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ASSESSMENT

Sierra Nevada Montane Meadows: Keystone Ecosystems for Carbon Stability and Ecosystem Services Under Climate Change

An Original Research Report for:

California's Fifth Climate Change Assessment

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About California's Fifth Climate Change Assessment

California's Climate Change Assessments are the state's scientific foundation for understanding future climate-related vulnerability across California's regions and systems. Senate Bill 1320 (Stern, 2020) requires the State to report the impacts and risks of climate change across California at least every five years, beginning with California's Fifth Climate Change Assessment (Fifth Assessment). Building on decades of climate research and previous Assessments, the Fifth Assessment presents new findings about California's climate future, with a dedicated focus on Tribal partnerships, public engagement, and communities most vulnerable to climate impacts.

The Fifth Assessment's research and tools are designed to fill knowledge gaps about California's climate future, inspire strategic climate actions, and shape planning, investments, and policies at the state, regional, and local scales. Guided by research priorities identified by state, Tribal, and local leaders, community representatives, and subject matter experts, its findings are designed to help illuminate potential climate futures, the challenges they may present, and the opportunities to build resilience through adaptation pathways.

For the full suite of Fifth Assessment research products, please visit: www.ClimateAssessment.ca.gov.

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Use of Artificial Intelligence (AI):
We acknowledge the use of AI tools in the preparation of this report. More specifically, ChatGPT was used to draft preliminary text based on detailed outlines developed by the authors for some sections of Chapter 2: Synthesis of Sierra Nevada Meadow Science. All AI-generated content was extensively reviewed, edited, and expanded upon through multiple rounds of revision to ensure accuracy. The authors take full responsibility for the content of the published article.

Abstract

Wet meadows are small mountain wetlands that that are interspersed throughout conifer forests of the Sierra Nevada, creating ecotones that support high biodiversity and biological activity. In this report, we synthesize the current state of meadow science to better understand the importance and function of wet meadows, along with their vulnerability to land use and climate change. Sierra Nevada wet meadows provide habitat for wildlife (including special status species), are critical components of watersheds that supply much of California's water, and store large amounts of soil carbon (237±69 Mg C ha^{-1} to 1m). Since Euro-American settlement, widespread meadow degradation has resulted in substantial loss of ecosystem function, including reductions in soil carbon, groundwater storage, and habitat value. Restoration of floodplain hydrology has the potential to reverse these trends, converting meadows from net carbon sources to sinks (net change: ~600 g C m^{-2} y^{-1}), increasing groundwater retention time (~16 days), reducing flood peaks (10-25%), and improving wildlife habitat and biodiversity. Wet meadows enhance watershed resilience and provide important climate refugia, but variation in ecosystem condition and hydrogeomorphic characteristics are also likely to influence their persistence under climate change.

To further evaluate wet meadows as a nature-based climate solution, we measured soil carbon age and persistence across 19 properly functioning, degraded, and restored meadows to 0.75 m. A large proportion of meadow carbon was stabilized through association with mineral particles (mean 64±17% of total soil carbon), with transit times up to ~5,000 years. Properly functioning meadows contained the highest concentrations of both mineral-associated and particulate organic carbon. Restoration increased mineral-associated carbon concentrations and carbon transit times relative to degraded meadows. These findings suggest that carbon stored in Sierra Nevada wet meadow soils is both persistent (mean transit time: 1,324 years) and responsive to management, highlighting meadow conservation and restoration as a durable nature-based climate solution.

Keywords: wetland, carbon sequestration, MAOM, radiocarbon, restoration

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Highlights

- Sierra Nevada wet meadows exhibit long-term resilience to past climate events, but loss of ecosystem services and critical habitat is likely under anthropogenic climate change – particularly in the absence of frequent fire and hydrologic restoration
- Indigenous groups have actively managed and maintained meadows for as long as they have existed in the region, but rapid degradation of meadows began with Euro-American settlement in the early 1800s, and by the early 1900s widespread loss of meadow function and resilience had already occurred
- Meadows are sustained by self-reinforcing feedbacks between vegetation, hydrology, and geomorphology, yet uncertainty about the characteristics of properly functioning meadows and drivers of resilience could hinder effective stewardship and restoration
- Variations in hydrogeomorphology and climate across the Sierra Nevada impact meadow formation and resilience and may be important drivers of the persistence of wet meadows under climate change
- Wet meadows are known to provide valuable habitat for wildlife; however, the relative importance and use of meadows have only been studied for a few species. More work is needed to effectively prioritize and structure restoration for maximum benefit to wildlife and biodiversity
- High rates of vegetative carbon inputs drive soil carbon sequestration and mineral-associated carbon formation in properly functioning and restored wet meadows, resulting in large reservoirs of soil carbon that may be durable to climate warming and can persist for thousands of years

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1: Introduction

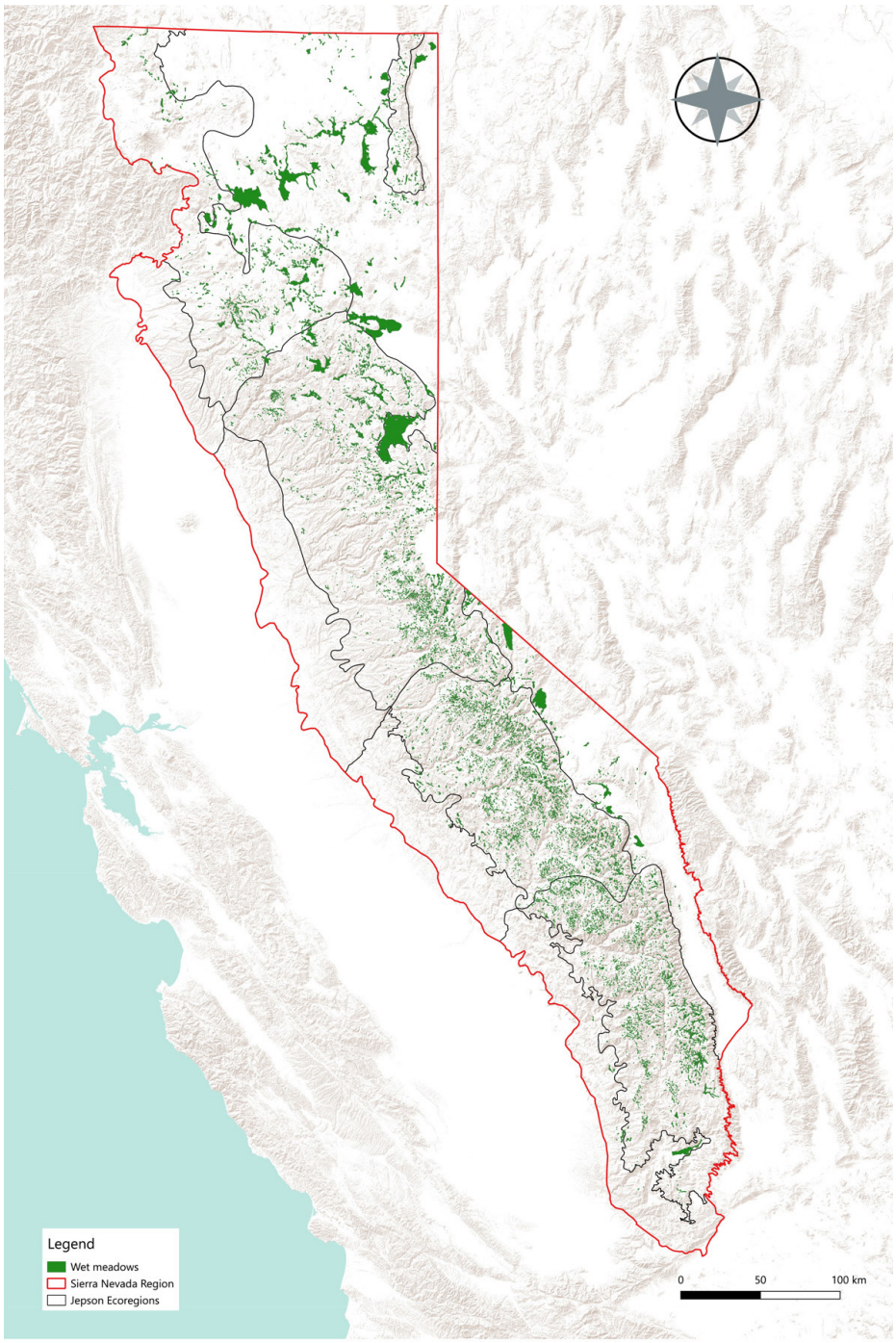
The Sierra Nevada range is often referred to as the "water tower" of California and Nevada because it accumulates snow during the winter months and receives high amounts of annual precipitation that flows downstream during dry periods to other parts of the state. This greater water availability coupled with topographic variability results in a high density and diversity of wetland environments (Cooper et al., 2012; Box 2.1). Mountain wetlands—including wet meadows, marshes, fens, and riparian areas—contribute disproportionately to biogeochemical cycles, watershed hydrology, and habitat. Yet, because of their geographic isolation and relatively small extent, mountain wetlands are often excluded from analyses or grouped with the surrounding uplands.

