are a number of plant and animal species that depend on the mosaic of meadow interior and edge habitat (Knopf and Samson 1994, Graber 1996); therefore, contemporary population trends for these meadow-dependent species can provide some insight into the NRV. For example, the presence of the Nokomis Fritillary butterfly (*Speyeria nokomis apacheana*), a meadow-adapted species currently in decline, reflects a period of wetter times (Shapiro 1996). Amphibian endemism in the Sierra is probably related to the climatic changes that occurred during the Holocene, causing population isolation and speciation (Graber 1996).

Current Conditions

Species Richness

Multiple meadow communities have been identified in contemporary meadows. Ratliff (1982, 1985) identified 21 vegetation series in meadows during the mid-1980's; Potter (2006) identified eight herbaceous forb dominated associations and nineteen graminoid dominated associations in meadows. A more recent analysis in Yosemite identified 29 meadow associations (Keeler-Wolf et al. 2012). A study of wet meadows in Sequoia and Kings Canyon National Parks identified 220 species in 0.04 hectares (Jones 2011). In contemporary meadows throughout the assessment area, common dominant species in wet meadows include Nebraska sedge (*Carex nebrascensis*) and when there is increased disturbance, Baltic rush (*Juncus balticus* subsp. *ater*) (Fites-Kaufman et al. 2007). Common open dry meadow species include sagebrush sedge (*Carex filifolia* var. *erostrata*), spike false oat (*Trisetum spicatum*), blue grass (*Poa stebbinsii*) in high elevation meadows and Douglas' sedge (*Carex douglasii*), Nevada blue grass (*Poa secunda*), oat grasses (*Danthonia* spp.), and needle grasses (*Achnatherum* and *Stipa* spp.) in low elevation meadows (Fites-Kaufman et al. 2007). The most common shrub species found within, and surrounding Sierra Nevada meadows are willows (*Salix* spp.) (Fites-Kaufman et al. 2007). Willows are often confined to low topographic positions along streams and where there is frequent flooding to provide a favorable moisture balance (Klikoff 1965). When the Sierra Nevada Ecosystem Project (SNEP) was conducted in 1996, there were 116 taxa of plants found in meadows that were considered rare and/or endemic (Shevock 1996).

When meadows convert into conifer or shrub stands, species diversity declines. In Sequoia and Kings Canyon National Parks, montane and subalpine forests and woodlands were identified as the least diverse habitats compared to montane and subalpine meadows which were the most diverse (Jones 2011). The most common tree species found within, and surrounding Sierra Nevada meadows is lodgepole pine (*Pinus contorta* var. *murrayana*) (Wood 1975). Many meadows are surrounded by a

dense growth of lodgepole, some a few hundred years old. It is also common to find clumps of mature lodgepole within the meadow, associated with a large rock or a well-drained site, as well as small stunted lone lodgepole in wetter parts of the meadow (Wood 1975). Other upland tree species that have been documented within meadows include ponderosa pine (*Pinus ponderosa*), Jeffery pine (*Pinus jeffreyi*), white fir (*Abies concolor*), western juniper (*Juniperus occidentalis*) (Norman and Taylor 2005), and aspen (*Populus tremuloides*) (Fites-Kaufman et al. 2007). While there are seven species of sagebrush known to occur in the Sierra Nevada (Weeden 1981), Rothrock sagebrush (*Artemisia rothrockii*) and big sagebrush (*Artemisia tridentata* ssp. *tridentata*) are the most common upland shrubs that invade meadows in the assessment area (Berlow et al. 2002, Wright and Chambers 2002).

Fifty-three percent of the 358 amphibians, reptiles, birds and mammals that occur on forest and range land of the western Sierra Nevada were identified as using meadows (Verner and Boss 1980). This includes 27 percent of the birds, 62 percent of the amphibians, 19 percent of the reptiles, and 30 percent of the mammals identified by Verner and Boss (1980). Some species are only found in meadows, while other species use meadows for forage and/or migration. Many of these have been identified as “at-risk” (Kattelman and Embury 1996). Grazing impacts bird species that utilize meadows by decreasing the density and height of herbaceous growth, which results in a decrease of food (primarily in the form of insects) (Graber 1996). Grazing has been implicated in the decline of willow flycatchers (*Empidonax traillii*) (Sanders and Flett 1989, Kattelman and Embury 1996) and great gray owls (*Strix nebulosa*) (Graber 1996, Powers et al. 2011). The federally endangered willow flycatcher is a species that has frequently been studied in the Sierra Nevada and it has been suggested that the decline of this species could represent the decline of other species (Kattelman and Embury 1996). The true toads (*Bufo* spp.) and true frogs (*Rana* spp.) are the most at risk due to habitat threats including grazing, stream channelization, dams, recreation, changes in hydrology, mining, and the introduction of exotic species (especially fish) (Jennings 1996). Six amphibians are restricted to the Sierra Nevada including the Yosemite toad (*Bufo canorus*), three species of salamanders in the genus *Hydromantes*, and two in the genus *Batrachoseps* (Graber 1996). The mountain yellow legged frog was the most abundant species in montane aquatic habitats during the 1800’s; however due to the introduction of non-native fish in the 1920’s, predation combined with disease outbreaks have caused a decline of this species (Hahn and Curnutt 2012).