Within the Sierra Nevada region, wetlands cover over 830,000 acres, or ~3% of the geographic area (United States Fish and Wildlife Service, 2004). Historically, this may have included up to 680,000 acres of wet meadows and over 5,000 acres of fens, though many have been degraded or converted to other land uses. The greatest number of meadows are located in the high Sierra Nevada; however, meadows in the Cascades and Modoc Plateau ecoregions are larger in size, and the greatest total area of historic wet meadow is found within the Modoc Plateau ecoregion (Fig. 1.1).

Long histories of anthropogenic disturbance (e.g., road construction, logging, grazing, agriculture, and fire suppression) have led to the degradation of meadows across the region and dramatically reduced the number of acres that currently support wet meadow habitat. These disturbances catalyze destabilizing feedbacks that lead to channel incision, increased depth to groundwater, changes in vegetation community composition, decreased rates of vegetative productivity, and loss of biodiversity (Essaid & Hill, 2014; Loheide & Gorelick, 2005, 2007). Stream channel incision, and the associated loss of hydrologic connectivity, also converts meadows from net carbon sinks to sources of carbon, further reducing ecosystem resilience and contributing to increasing levels of atmospheric carbon dioxide (Reed et al., 2021). Restoration of floodplain hydrology has been shown to stem carbon losses from degraded meadows and reestablish conditions for soil carbon sequestration (Reed et al., 2022). Further, chemical and physical stabilization of carbon on the surface of soil particles may contribute to the persistence of this newly sequestered carbon. Yet, the long-term persistence of carbon in Sierra Nevada wet meadows—along with the impacts of disturbance and restoration on rates of carbon transit—remain largely unexplored. In order for conservation and management to adequately adapt to changing climate conditions, we need a solid understanding of meadow ecosystem function, the impacts of restoration, and the potential for climate change to alter the ecosystem services they provide and the biodiversity they support.

In this project, we address this need by summarizing the state of the science of Sierra Nevada wet meadow ecosystems and identifying critical gaps in knowledge (Chapter 2). This synthesis covers geomorphology, hydrology, biogeochemistry, and biodiversity of meadows with the goal of better understanding the importance of meadows on the landscape. We explore drivers of ecosystem resilience and vulnerabilities to climate change, along with the impacts of anthropogenic disturbance and restoration on ecosystem function. Additionally, we conduct original science to address an important unknown for climate change adaptation—the long-term persistence of soil carbon in Sierra Nevada wet meadows (Chapter 3). This work combines soil fractionation with radiocarbon dating and transit time modeling in soils from 19 meadows spanning a range of conditions to better understand how carbon cycles in wet meadow ecosystems and provide information about what may be expected of these substantial carbon stocks under future climate conditions.

Figure 1.1: Historic meadows within the Sierra Nevada and southern Cascade regions of California.



Across the region there are almost 16,000 meadows covering more than 680,000 acres. Meadows range in size from 0.05 – 80,624 acres (mean = 42.6 acres, median = 3.4 acres). The red line denotes the boundary of the region, and grey lines show ecoregions within the Sierra Nevada.

2: Synthesis of Sierra Nevada Meadow Science

2.1: The Disproportionate Impact of Meadows

Wet meadows are groundwater-dependent, mineral soil wetlands that occur at all elevation zones within the Sierra Nevada, from foothills to alpine. Low gradient topography and sinuous stream channels slow the flow of water through the ecosystem, contributing to groundwater recharge (Loheide et al., 2009) and attenuating high flow events (Hammersmark et al., 2008; Tague et al., 2008). Shallow groundwater tables and extended periods of saturated and moist soil conditions support diverse herbaceous vegetation interspersed with shrubs and occasionally trees (Allen-Diaz, 1991; Loheide & Gorelick, 2007; Lowry et al., 2011). These productive communities of wetland vegetation provide critical habitat for a wide range of species including invertebrates, birds, mammals, amphibians, and native fish. Productive herbaceous vegetation with dense fine root mats also stabilizes stream channels (Toledo & Kauffman, 2001) and drives high rates of carbon sequestration that supports large soil carbon stocks (Norton et al., 2011, 2014; Reed et al., 2021).

Occurring at the terrestrial-aquatic interface, wet meadows are zones of enhanced biogeochemical activity. While they cover less than 3% of the Sierra Nevada, wet meadows may contain 12-30% of the soil organic carbon stocks (Norton et al., 2011, 2014). Meadows with properly functioning hydrology and dense wetland vegetation can store as much carbon in the top 3 feet (1 m) of soil as Sierra Nevada mixed conifer forest contains above- and belowground combined (Mattson & Zhang, 2019; Reed et al., 2021). However, data from wet meadows across the Sierra Nevada show that soil carbon stock is highly variable and likely influenced by parent material, climate, and disturbance history; soil carbon densities range from 6.09 kg C m^{-2} to 18.62 kg C m^{-2} in the top 1 foot (0.3 m) of soil (mean ± SD = 10.81 ± 2.49 kg C m^{-2}, n = 23 meadows) and from 15.26 kg C m^{-2} to 38.05 kg C m^{-2} in the top 3 feet (1 m) of soil (mean ± SD = 23.68 ± 6.91 kg C m^{-2}, n = 14 meadows; Reed et al., 2021, 2022). These values are similar to densities of soil carbon reported for other blue and teal carbon ecosystems, including Rocky Mountain beaver meadows (Laurel & Wohl, 2019), mangroves (Macreadie et al., 2021), and tidal marshes (Macreadie et al., 2021).