In addition to providing habitat for a large number of vertebrates, meadows provide habitat for a large number of invertebrates. In general, fens have greater macroinvertebrate diversity than other meadows (Holmquist et al. 2011). Holmquist et al. (2011) identified 14,805 invertebrates from 147 families in terrestrial and aquatic meadow habitat in the southern portion of the assessment area. Pack stock grazing had limited negative impact on faunal diversity (Holmquist et al. 2013).

Non-native invasive plants

Non-native invasive plants have been dispersed beyond their natural range and historic distribution through human activities (Schwartz et al. 1996). By definition, non-native species in California are those that were introduced after European contact in 1769. The California Invasive Plant Council has

estimated that approximately 100 invasive species occur in the Sierra Nevada and 43 of these are of high management concern (Cal-IPC 2011). Of these 43 species, 18 species invade meadow ecosystems (Cal-IPC 2006). The most common non-native species in Sierra Nevada meadows is Kentucky bluegrass (*Poa pratensis*), which appears to be increasing (Menke et al. 1996). While the frequency, abundance, and cover of non-native species in Sierra Nevada meadows have not been well documented, there are some landscape-level trends that have emerged. The number of non-native species in high elevation meadows is generally fewer than the number of non-native species in meadows at lower elevations (D'Antonio et al. 2004, Underwood et al. 2004, Klinger et al. 2006). This general trend may be due to the inability of many non-native species to survive at higher elevations (Klinger et al. 2006) or to the lower frequency of non-native species introductions in high elevation habitats (Schwartz et al. 1996). The abundance of non-native invasive species may also increase during drought years; for example, in their study of meadows in the central Sierra Nevada, Kluse and Diaz (2005) found that *Poa pratensis* increased in sites with lower soil moisture, while the native bunchgrass *Deschampsia cespitosa* was excluded from drier sites.

Comparison of Current Conditions to NRV

Shifts in species composition have occurred in Sierra Nevada meadows during the past 10,000 years (Wood 1975, Koehler and Anderson 1994, Dull 1999); therefore, range expansions or invasions of some native species into meadows are to be expected and may fall within the NRV (D'Antonio et al. 2004). One exception to this is the introduction and invasion of Sierra meadows by highly aggressive non-native species, which by definition are outside the NRV. Some meadows may still be within NRV where no non-native invasive species have been introduced. There has also been an increase of conifers and shrub species within meadows, shifting open meadows to shrub and woodland meadows causing a decrease in meadow diversity. Moderate grazing can result in increased native plant diversity in wet and mesic meadows and decreased diversity in dry meadows (Ratliff 1985). The diversity of vegetation in meadows may thus be greater than under NRV in wet meadows, especially related to forb diversity.

While expansions and contractions of native species are within the NRV, the rate at which we are losing species is outside of the NRV. Barnosky and others (2011) conclude that global extinction rates are higher than what would be expected under the NRV. The diversity of meadow-dependent animal species, especially birds and amphibians, is lower than the NRV due to the decline of at-risk species. The diversity of vegetation in meadows may be greater than under historic conditions in wet meadows, especially related to forb diversity which has likely increased in response to grazing.

Potential Effects from Future Climate

Pollen analyses reveal that community assemblages were generally dissimilar to widespread plant communities of today (Jackson 2006). This suggests that current plant communities will probably not simply migrate intact to higher latitudes and elevations with warming climates but will likely differ compositionally from contemporary assemblages (Romme et al. 2012), forming novel assemblages. Future changes in climate will affect the abundance, size, and phenology of individual species (de

Valpine and Harte 2001). In some portions of the assessment area, increasing temperatures combined with drier summers (Dettinger 2005) will decrease the abundance of species dependent on hydric and mesic wetland conditions, especially species that have a narrow thermal tolerance (Table 8). During a warming experiment on meadow forbs, deValpine and Harte (2001) found that while biomass did not change significantly, individual species contributions changed; early flowering species responded negatively to the warming.

Changing climatic conditions and the evolution of high-elevation ecotypes may increase the future vulnerability of high elevation Sierra Nevada meadows to invasion by non-native species (Schwartz et al. 1996). Many non-native invasive species are generalists, with broad ecological tolerances; therefore, as temperatures across the Sierra Nevada continue to increase and some meadows become drier, the vulnerability of Sierra Nevada meadows to invasion by non-native species will most likely increase. The California Invasive Plant Council modeled the potential response of 29 non-native plant species in the Sierra Nevada to future climate projections and determined that eight invasive meadow or riparian species could increase their range by the year 2050; of these, six species were predicted to increase by 15 to 99 percent and two species were projected to increase by more than 100 percent (Cal-IPC 2011). Changing climate combined with increasing extinction will continue to move meadow diversity further from NRV during the principal reference period.

ACKNOWLEDGEMENTS

We would like to extend great thanks to all of people who reviewed this document. Their suggestions significantly improved the content and structure of this chapter. Thanks to: Amy Merrill, Becky Estes, Dave Weixelman, Erik Frenzel, Heather Stone, Hugh Safford, Sarah Sawyer, and Sylvia Haultin.

LITERATURE CITED

- Abbott, L. B., R. D. Pieper, and K. E. Young. 2003. Analysis of residual biomass monitoring program in Sequoia and Kings Canyon National Parks., New Mexico State University, Las Cruces, NM.
- Allen, B. H. 1987. Forest and Meadow Ecosystems in California. *Rangelands* 9:125-128.
- Allen-Diaz, B. H. 1991. Water-table and plant-species relationships in Sierra-Nevada meadows. *American Midland Naturalist* 126:30-43.
- Anderson, M. K. 1994. Prehistoric anthropogenic wildland burning by hunter-gatherer societies in the temperate regions: A net source, sink, or neutral to the global carbon budget? *Chemosphere* 29:913-934.
- 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. 1987. Late-Quaternary environments of the Sierra Nevada, California. The University of Arizona, Ann Arbor, MI.
- Anderson, R. S. 1990. Holocene forest development and paleoclimates within the central Sierra Nevada, California. *The Journal of Ecology*:470-489.
- Anderson, R. S. 1996. Postglacial biogeography of Sierra lodgepole pine (*Pinus contorta* var *murrayana*) in California. *Ecoscience* 3:343-351.
- Anderson, R. S., and S. L. Carpenter. 1991. Vegetation changes in Yosemite Valley, Yosemite National Park, California, during the protohistoric period. *Madrono* 38:1-13.
- Anderson, R. S., and S. J. Smith. 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. *Geology* 22:723-726.
- Anderson, R. S., and S. J. Smith. 1997. NATO ASI Series, Sediment Records of Biomass Burning and Global Change. Springer-Verlag, Berlin Heidelberg.
- Austin, J. T. 2012. Floods and Droughts in the Tulare Lake Basin. Sequoia Natural History Association, Three Rivers, CA.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. M. Marshall, Jenny L., E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51-57.
- Bartolome, J. W., D. C. Erman, and C. F. Schwarz. 1990. Stability and Change in Minerotrophic Peatlands, Sierra Nevada of California and Nevada, Berkeley, CA.
- Bauer, K. M., E. L. Berlow and C. M. D'Antonio. 2002. The Relationship between Climate and Rothrock Sagebrush Colonization Patterns. *Journal of Range Management* 55:620-625.
- Beesley, D. 1996. Reconstructing the Landscape: An Environmental History, 1820-1960. Pages 3-24 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.
- Benedict, N. B., and J. Major. 1982. A physiographic classification of subalpine meadows of the Sierra Nevada, California. *Madrono* 29:1-12.
- 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.
- Boyd, R. S., R. A. Woodward, and G. Walter. 1993. Fire effects on a montane Sierra Nevada meadow. *California Fish and Game* 79:115-125.
- Bradley, H. C. 1911. The passing of our mountain meadows. *Sierra Club Bulletin*, Volume 8, pp. 39-42.
- Brown, J. R., and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385-2396.
- Buechner, H. K. 1960. The Bighorn Sheep in the United States, Its Past, Present, and Future. *Wildlife Monographs*:3-174.
- CAL-Fire. 2012. Fire Perimeters California [ds396].
- Cal-IPC. 2006. California Invasive Plant Inventory. Cal-IPC Publication 2006-02. California Invasive Plant Council, Berkeley, CA.
- Cal-IPC. 2011. Prioritizing regional response to invasive plants in the Sierra Nevada. Cal-IPC Publication 2011-1. California Invasive Plant Council, Berkeley, CA. Available: www.cal-ipc.org.
- Carson, E. C., J. C. Knox, and D. M. Mickelson. 2007. Response of bankfull flood magnitudes to Holocene climate change, Uinta Mountains, northeastern Utah. *Geological Society of America Bulletin* 119:1066-1078.
- Chambers, J. C., and J. R. Miller. 2011. *Geomorphology, Hydrology, and Ecology of Great Basin Meadow Complexes: Implications for Management and Restoration*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Chang, C. 1996. Ecosystem responses to fire and variations in fire regimes. Pages 1071-1099 *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.
- Chytrý, M., L. Tichý, and J. Roleček. 2003. Local and regional patterns of species richness in Central European vegetation types along the pH/calcium gradient. *Folia Geobotanica* 38:429-442.
- Coughenour, M. B. 2006. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44:530-542.
- Davis, O. K., and M. J. Moratto. 1988. Evidence for a warm dry early Holocene in the western Sierra Nevada of California: pollen and plant macrofossil analysis of Dinkey and Exchequer Meadows. *Madroño* 35:132-149.
- Davis, O. K., and D. S. Shafer. 2006. *Sporormiella* fungal spores, a palynological means of detecting