High rates of primary productivity, particularly belowground, drive annual rates of modern carbon sequestration in hydrologically functioning meadows that are similar to other wetlands and exceed values reported for temperate and tropical forests (505.64 ± 239.57 g C m^{-2} y^{-1}; Blackburn et al., 2021; Luyssaert et al., 2007; Reed et al., 2021; Temmink et al., 2022). Globally, wetlands are the largest natural source of methane to the atmosphere (Kayranli et al., 2010). However, in a survey of meadows

across the Sierra, Reed et al. (2021) found that only five of 13 meadows were net sources of methane, with annual rates ranging from 0.04 – 4.8 g C-CH_4 m^{-2} y^{-1}. Periods of methane emission early in the growing season were followed by methane uptake as water tables dropped later in the summer. Even accounting for long-term global warming potential, methane emissions offset less than 10% of net carbon sequestration, and methane emissions were only greater than 1% of the net carbon budget in the wettest meadow sampled (Reed et al., 2021). Blankinship & Hart (2014) similarly found that net methane emission was rare, and methane uptake consistently occurred, particularly under drier conditions. Higher mineral soil content in meadows relative to peatlands and organic soil wetlands may also increase the residence time of this newly sequestered carbon through physico-chemical interactions with the mineral matrix (see Chapter 3 for more details).

Wet meadows provide critical habitat and are key to supporting biodiversity in the Sierra Nevada. Many species are dependent on meadows, disproportionately use meadows, or reach their greatest abundance in meadows; it is estimated that 20% of terrestrial vertebrates in the Sierra Nevada are dependent riparian habitats, including meadows, to sustain viable populations (Graber, 1996). Healthy meadows support a high abundance and diversity of breeding birds (Campos & Burnett, 2014) and a bird community distinct from adjacent upland habitats (Siegel & DeSante, 1999). In the Northern Sierra and Southern Cascades, Humple and Burnett, (2010) found Yellow Warblers (*Setophaga petechia*) to be 31 times more abundant in meadows than in upland habitats. The productivity of birds breeding in wet meadows may be higher than the surrounding upland habitats (Cain III & Morrison, 2003). Adult survival rates are also higher relative to other riparian habitats in the greater region (Burnett et al., 2004). During the post-breeding period meadows can support a high abundance of species that breed in adjacent or lower elevation upland habitats, in addition to meadow breeding birds (Burnett & Geupel, 2001).

California's state fish, the California golden trout, is dependent on meadows in its native range (Moyle, 2002). Several species of amphibians (Brown et al., 2014; Shaffer et al., 2000) and macro invertebrates (Albu & Albu, 2023; Erman, 1996; Jewett Jr., 1963; Wagner & Crabtree, 2018) are also endemic to Sierra Nevada wet meadows. Native species of amphibians depend on the complexity of healthy meadows at all life stages, particularly at lower and mid-elevations where lakes are limited (Morton & Pereyra, 2010; Savage et al., 2010; Yarnell et al., 2019). As diverse and semi-permanent islands of flowering plants in a sea of gymnosperms, wet meadows and fens contain many plant species absent from surrounding habitats (Baldwin et al., 2012). Consequently, they support higher abundances of bumble bees, butterflies, and other insects than the surrounding forests (Holmquist et al., 2011; Tarbill et al., 2023).

Sierra Nevada meadows may also be important for mammals of all sizes, from small rodents to large carnivores. Some mammals (e.g., meadow voles, bats, and female mule deer) preferentially use meadows or riparian areas relative to the surrounding uplands (Campos, 2023; Kalinowski et al., 2014; Loft et al., 1991). One report shows that bat activity may be two to three times higher in meadows than nearby forests (Campos, 2023). Other species (e.g., pine marten (*Martes martes*)) prefer meadow edge habitat (Spencer et al., 1983) or rely on meadows for foraging (e.g., Great-gray Owl (*Strix nebulosa*); Kalinowski et al., 2014). One mammal, the American beaver (*Castor canadensis*), is thought to play a keystone role in shaping meadow form and function (Polvi & Wohl, 2012). Active beaver modification of riparian areas and meadows increases habitat abundance and diversity, indirectly benefiting other species while also supporting ecosystem function and resilience (Wohl, 2021). Wet meadows are crucial habitat for many special status species including four species of birds (Greater Sandhill Crane (*Grus canadensis*), Great Gray Owl (*Strix nebulosa*), Willow Flycatcher (*Empidonax traillii*), and Yellow Warbler (*Setophaga petechia*)) and five amphibians (Cascade's Frog (*Rana cascadae*), Sierra Nevada Yellow-legged Frog (*Rana sierrae*), southern Mountain Yellow-legged Frog (*Rana muscosa*), Yosemite Toad (*Anaxyrus canorus*), and Long-toed Salamander (*Ambystoma macrodactylum*)). Streams in some wet meadows also provide important habitats for a number of native trout species including Eagle Lake Rainbow (*Oncorhynchus mykiss aquilarum*), Lahontan Cutthroat (*Oncorhynchus henshawi henshawi*), and California Golden Trout (*Oncorhynchus aguabonita*) and are important habitats for large numbers of mammals including migratory deer. However, many of the reports on meadow use by wildlife are based on expert opinion, and only a few species' habitat use patterns have been documented with empirical data.

2.1.1: Scope of the Synthesis

The objective of this synthesis is to summarize the current state of the science around Sierra Nevada wet meadows along with the impacts of anthropogenic disturbance, climate change, and restoration on ecosystem function in meadows. We focus primarily on peer-reviewed scientific literature but have supplemented our review with reports, dissertations, and master's theses where other studies were unavailable. We also endeavored to limit our review to work done in the Sierra Nevada. Wet meadows exist in mountain ranges throughout the world, but meadow research from other regions may be less relevant due to differences in climate, geology, and land-use history. Where literature was lacking on Sierra Nevada meadows, we have included findings from other regions while noting the location of those findings. Wet meadows are one type of mountain wetland found within the Sierra Nevada—along with marshes, fens, and riparian areas. As detailed in Box 2.1, wet meadows are distinguished from other mountain wetlands by differences in their hydroperiod, substrate, and vegetation. The definitions presented here, along with other methods of wetland taxonomy (e.g., Ratliff, 1982, 1985; Weixelman et al., 2011), help us

conceptualize wet meadow environments and meet the human need to describe and categorize ecosystems. However, in reality, many mountain wetlands fall somewhere along a continuum between wetland types and coexist in diverse wetland complexes supported by dynamic combinations of snowmelt, surface flows, and groundwater. This synthesis focuses primarily on wet meadows but includes some discussion of other mountain wetland ecosystems. Many of the benefits and functions of wet meadows discussed here apply to other mountain wetlands as well.

Box 2.1: Taxonomy of mountain wetlands

Wet meadows: groundwater-dependent, mineral soil wetlands that occur in all elevation zones within the Sierra Nevada from the foothills to the alpine zone. Wet meadows occur in low gradient basins where water and fine sediment accumulate from the surrounding uplands, creating extended periods of saturated soil conditions that support hydric and mesic vegetation (Allen-Diaz, 1991; Hammersmark et al., 2008; Loheide et al., 2009). Wet meadows are not perennially saturated and, as a result, have little or no peat accumulation.

Fens: perennially saturated, groundwater-supported, peat-forming wetlands that occur in isolation or adjacent to wet meadows in the Sierra Nevada (Cooper et al., 2012; Wolf & Cooper, 2015). Fens form through infilling of small lakes or ponds, where groundwater discharges from geologic discontinuities, or at localized points of groundwater discharge including discharge slopes (Wolf & Cooper, 2015).

Marshes: periodically inundated with standing water that limits vegetation to aquatic or emergent herbaceous species but may also dry out during periods of drought.

Riparian areas: form along stream channels and often occur at steeper slopes or in narrow drainages than wet meadows. Woody species (e.g. aspen, alder, and willow) are common in riparian areas and may be more dominant than in meadows (Cooper et al., 2012).

2.2: Meadow Formation and Function

2.2.1: Formation and Persistence of Sierra Nevada Meadows

At the geologic core of the range lies the Sierra Nevada Batholith, a large mass of igneous rock primarily composed of fractured granites that formed 87-115 million years ago. Debate persists over the timing of the primary uplift of the Sierra Nevada. However, recent studies suggest Early and Late Cenozoic uplift phases, punctuated by periods of erosion and complex incision (Beeson & McCoy, 2022; Wakabayashi &

Sawyer, 2001). There is also evidence that relatively recent (2-11 Ma) uplift may have occurred and contributed to meadow formation (Beeson & McCoy, 2022). During the Miocene (20–5 Ma), portions of the northern and central Sierra Nevada region were blanketed by lava and pyroclastic flows, producing thick soils and deep aquifers with high water storage capacity (Ericson et al., 2005). In contrast, extensive and repeated Pleistocene glaciations sculpted deep valleys that transported sediment and altered drainage networks in the central and southern regions (Huber, 1990; Small & Anderson, 1995). These glacial events left a legacy of thin soils and exposed bedrock in many southern Sierra headwater streams (Ericson et al., 2005) but also contributed to the formation of low-gradient surfaces upon which many meadows are formed (Wood, 1975).

Low-gradient basins provide the geomorphic conditions needed for meadow formation—what Benedict and Major (1982) termed the "geologic stability" of meadows. In turn, biological stability—an ecosystem's ability to persist and recover—depends on the combination of geology, climate, and successional processes. Traditional models have framed meadow development as a linear progression from open water to marsh, meadow, and ultimately forest, driven by processes of sediment accumulation and ecological succession. This simplified framework has contributed to the idea that meadows are fragile and transitional ecosystems and would imply that meadow formation is limited to places that were once open water (e.g., proglacial lakes or tarns). However, few meadows in the Sierra Nevada are underlain by lake deposits, and many occur on slopes, in unglaciated valleys, or interfluves, suggesting that hydrogeomorphic factors that promote shallow water tables may instead be the critical driver of meadow distribution and persistence In the Sierra Nevada (Wood 1975).

Palaeoecological evidence supports the idea that meadows are resilient and persistent ecosystems with levels of biological stability that mirror the surrounding forest; buried layers of peat over 10,000 years old appear in meadows throughout the Sierra Nevada (Anderson & Smith, 1994; Wood, 1975). Further, alternating alluvial- and forest-derived layers in many meadow palaeoecological records suggest climate-induced shifts in precipitation and vegetation, not orderly succession, govern meadow development and persistence. During periods of extreme drought and warm-dry conditions (e.g., the early Holocene and Medieval Climate Anomaly), many meadows transitioned to forests or other xeric vegetation (Koehler & Andrson, 1994; Wood, 1975). In contrast, during cooler and wetter periods (e.g., late Holocene neoglacial cooling and the Little Ice Age) higher groundwater levels excluded conifers, initiated conditions for peat formation, and led to meadow reestablishment (Koehler & Andrson, 1994).

Biotic agents have also played an important role in shaping Sierra Nevada meadows. Fallen trees can trap sediment and contribute to the formation of low gradient basins (Koehler & Andrson, 1994). Beaver are also capable of transforming streams into

ponded wetlands, altering hydrologic flows, sediment retention, and vegetation community composition (Westbrook et al., 2011). Ethnographic and physical evidence indicates that beaver were present in the Sierra above 1,600 feet (James & Lanman, 2012; Lanman et al., 2012), and remnants of historic dams are still found, often exposed by stream channel incision. Research in the Colorado Rocky Mountains has described how beaver dams, and their occasional failure, can have long-term impacts on both small headwater systems and larger floodplain terraces (Polvi & Wohl, 2012; Westbrook et al., 2011).

2.2.2: Ecosystem Function in Meadows

Ecosystem function in wet meadows depends on stabilizing feedbacks between vegetation, biota, hydrology, and geomorphology and frequent influence from natural disturbances (e.g., floods and fire). These feedbacks are critical for meadow formation, help ensure long-term persistence under changing climate conditions, contribute to ecosystem services, and help support high levels of biodiversity (Fig. 2.1).

2.2.2.1 Hydrology

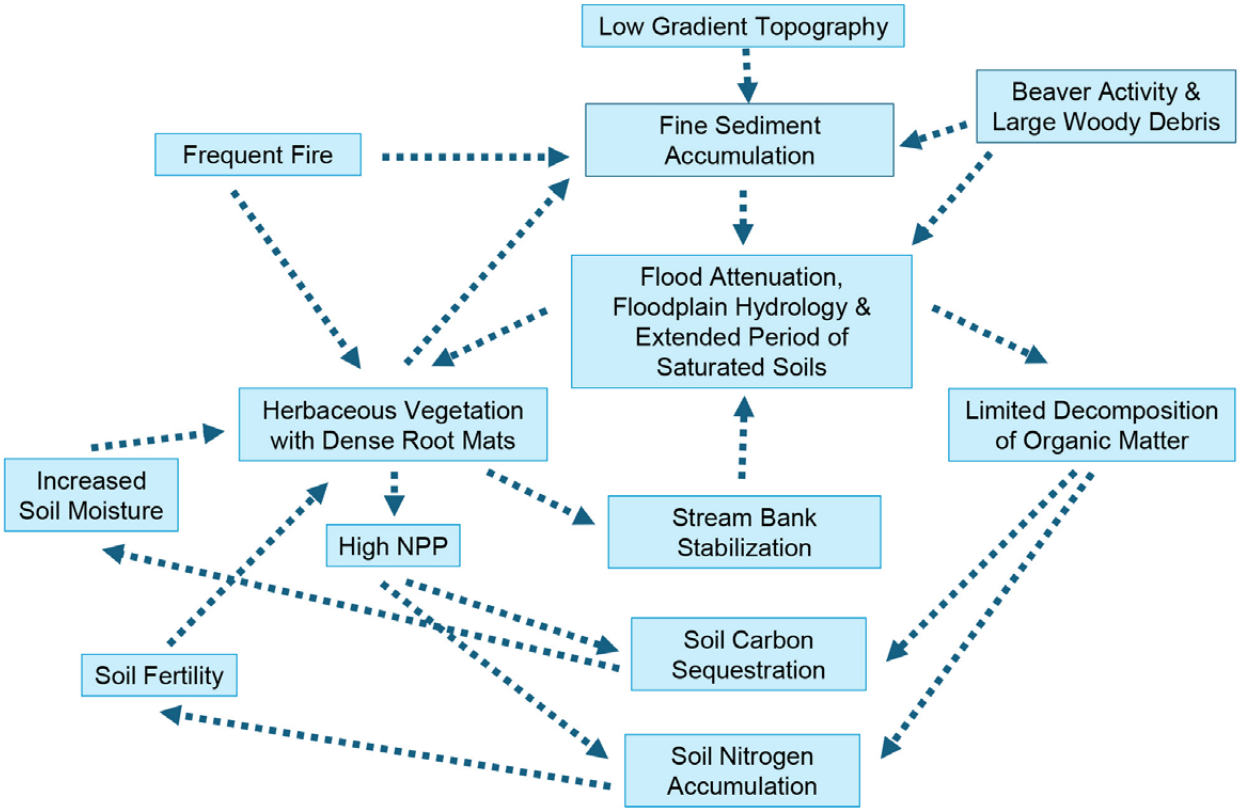
Accumulation of fine sediment in low-gradient valleys slows the flow of water through meadows, dispersing high flows and creating prolonged periods of saturated soils that support hydric and mesic vegetation (Fig. 2.1; Loheide et al., 2009). Dense root mats of herbaceous wetland species stabilize fine sediments and shallow streambanks, enhancing lateral connectivity and infiltration during high flows (Micheli & Kirchner, 2002). In addition to overbank flows, wet meadow vegetation is sustained by groundwater inputs that help maintain shallow water tables through the region's warm, dry summers (Loheide et al., 2009; Lowry & Loheide, 2010).