- herbivore density. *Paleogeography, Palaeoclimatology, Paleoecology* 237:40-50.
- de Valpine, P., and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82:637-648.
- Debenedetti, S. H., and D. J. Parsons. 1979. Natural fire in subalpine meadows – a case description from the Sierra Nevada. *Journal of Forestry* 77:477-479.
- Debenedetti, S. H., and D. J. Parsons. 1984. Postfire succession in a Sierran subalpine meadow. *American Midland Naturalist* 111:118-125.
- Dettinger, M. D. 2005. From climate-change spaghetti to climate-change distributions for 21st Century California. *San Francisco Estuary and Watershed Science* 3.
- Dodd, M. B., W. K. Lauenroth, I. C. Burke, and P. L. Chapman. 2002. Associations between Vegetation Patterns and Soil Texture in the Shortgrass Steppe. *Plant Ecology* 158:127-137.
- Dull, R. A. 1999. Palynological evidence for 19th century grazing-induced vegetation change in the southern Sierra Nevada, California, USA. *Journal of Biogeography* 26:899-912.
- Dwire, K., and J. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management* 178:61-74.
- Dwire, K. A., J. B. Kauffman, and J. E. Baham. 2006. Plant species distribution in relation to water-table depth and soil redox potential in Montane riparian meadows. *Wetlands* 26:131-146.
- D'Antonio, C. M., E. L. Berlow, and K. A. Haubensak. 2004. Invasive exotic plant species in Sierra Nevada ecosystems. Pages 175-184 in D. D. Murphy and P. A. Stine, editors. *Proceedings of the Sierra Nevada science symposium*; USDA Forest Service Gen. Tech. Rep. PSW-GTR-193. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Edwards, S. W. 1992. Observations on the prehistory and ecology of grazing in California. *Fremontia* 20:3-11.
- Ernst, E. F. 1949. Vanishing meadows in Yosemite Valley. *Yosemite Nature Notes* 28:34-41.
- Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 456-501 in M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. *Terrestrial Vegetation of California*. Third Edition. University of California Press, Berkeley.
- Frenzel, E. 2012. Using prescribed fire to restore tree-invaded mountain meadows: a case study from the Lake Tahoe Basin, California and Nevada USA. University of California, Davis, Davis, CA.
- Fryjoff-Hung, A., and J. Viers. 2012. Sierra Nevada Multi-Source Meadow Polygons Compilation (v 1.0). Page <http://meadows.ucdavis.edu/>. Center for Watershed Sciences, UC Davis, Davis, CA.