Groundwater can enter meadows through upward flow from bedrock (basal flow), lateral inflow from adjacent slopes, or stream recharge (Loheide et al., 2009). The rate and distribution of groundwater movement into and out of meadows are governed by the ability of water to move through meadow sediments and the surrounding bedrock, known as hydraulic conductivity (Essaid & Hill, 2014; Hill & Mitchell-Bruker, 2010; Loheide et al., 2009). Across the region, bedrock hydraulic conductivity varies widely, from roughly 1 cm/s in the fractured basalt of northern and northeastern Sierra Nevada to as low as 10-9 cm/s in unglaciated granite of the central Sierra (Hill & Mitchell-Bruker, 2010). Within meadows, hydraulic conductivity can also vary with depth, influencing both the direction and magnitude of groundwater discharge (Hill & Mitchell-Bruker, 2010; Loheide et al., 2009). Wet meadow conditions are generally favored by high rates of groundwater inflow from bedrock with high hydraulic conductivity into meadow sediments with lower hydraulic conductivity, producing a higher ratio of lateral to basal groundwater inflow (Essaid and Hill, 2014, Loheide et al., 2009).

Low gradient topography and fine sediments stabilized by dense root mats also increase the residence time of water in wet meadows and promote mixing of surface water with shallow groundwater. This hyporheic exchange may be further enhanced in wet meadows by snowmelt-induced pumping and water table fluctuations linked to diel variation in rates of evapotranspiration (Loheide II & Lundquist, 2009). Groundwater and surface water exchange contributes to thermal stratification of pools, creating refugia for cold-water fish species including salmonids (Lucas et al., 2016). In other wetland systems, hyporheic exchange has also been shown to attenuate contaminants through biodegradation, sorption, and phytoremediation (Johnston, 1991; Overton et al., 2022; Reddy et al., 1999). Properly functioning riparian meadows in the southern Sierra Nevada have been shown to remove anthropogenic nitrogen from runoff; robust microbial and vegetation communities in meadow soils assimilate nitrogen flushed from upland soils by spring runoff (Sickman et al., 2003; Williams et al., 1995). The capacity of Sierra Nevada meadows to filter other contaminants, however, remains unknown. In general, the degree of hydrologic connectivity between a wetland and the surrounding watershed impacts both the type and concentration of contaminant inputs as well as the rate of biogeochemical transformation of these inputs. The duration and seasonality of inundation may also impact the capacity of wetlands to alter water chemistry (Schlesinger & Bernhardt, 2013; Winikoff & Finlay, 2023).

Little work has been done to assess the capacity of meadows to attenuate flood events downstream. Increases in stream channel sinuosity and floodplain connectivity linked to restoration in low gradient meadows have been shown to delay and reduce the magnitude of high flow events (Hammersmark et al., 2008; Ohara et al., 2014; Tague et al., 2008). In the southwestern United States, larger wetlands and those higher up in the watershed were shown to have the greatest impacts on downstream flood depth and duration (Tang et al., 2020). However, other studies have noted the challenges associated with quantifying the impact of headwater wetlands on flood attenuation due to processes operating elsewhere in the catchment (Hoden 2013). Meadow vegetation type (which impacts flow resistance), proximity to perennial stream channels, hydraulic conductivity, slope, upland topography, and soil moisture status may additionally impact flood attenuation capacity (Acreman & Holden, 2013; Ameli & Creed, 2019), and the influence of these factors on Sierra Nevada meadows needs to be better understood.

Figure 2.1: Model of stabilizing feedbacks that support wet meadow formation and ecosystem function.



This model shows stabilizing feedbacks in low gradient, riparian meadows where low gradient topography and fine sediment stabilized by dense root mats slow the flow of water through the ecosystem, creating conditions that support wetland vegetation and high rates of carbon accumulation. In discharge slope wetlands and groundwater dependent wetlands, perennial groundwater discharge supports hydric vegetation that provide valuable habitat and carbon sequestration.

It is important to note that most existing knowledge of Sierra Nevada meadow hydrology comes from studies evaluating the impacts of hydrologic restoration, rather than studies on the functioning of undegraded meadows. Further, many rely on models validated with data from a single site to simulate groundwater recharge, flood attenuation, and streamflow under varying levels of channel incision. Models can be useful for systematically exploring hydrologic responses to incision and restoration, particularly given the impact of interannual climate variability on meadow hydrology (Essaid & Hill, 2014; Ohara et al., 2014). However, the paucity of research on pristine or properly functioning meadows limits our ability to assess baseline function and determine whether restoration activities are successful in restoring hydrologic processes.

2.2.2.2 Vegetation

Wet meadows have diverse and productive vegetative communities composed of species that have adapted to grow in mountain wetland conditions—relatively short growing seasons, extended periods of saturated soil conditions, and frequent disturbance from overbank flooding. As a result, meadow vegetation is dominated by disturbance-adapted, herbaceous hydric and mesic species, including sedges (*Carex* spp.), rushes (*Juncus* spp.), grasses, and perennial forbs (Allen-Diaz 1991, Sanderson 1967, Strand 1972). In ungrazed wet meadows, aboveground herbaceous vegetation can be 2-3 feet (1 m) high by mid-summer at montane elevations and 1 foot (0.3 m) high in subalpine meadows (Wood, 1975). Up to 80% of vegetation biomass in some common wet meadow species occurs belowground as sinuous fine roots and rhizomes that stabilize the soil and influence biogeochemical processes (Dwire et al., 2004; Reed et al., 2021). In addition to herbaceous plants, many wet meadows contain woody shrubs like willows (*Salix* sp.), which increase the habitat complexity and functional diversity of the overall vegetation community.

Water table depth and seasonal patterns of water table fluctuations, water chemistry, and elevation are the primary drivers of vegetation community composition in wet meadows (Allen-Diaz, 1991; Hammersmark et al., 2009, 2010; Jones, 2011; Wolf & Cooper, 2015). Saturated soils early in the growing season create anaerobic conditions that exclude xeric species, including most conifers and upland shrubs (Fig. 2.1; Dwire et al., 2006; Loheide & Gorelick, 2007; Lowry et al., 2011), and support highly productive hydric and mesic vegetation (Allen-Diaz, 1991). In order for hydric and mesic species to reproduce, water tables must remain within 3 feet (1 m) of the soil surface through peak productivity (Loheide & Gorelick, 2007). Following senescence, shallow water tables are no longer required for vegetative growth (Loheide & Gorelick, 2007) and can drop below 3 feet (1 m) later in the summer, even in meadows with connected floodplain hydrology (Hammersmark et al., 2009). Meadows with fine grained soils can support hydric and mesic vegetation with slightly deeper water tables as high rates of capillary action allow larger volumes of water to be stored in the soil above the water table. Higher concentrations of soil organic matter also increase the amount of plant available water that can be stored in the rooting zone, delaying the onset of water stress in plants by days to weeks (Ankenbauer & Loheide, 2017).