- Graber, D. M. 1996. Status of terrestrial vertebrates - Chapter 25. Pages 709-734 Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis, CA.
- Graumlich, L. J. 1993. A 1000-year record of temperature and precipitation in the Sierra-Nevada. *Quaternary Research* 39:249-255.
- Green, D. M., and J. B. Kauffman. 1995. Succession and Livestock Grazing in a Northeastern Oregon Riparian Ecosystem. *Journal of Range Management* 48:307-313.
- Gross, S., D. Weixelman, H. Safford, and E. Frenzel. 2013. (manuscript in progress) Using an Ecological Framework to Track Meadow Function in the Lake Tahoe Basin, CA and NV.
- Gruell, G. E. 2001. Fire in Sierra Nevada forests: a photographic interpretation of ecological change since 1849. Mountain Press Pub. Co., Missoula, Mont.
- Hahn, B. A., and J. L. Curnutt. 2012. Using historical ecology to inform wildlife conservation, restoration, and management. Pages 207-208 in J. A. Wiens, G. D. Hayward, H. D. Safford, and C. M. Giffen, editors. *Historical Environmental Variation in Conservation and Natural Resource Management*. Wiley-Blackwell - A John Wiley & Sons, Ltd, Publication.
- Hanley, T. A., and K. A. Hanley. 1982. Food Resource Partitioning by Sympatric Ungulates on Great Basin Rangeland. *Journal of Range Management* 35:152-158.
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate warming experiment. *Science (New York, NY)* 267:876.
- Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America* 101:12422-12427.
- Helms, J. A. 1987. Invasion of *Pinus contorta* var. *murrayana* (Pinaceae) into mountain meadows at Yosemite National Park, California. *Madrono* 34:91-97.
- Hess, G. W. 2002. Updated techniques for estimating monthly streamflow-duration characteristics at ungaged and partial-record sites in central Nevada. DTIC Document.
- Hobbs, N. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Holmquist, J. G., J. R. Jones, J. Schmidt-Gengenbach, L. F. Pierotti, and J. P. Love. 2011. Terrestrial and Aquatic Macroinvertebrate Assemblages as a Function of Wetland Type across a Mountain Landscape. *Arctic, Antarctic, and Alpine Research* 43:568-584.

- Holmquist, J. G., J. Schmidt-Gengenbach, and S. A. Haultain. 2013. Effects of a Long-Term Disturbance on Arthropods and Vegetation in Subalpine Wetlands: Manifestations of Pack Stock Grazing in Early versus MidSeason. *PloS one* 8:e54109.
- Howes, B. L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation-Reduction Potentials in a Salt Marsh: Spatial Patterns and Interactions with Primary Production. *Limnology and Oceanography* 26:350-360.
- Jackson, S. T. 2006. Vegetation, environment, and time: The origination and termination of ecosystems. *Journal of Vegetation Science* 17:549-557.
- Jennings, M. R. 1996. Status of amphibians - Chapter 31. Pages 921-944 *Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options.* University of California, Centers for Water and Wildland Resources, Davis, CA.
- Johnson, B. R. 1986. Influence of Soil Moisture, Herbaceous Competition, and Small Mammals on Lodgepole Pine (*Pinus contorta* var. *murrayana* (Grev & Balf) Engelm) Seedling Establishment in Sierra Nevada Meadows of California. University of California, Davis.
- Jones, J. R. 2011. Patterns of Floristic Diversity in Wet Meadows and Fens of the Southern Sierra Nevada, California, USA. Colorado State University, Fort Collins, CO.
- Kattelman, R. 1996. Hydrology and Water Resources. Pages 855-920 *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.
- Kattelman, R., and M. Embury. 1996. Riparian Areas and Wetlands - Chapter 5. *Sierra Nevada Ecosystem Project: Final report to Congress, vol. III, Assessments and scientific basis for management options.* University of California Centers for Water and Wildland Resources, Davis, CA.
- Keeler-Wolf, T., P. E. Moore, E. T. Reyes, J. M. Menke, D. N. Johnson, and D. L. Karavidas. 2012. Yosemite National Park vegetation classification and mapping project report. Natural Resource Report NPS/YOSE/ NRR-2012/598. National Park Service, Fort Collins, Colorado.
- Kie, J. 1996. The effects of cattle grazing on optimal foraging in mule deer (*Odocoileus hemionus*). *Forest Ecology and Management* 88:131-138.
- Kie, J., and B. Boroski. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. *Journal of Range Management* 49:482-488.
- Kim, J. G., and E. Rejmankova. 2001. The palaeoecological record of human disturbance in wetlands of the Lake Tahoe Basin. *Journal of Paleolimnology* 25:437-454.