Physiological traits that enable wet meadow vegetation to cope with short growing seasons and shallow water tables also allow them to respond rapidly to fluvial disturbances and fire. Allocation of nutrients and nonstructural carbohydrates to belowground biomass following peak productivity in sedges, rushes, and perennial herbs facilitates rapid growth following spring snowmelt and aids regeneration after fire (Bernard et al., 1988; Steele et al., 1984). Clonal reproduction in many sedges and rushes also facilitates rapid recovery following fluvial disturbance and fire. In order to maintain aerobic root respiration under saturated soil conditions, roots of

wetland plants release oxygen into the soil through aerenchymous tissues (Mainiero & Kazda, 2005). This oxygen release allows for nutrient absorption and root growth under saturated conditions while also impacting soil microbial communities and biogeochemical processes (Waldo et al., 2022).

2.2.2.3 Biogeochemistry

The biogeomorphic feedbacks that form and sustain wet meadows include self-reinforcing interactions among vegetation, hydrology, and geomorphology that drive biogeochemical reactions and rates of carbon sequestration. In contrast to "decomposition limiting" wetlands, where environmental controls on decomposition lead to net carbon accumulation despite lower levels of productivity, wet meadows are "productivity stimulating" ecosystems where carbon storage is driven by high rates of carbon inputs. These inputs come from feedbacks that increase resource availability, stimulate vegetative productivity, and lead to high rates of organic matter production (Morra et al., 2023c; Reed et al., 2021; Temmink et al., 2022). Using a biometric approach to quantifying annual net carbon fluxes, Reed et al. (2021) found that rates of heterotrophic respiration were not significantly different between meadows that were gaining and losing carbon, and heterotrophic respiration remained high even under saturated soils conditions. Net carbon inputs, on the other hand, were significantly different between meadows and appear to be the primary driver of the direction and magnitude of net carbon flux (Morra et al., 2023c; Reed et al., 2021). High rates of vegetative carbon inputs in wet meadows are sustained by optimal growing conditions for hydric and mesic vegetation—extended periods of saturated and moist soils, sufficient nutrients, warm growing season temperatures, ample sunlight, and low carbon use efficiency. However, controls on vegetative growth and the impacts of changing environmental conditions on belowground carbon allocation in these ecosystems remain largely unexplored (but see Morra et al., 2023c).

High rates of belowground vegetative productivity also contribute to the persistence of soil carbon in meadows through associations between organic molecules and mineral soil (Morra et al., 2023b). Carbon that is stabilized through mineral association is considered to be more persistent than particulate organic matter and may remain in the ecosystem for hundreds to thousands of years (Torn et al., 1997, 2009, but see Jilling et al., 2025). Wet meadows have been shown to store high concentrations of carbon associated with soil minerals relative to other ecosystems (see Chapter 3: Soil Carbon Age and Persistence Technical Report for more details). Further, the formation and persistence of mineral associated organic matter appears to be driven by high rates of productivity and belowground carbon allocation (Bagcilar et al., 2024; Morra et al., 2023b).

Higher soil mineral content in meadows relative to other wetlands provide alternate electron acceptors that suppress methane production and contribute to high rates of soil respiration during periods of low soil oxygen (Reed et al., 2021, 2023). Seasonal

fluctuations in water tables and release of oxygen belowground by aerenchymous plants with dense root mats may further help maintain soil oxidation-reduction potentials above the zone of high methane emissions and increase the availability of alternate electron acceptors for heterotrophic respiration (Mainiero & Kazda, 2005; Reed et al., 2023). Preliminary findings suggest that Sierra Nevada wet meadows may be able to act as terrestrial carbon sinks without producing substantial amounts of methane to the atmosphere; however, the drivers and controls on methane fluxes in wet meadows remain largely unexplored.

Compared to water and carbon cycles, the roles of other element cycles, their interactions, and microbial influences in Sierra Nevada wet meadows are less understood. Nutrient availability has been shown to limit vegetative growth in European wet meadows (van der Hoek et al., 2004; Venterink, 2001) and alpine grasslands in the Qinghai-Tibetan Plateau (Dong et al., 2023; Sun et al., 2023). Globally, nutrient limitations and microbial activity are widely recognized as constraining rates of carbon sequestration and stabilization (Cotrufo et al., 2013, 2019; Sokol & Bradford, 2019). Yet, the limits to vegetative growth and carbon sequestration in Sierra Nevada wet meadows have not been studied.

2.2.2.4 Biodiversity

Patterns of high biodiversity in meadows likely stem from the wide range of hydrologic niches, which support diverse vegetation communities (Allen-Diaz, 1991; Lowry et al., 2011), and in turn, provide habitats for a variety of wildlife (Tarbill et al., 2023, 2024). In addition, long-term processes, such as repeated glaciation cycles, have shaped species distributions and diversification of Sierra Nevada ecosystems, contributing to the biodiversity observed today (Weng et al., 2021).

Bird communities in Sierra Nevada meadows reflect this ecological complexity. Meadow-dependent species rely on a variety of habitat and vegetation structures (Cain III & Morrison, 2003; Campos et al., 2020; Campos & Burnett, 2014; Ivey & Herziger, 2001; Mathewson et al., 2012). For example, willow thickets provide essential nesting and foraging habitat for many species such as Willow Flycatcher (*Empidonax traillii*), while wetter, open meadows support species like Sandhill Crane (*Grus canadensis*) and Wilson's Snipe (*Gallinago delicata*) (Campos et al., 2020; Ivey & Herziger, 2001; Mathewson et al., 2012). Habitat modification, whether through hydrologic degradation or changes in vegetation composition and structure, has been linked to shifts in these bird communities (Campos et al., 2020). Species distributions also vary with elevation (Siegel et al., 2014), and, as a result, few individual meadows support the full diversity of meadow-associated birds found across the Sierra Nevada.

Fish-bearing streams in meadows are predominantly small first and second order streams with small catchment areas. Hydrologic variables (i.e., annual 7-day minimum discharge, maximum winter discharge, and number of distinct winter floods) and habitat variables (i.e., percentage of pool habitat, percentage of gravel substrate, sedges, undercut banks, and aquatic vegetation) explain most of the variation in assemblage structure of native fishes that have been studied (Kiernan & Moyle, 2012; Knapp et al. 1998; Matthews, 1996a, 1996b). Interactions between surface water and groundwater in meadows, along with shade provided by streamside shrubs, help maintain cooler stream temperatures and provide refugia for cold water fish (Lucas et al., 2016).

Wet meadows are also hot spots of vegetative diversity, however, few quantitative assessments of their contribution to biodiversity of the Sierra Nevada have been conducted. Jones (2011) measured floristic diversity across Sequoia and Kings Canyon National Parks and found that montane and subalpine wet meadows were among the most species rich assemblages. Combined, these two ecosystem types had the highest number of species and 12% of species with special status, even though wet meadows covered only 2% of the study area (Jones, 2011). Biological diversity and the distribution of species richness within meadows may also be driven by water table and oxygen availability. Studies in wet meadows in northeastern Oregon and the Qinghai-Tibetan Plateau have found species richness to be inversely related to water table depth and aboveground biomass and positively related to soil oxygen availability (Dwire et al., 2004; Wu et al., 2013). However, similar assessments have not been made for the Sierra Nevada.

2.3: Vulnerabilities and Stressors

2.3.1: Anthropogenic Disturbance

2.3.1.1 Historic Disturbances

Humans have likely utilized Sierra Nevada meadow resources and, to varying degrees, managed these meadows for as long as they have existed in the region. Historically, Indigenous groups used management practices including fire, pruning, selective harvesting, sowing, and weeding to maintain open meadows, improve forage, and increase patches of selective vegetation (Anderson & Moratto, 1996; McMillin, 1956). For example, Indigenous groups throughout the Sierra harvested willow from meadows for basketry; fire and pruning were employed to create willow stalks that were suitably thin, strong, and pliable for weaving (Anderson, 1999). The impacts of Indigenous management practices likely varied across the range with tribe and cultural objectives, but their influence on ecosystem structure and function in Sierra Nevada meadows should not be overlooked (Anderson & Carpenter, 1991; Anderson & Stillick, 2013; Klimaszewski-Patterson & Mensing, 2016).

Early exploration of the Sierra Nevada by Euro-Americans was conducted, in large part, by trappers in search of beaver pelts. Heavy trapping during the early 1800s led to the near, if not complete, extirpation of beavers from the central and southern Sierra Nevada by the mid-1800s (Lanman et al., 2012). Beaver persisted longer in some areas of the northern and northeastern Sierra Nevada, but by the beginning of the 1900s population levels across the state had declined so low that the state legislature afforded complete protection to beaver in 1911 (Tappe, 1942).

Beginning in the Gold-Rush era of the 19th century, Euro-American settlers heavily utilized meadows in the Sierra Nevada for sheep grazing. The near-simultaneous acquisition of California by the United States and the discovery of gold on the west slope of the Sierra Nevada resulted in a massive influx of people and animals to the region. The year 1848 demarcates a transition in California from a "tranquil, pastoral region" to one of "intense, almost violent activity" (Burcham, 1981a). The ensuing decade (1850-1860) has been described as a "cattle boom," with ~250,000 cattle in 1850 and ~1 million cattle in 1860 (Burcham, 1981a). Widespread floods followed by intense drought in the early 1860s led to the loss of >200,000 cattle and transformations in the cattle industry (Burcham, 1981b). As a result, many ranchers shifted to sheep and looked to pastures in the Sierra Nevada. In 1850, there were only 17,500 sheep in California. By 1860, there were over 1 million, and, by 1880, there were roughly 5 million sheep (Burcham, 1981a; Menke et al., 1996). Commensurate with this activity, wetlands in the Sierra Nevada—particularly wet meadows and fens—suffered rapid degradation (Menke et al., 1996). By the early 1900s, land managers were concerned about the condition of meadows, but significant reductions to grazing animal numbers did not occur until the 1920s -1930s. By that time, stream channel incision was common in meadows throughout the region, and incision depths up to 15 feet (5 m) were reported (Hughes, 1934). Use increased again during World War II, and pack stock replaced livestock as soon as the National Parks were created; however, utilization rates never reached pre-1920 levels (Menke et al., 1996).

Hydraulic mining also began in the Sierra Nevada in the 1850s, resulting in the accumulation of massive amounts of sediment in streams and rivers throughout the region. Channel incision ensued as streams adjusted to increased sediment load, and altered flows and channel incision were present in most mountain channels by the turn of the century (James, 1994). This period of mining activity impacted the surrounding forest as trees were extensively harvested to support mining operations, provide fuel, and construct shelter. The change in upland forest structure may have also influenced erosion and sedimentation rates in Sierra Nevada meadows.

Construction of roads and railroads for transportation and logging created concentrated flow paths that further contributed to stream channel incision and loss of meadow habitat, though the extent of this impact has not been documented (Soil Conservation Service, 1989; Wemple et al., 1996). Fire suppression began in the early

1900s, and fire was virtually eliminated as an important ecological factor by 1920 (Kilgore & Taylor, 1979). However, the removal of Indigenous groups from the Sierra Nevada likely resulted in less fire in meadows prior to direct fire suppression efforts (Anderson & Stillick, 2013; Klimaszewski-Patterson & Mensing, 2016).

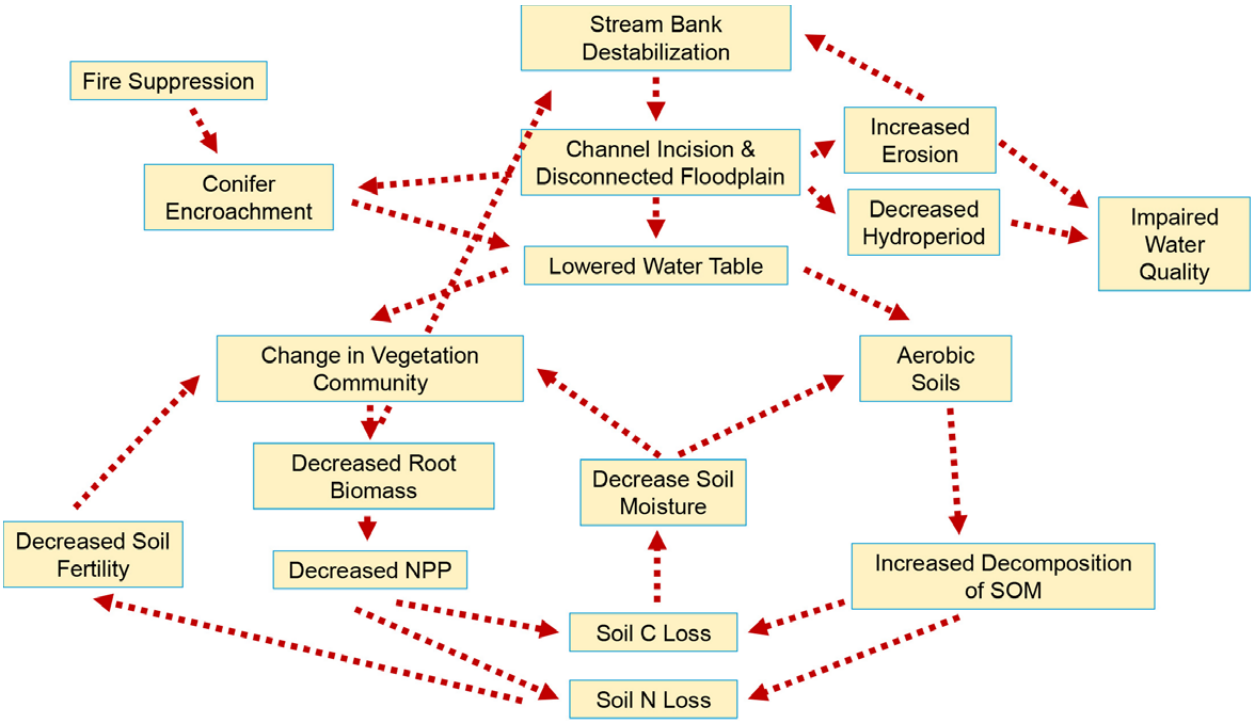
2.3.1.2 Impacts of Anthropogenic Disturbance

The number of meadows across the Sierra Nevada that currently exist in a degraded condition remains unknown. However, commonly cited estimates (upscaled from smaller assessments) are that 40-70% of meadows have been degraded, primarily as a result of anthropogenic activities (Hunsaker et al., 2015; National Fish and Wildlife Foundation, 2010). Degradation of ecosystem function in meadows arises from activities that alter the stabilizing biotic and geomorphic feedbacks mediated by soil-plant-water interactions. Intentional or unintentional disturbances propagated by human land use can catalyze self-reinforcing feedbacks that lead to channel incision, changes in vegetative community composition, altered biogeochemistry, and habitat loss (Fig. 2.2).