- Kinney, W. C. 1996. Conditions of Rangelands before 1905. Pages 31-45 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.
- Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in central Sierra Nevada. *Ecological Monographs* 35:178-&.
- Klinger, R., E. C. Underwood, and P. E. Moore. 2006. The role of environmental gradients in non-native plant invasion into burnt areas of Yosemite National Park, California. *Diversity and distributions* 12:139-156.
- Kluse, J. S., and B. H. A. Diaz. 2005. Importance of soil moisture and its interaction with competition and clipping for two montane meadow grasses. *Plant Ecology* 176:87-99.
- Knopf, F. L., and F. B. Samson. 1994. Scale perspectives on avian diversity in western riparian ecosystems. *Conservation Biology* 8:669-676.
- Koehler, P. A., and R. S. Anderson. 1994. The paleoecology and stratigraphy of Nichols Meadow, Sierra National Forest, California, USA. *Paleogeography Palaeoclimatology Paleoecology* 112:1-17.
- Kondolf, G. M., R. Kattelman, M. Embury, and D. C. Emran. 1996. Status of Riparian Habitat. Pages 1009-1030 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.
- Kosco, B. H., and J. W. Bartolome. 1981. Forest grazing: past and future. *Journal of Range Management* 34:248-251. Lawton, H. W., P. J. Wilke, M. DeDecker, and W. M. Mason. 1976. Agriculture among the Paiute of Owens Valley. *Journal of California Anthropology*:13-50.
- Lloyd, A. H., and L. J. Graumlich. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology* 78:1199-1210.
- Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer the influence of cattle grazing. *Journal of Wildlife Management* 55:16-26.
- Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. *Journal of Wildlife Management* 51:655-664.
- Loheide, S. P., R. S. Deitchman, D. J. Cooper, E. C. Wolf, C. T. Hammersmark, and J. D. Lundquist. 2009. A framework for understanding the hydroecology of impacted wet meadows in the Sierra Nevada and Cascade Ranges, California, USA. *Hydrogeology Journal* 17:229-246.
- Loheide, S. P., and S. M. Gorelick. 2007. Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. *Water Resources*

Research 43.

- Loomis, J. B., E. R. Loft, D. R. Updike, and J. G. Kie. 1991. Cattle-deer interactions in the Sierra Nevada - a bioeconomic approach. *Journal of Range Management* 44:395-399.
- Lowry, C. S., S. P. Loheide, C. E. Moore, and J. D. Lundquist. 2011. Groundwater controls on vegetation composition and patterning in mountain meadows. *Water Resources Research* 47.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist*:757-773.
- McKelvey, K. S., and J. D. Johnston. 1992. Historical perspectives on forests of the Sierra Nevada and the Transverse Ranges of southern California: forest conditions at the turn of the century. J. Verner, KS McKelvey, BR Noon, RJ Gutiérrez, GI Gould, Jr., and TW Beck, technical coordinators. *The California Spotted Owl: A Technical Assessment of its Current Status*. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-133:225-246.
- McMillin, J. H. 1950. The aboriginal human ecology of the Mountain Meadows area in southwestern Lassen County, California. Sacramento State College, Sacramento, California.
- McNaughton, S. J. 1993. Grasses and grazers, science and management. *Ecological Applications* 3:17-20.
- Menke, J. W., C. Davis, and P. Beesley. 1996. Rangeland Assessment. in V. I. Sierra Nevada Ecosystem Project: Final report to Congress, Assessments, Commissioned Reports, and Background Information., editor. University of California, Davis: Centers for Water and Wildland Resources.
- Meyer, C. B., D. H. Knight, and G. K. Dillon. 2005. Historic range of variability for upland vegetation in the Bighorn National Forest, Wyoming. General Technical Report RMRS-GTR-140. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Micheli, E. R., and J. W. Kirchner. 2002a. Effects of wet meadow riparian vegetation on streambank erosion. 1. Remote sensing measurements of streambank migration and erodibility. *Earth Surface Processes and Landforms* 27:627-639.
- Micheli, E. R., and J. W. Kirchner. 2002b. Effects of wet meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. *Earth Surface Processes and Landforms* 27:687-697.
- Millar, C., and W. Woolfenden. 1999. The role of climate change in interpreting historical variability. *Ecological Applications* 9:1207-1216.
- Millar, C. I. 1996. The Mammoth-June Ecosystem Project, Inyo National Forest. Pages 1273-1346 *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.
- Millar, C. I., R. D. Westfall, D. L. Delany, J. C. King, and L. J. Graumlich. 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. *Arctic Antarctic and Alpine Research* 36:181-200.
- Miller, J., D. Germanoski, K. Waltman, R. Tausch, and J. Chambers. 2001. Influence of late Holocene hillslope processes and landforms on modern channel dynamics in upland watersheds of central Nevada. *Geomorphology* 38:373-391.
- 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 areas: Ecology, management, and restoration*. Island Press, Washington, D.C.
- Miller, N. L., K. E. Bashford, and E. Strem. 2003. Potential impacts of climate change on California hydrology. *Journal of the American Water Resources Association* 39:771-784.
- Momsen, J. H. 1996. Agriculture in the Sierra. Pages 497-528 *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.
- Moritz, M., E. Batllori, M. Krawchuk, M. D. Schwartz, and Nydick. 2013. Southern Sierra ecoregional fire management exercise based on modeling plausible future scenarios: future fire occurrence section. Report in preparation for Sequoia and Kings Canyon National Parks and Sequoia National Forest. California Cooperative Ecosystem Studies Unit, National Park Service, Task Agreement No. J8C07100024.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by Beaver. *BioScience* 38:753-762.
- National Research Council. Committee on Restoration of Aquatic, E.-S., P. Public, S. National Research Council. Water, B. Technology, G. National Research Council. Commission on, and Resources. 1992. *Restoration of aquatic ecosystems: science, technology, and public policy*. National Academies Press.
- Norman, S. P., and A. H. Taylor. 2003. Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California, USA. *Journal of Biogeography* 30:1081-1092.
- Norman, S. P., and A. H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. *Forest Ecology and Management* 215:51-68.
- Norton, J. B., L. J. Jungst, U. Norton, H. R. Olsen, K. W. Tate, and W. R. Horwath. 2011. Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows. *Ecosystems* 14:1217-1231.

- Null, S. E., J. H. Viers, and J. F. Mount. 2010. Hydrologic Response and Watershed Sensitivity to Climate Warming in California's Sierra Nevada. *PLoS ONE* 5:e9932.
- Odion, D. C., T. L. Dudley, and C. M. D'Antonio. 1988. Cattle grazing in southeastern Sierran meadows: ecosystem change and prospects for recovery. Pages 277-292 in *Plant biology of eastern California*, Mary DeDecker Symposium. White Mountain Research Station, Los Angeles, California, USA.
- Parker, A. J. 2002. Fire in Sierra Nevada forests: evaluating the ecological impact of burning by Native Americans. *Fire, native peoples, and the natural landscape*. Edited by TR Vale. Island Press, Washington, DC:233-267.
- Patterson, L., and D. J. Cooper. 2007. The use of hydrologic and ecological indicators for the restoration of drainage ditches and water diversions in a mountain fen, Cascade Range, California. *Wetlands* 27:290-304.
- Peart, D. R. 1989. Species Interactions in a Successional Grassland. III. Effects of Canopy Gaps, Gopher Mounds and Grazing on Colonization. *Journal of Ecology* 77:267-289.
- Pettit, N., and R. Naiman. 2007. Fire in the riparian zone: Characteristics and ecological consequences. *Ecosystems* 10:673-687.
- Polley, H. W., H. S. Mayeux, H. B. Johnson, and C. R. Tischler. 1997. Viewpoint: Atmospheric CO₂, Soil Water, and Shrub/Grass Ratios on Rangelands. *Journal of Range Management* 50:278-284.
- Potter, D. A. 2006. Riparian Plant Community Classification: West Slope, Central and Southern Sierra Nevada, California.
- Powers, B., M. D. Johnson, J. A. LaManna, and A. Rich. 2011. The Influence of Cattle Grazing on Pocket Gophers in the Central Sierra Nevada Mountains, California: Potential Implications for Great Gray Owls. *Northwestern Naturalist* 92:13-18.
- Pyke, D. A., M. L. Brooks, and C. D'Antonio. 2010. Fire as a Restoration Tool: A Decision Framework for Predicting the Control or Enhancement of Plants Using Fire. *Restoration Ecology* 18:274-284.
- Ratliff, R. D. 1982. A Meadow Site Classification for the Sierra Nevada, California. in U. S. D. o. A. F. Service, editor. *Pacific Southwest Forest and Range Experiment Station*, Berkeley, California.
- Ratliff, R. D. 1985. Meadows in the Sierra Nevada of California: state of knowledge. Gen. Tech. Rep. PSW-84. 52 p. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- Romme, W. H., J. A. Wiens, and H. D. Safford. 2012. Setting the stage: Theoretical and conceptual background of historical range of variation. Page 3 in J. A. Wiens, G. D. Hayward, H. D. Safford,

and C. Giffen, M., editors. Historical Environmental Variation in Conservation and Natural Resource Management.

Safford, H. D., and K. M. Van de Water. 2013. (manuscript in progress). Mapping temporal changes in fire frequency across a fire-prone landscape: patterns in fire return interval departure (FRID) on National Forest lands in California, USA. Page 95.

Sanders, S. D., and M. A. Flett. 1989. Montane riparian habitat and willow flycatchers: threats to a sensitive environment and species.-. Pages 262-266. DL Abell (Tech Coord).

Schwartz, M. W., D. J. Porter, J. M. Randall, and K. E. Lyons. 1996. Impact of nonindigenous plants. 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.

Shapiro, A. M. 1996. Status of Butterflies - Chapter 27. Pages 743-757 Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis, CA.

Shevock, J. R. 1996. Status of rare and endemic plants - Chapter 24. Pages 743-757 Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis, CA.

Skinner, C. N., and C. Chang. 1996. Fire regimes, past and present. Sierra Nevada Ecosystem Project, final report to congress, vol. 2, assessment and scientific basis for management options, Wildlands Center Research Report Davis, CA:1041-1069.

SNEP. 1996. Rangelands - Chapter 7. Pages 113-122 Sierra Nevada Ecosystem Project, Final Report to Congress, vol. I, Assessment Summaries and Management Strategies. University of California, Centers for Water and Wildland Resources.

Steward, J. H. 1933. Ethnography of the Owens Valley Paiute. University of California Publications in American Archaeology and Ethnology 33:233-350.

Taylor, A. H. 1990. Tree invasion in meadows of Lassen-Volcanic-National-Park, California. Professional Geographer 42:457-470.

Tilman, D. 1987. Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. Ecological Monographs 57:190-214.

Underwood, E. C., R. Klinger, and P. E. Moore. 2004. Predicting patterns of non-native plant invasions in Yosemite National Park, California, USA. Diversity and distributions 10:447-459.

- USDA, F. S. 2011. Grazing statistical summary. Retrieved from USDA Forest Service website: <http://www.fs.fed.us/rangelands/reports/index.shtml>.
- USDA, F. S. 2012. Region 5 Range Long Term Monitoring Project. USDA Pacific Southwest Region, Vallejo, CA. Vale, T. R. 1977. Forest Changes in the Warner Mountains, California. *Annals of the Association of American Geographers* 67:28-45.
- Vale, T. R. 1987. Vegetation change and park purposes in the high elevations of Yosemite-National-Park, California. *Annals of the Association of American Geographers* 77:1-18.
- Van Auken, O. W., and J. K. Bush. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology* 78:1222-1229.
- Van de Water, K., and M. North. 2010. Fire history of coniferous riparian forests in the Sierra Nevada. *Forest Ecology and Management* 260:384-395.
- 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.
- Vankat, J. 1977. Fire and man in Sequoia-National-Park. *Annals of the Association of American Geographers* 67:17- 27.
- Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia-National-Park, California. *Journal of Biogeography* 5:377-402.
- Veblen, T., W. Baker, G. Montenegro, T. Swetnam, and C. Baisan. 2003. Tree-Ring Reconstructions of Fire and Climate History in the Sierra Nevada and Southwestern United States. Pages 158-195 *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Springer New York.
- Verner, J., and A. S. Boss. 1980. California wildlife and their habitats: western Sierra Nevada. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.
- Viers, J. H., S. E. Purdy, R. A. Peek, A. Fryjoff-Hung, N. R. Santos, J. V. E. Katz, J. D. Emmons, D. V. Dolan, and S. M. Yarnell. 2013. Montane Meadows In The Sierra Nevada.
- Wagner, F. H. 1989. Grazers, past and present. Pages 151 - 162 in L. F. Huenneke and H. Mooney, editors. *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic Publishers, Dordrecht - Printed in the Netherlands.
- Wasserman, N. 2008. Repeat Photograph and the Sierra Nevada Mountains. 100 Years in Tuolumne. Weeden, N. 1981. *A Sierra Nevada Flora*. Wilderness Press.
- Weixelman, D. A., and S. E. Gross. 2013. (manuscript in progress) Plant functional types in relation to disturbance and hydrology in mountain meadows, Sierra Nevada and Southern Cascade ranges, CA.

- Weixelman, D. A., B. Hill, D. J. Cooper, E. L. Berlow, J. H. Viers, S. E. Purdy, A. G. Merrill, and S. G. Gross. 2011. Meadow Hydrogeomorphic Types for the Sierra Nevada and Southern Cascade Ranges in California - A Field Key. Page 34 in U. S. D. o. Agriculture, editor. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Vallejo, CA.
- Weixelman, D. A., and D. C. Zamudio. 2001. Determining ecological status of Sierra Nevada Mountain meadows using plant frequency and soil characteristics. Pages 436-471 in California riparian systems: processes and floodplains management, ecology, and restoration. 2001 Riparian Habitat and Floodplains Conference Proceedings, Riparian Habitat Joint Venture, Sacramento, CA.
- Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78:751-763.
- Westoby, M. 1985. Does heavy grazing usually improve the food resource for grazers? *The American naturalist* 126. Wood, S. H. 1975. Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. Dissertation, California Institute of Technology, Pasadena, California, USA.
- Woolfenden, W. B. 1996. Quaternary Vegetation History. Pages 47-70 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.
- 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.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin. 1995. Steppe-tundra transition A herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist* 146:765-794.