2.3.1.2.1 Hydrologic Alterations

Hydrologic function in meadows can be impacted by activities directly aimed at altering flow or reducing the period of soil saturation (e.g., channelization, diversion, stream straightening, drainage, or culvert construction) or as an unintended consequence of activities in meadows and the surrounding uplands (e.g., grazing, logging, road and railroad construction, wildfire, and climate change). Whether intentional or not, these activities concentrate flows and increase erosive forces, leading to streambank destabilization and further channel incision (Fig. 2.2). Stream channel incision decouples groundwater from surface processes, significantly lowering water tables and reducing groundwater storage capacity (Essaid & Hill, 2014; Loheide et al., 2009; Loheide & Gorelick, 2007). Steep hydraulic gradients toward the incised channel can shift the direction of flow from down-valley to almost exclusively toward the channel, decreasing the residence time of groundwater and altering the timing and magnitude of baseflow (Loheide & Gorelick, 2007). Model simulations suggest that even moderate levels of stream channel incision (<3 feet; <1 m) result in reduced groundwater recharge, faster drainage following snowmelt, and extended periods of aerobic soil conditions during the growing season (Essaid & Hill, 2014; Nash et al., 2018). Groundwater storage loss and seasonal fluctuations in groundwater levels increase with incision depth. Under reduced precipitation scenarios, groundwater recharge during wet years may not be sufficient to offset incision-induced losses in degraded meadows, leading to a net loss of groundwater storage over time (Essaid & Hill, 2014).

Figure 2.2: Model of self-reinforcing feedbacks that lead to meadow degradation.



Degradation is generally initiated through a combination of concentration of flows and loss of stabilizing vegetation or conifer encroachment resulting from fire suppression. Once the stabilizing plant-soil-water feedbacks have been disrupted, self-reinforcing feedbacks can move the ecosystem to an alternative stable state with reduced ecosystem function and without the capacity to self-repair.

Increased depth of groundwater and the consequent prolonged drying of surface soils following stream channel incision can also result in the conversion of vegetation from hydric to xeric communities (Fig. 2.2; Loheide & Gorelick, 2005, 2007). Shifts in vegetation community composition are often greatest near the stream channel where hydrologic gradients are the steepest (Loheide et al., 2009). However, the areal extent of groundwater decline and patterns of vegetation change are influenced by meadow and bedrock hydraulic properties that impact the distribution of lateral and basal groundwater flows, in addition to incision depth (Essaid & Hill, 2014; Loheide et al., 2009). Replacement of hydric and mesic vegetation by xeric species with lower root biomass reduces stream bank stability and accelerates rates of erosion and channel incision, creating self-reinforcing feedbacks that can lead to an incised alternative stable state (Fig. 2.2; Micheli & Kirchner, 2002; Toledo & Kauffman, 2001). In meadows with greater groundwater inputs as lateral flows, the margins of the meadow may continue to support wet meadow vegetation. However, establishment of xeric species, including conifers and sagebrush, near stream channels can lead to additional losses of soil moisture through evapotranspiration and accelerate the conversion of wet meadow vegetation to upland species (Boisramé et al., 2017).

The impacts of anthropogenic disturbance on meadow biogeochemistry are largely the product of interactions among plants, water, and soil. Meadows with shallow stream channels and good lateral floodplain connectivity have high rates of primary productivity and vegetative carbon inputs, while meadows with incised stream channels have significantly higher cover of bare ground, lower rates of primary productivity, and lower rates of belowground carbon allocation (Fig. 2.2; Reed et al., 2021). As a result, hydrologically disturbed meadows may be large net sources of carbon to the atmosphere (200-500 g C m^{-2} y^{-1}; Reed et al., 2021). Such high rates of carbon loss, sustained by large extant soil carbon stocks consumed by microbial processing, may result in the loss of 1-3% of total soil carbon stock annually (Reed et al., 2021). Norton et al. (2011) found that soil carbon stocks in hydrologically "nonfunctioning" meadows in the central Sierra Nevada were significantly lower than in "properly functioning" or 'functioning-at risk" meadows. Further, the difference between meadows conditions was ~5 kg C m^{-2}, signifying a potential loss of ~30% of the soil carbon stock since disturbance began in what are currently hydrologically "nonfunctioning" meadows (Norton et al., 2011). Norton et al. (2011) also suggests that hydrological alteration of wet meadows leads to increased rates of nitrogen mineralization, shifting meadows from net sinks to sources of reactive nitrogen to stream water.

Changes in soil organic carbon strongly affect soil-plant-water interactions as loss of organic matter can lead to disproportionately large declines in water retention. This creates a self-reinforcing feedback where drier soils lead to transitions to xeric vegetation communities and loss of soil organic matter, further reducing soil moisture (Ankenbauer & Loheide, 2017; Reed et al., 2021). Ankenbauer & Loheide (2017) simulated the effect of soil organic matter on water availability in Sierra Nevada wet meadows and showed that soils with high organic matter (20% by mass) provided 35 more days of water-stress free conditions for vegetation compared with soils that had no organic matter.

All aquatic ecosystems in the Sierra Nevada have experienced loss of biotic integrity to some degree, largely as a result of hydrologic alterations (Moyle, 1996). In an assessment of watersheds in the Sierra Nevada (excluding the northeastern Sierra Nevada region), Moyle & Randall (1998) found that more than half of the native aquatic biota—namely fishes and frogs—were in poor to fair condition. Focusing on meadows specifically, Purdy et al. (2012) found 75-81% of sites sampled to be in poor to fair condition with respect to fish and amphibian biotic indices. This contrasts other indices of integrity for macroinvertebrates, physical habitat, and vegetation which rate 44%, 26%, and 18% of the same meadows to be in poor to fair condition, respectively (Purdy et al., 2012). The poor condition of many meadows across the Sierra Nevada contributes to the vulnerability of aquatic ecosystems under changing climate conditions. However, restoration of aquatic ecosystems also becomes increasingly unlikely as climate change asserts additional stress on these systems, further favoring alien species and giving rise to novel ecosystems (Moyle, 2014).

Altered hydraulic function in Sierra Nevada meadows reduces habitat heterogeneity and disrupts natural flow regimes, with significant consequences for biodiversity. Many aquatic and semi-aquatic species are highly specialized to particular hydrologic conditions. For example, mosquitoes and damselflies thrive in no-flow systems, whereas mayflies (Ephemerellidae) require flowing water (Holmquist, 2011). Foothill yellow-legged frogs are restricted to streams with natural flow regimes (Kupferberg et al., 2011), while Yosemite toads, Sierra yellow-legged frogs, and Mountain yellow-legged frogs depend on permanent pond habitats (Roche et al., 2012; Knapp et al., 2003). Connectivity among streams, floodplains, and side channels, combined with a diversity of pools and pond sizes, creates thermal heterogeneity that supports diverse macroinvertebrate assemblages (Noone et al., 2024) and facilitates amphibian dispersal (Berlow et al., 2013; Knapp et al., 2003). Loss of these hydrologic functions therefore reduces species diversity and limits the resilience of meadow ecosystems.

2.3.1.2.2 Grazing

Historic grazing, and the manipulation of meadow hydrology to support grazing, have contributed to the widespread degradation of wet meadows in the Sierra Nevada. However, meadows provide valuable forage, and grazing remains one of the most common uses of wet meadows on both private land and National Forests. While moderate grazing may be compatible with conservation objectives (Holmquist et al., 2010, 2013; Roche et al., 2012; Schmidt et al., 2005, but see Hatfield & LeBuhn, 2007), heavy grazing has been associated with negative ecological outcomes and loss of ecosystem integrity (Freitas et al., 2014; Hatfield & LeBuhn, 2007; Herbst et al., 2012; Holmquist et al., 2014; Loft et al., 1991; Vernon et al., 2022).

Grazing impacts ecosystem stability and function in meadows primarily through removal of vegetation (Loft et al., 1987) and physical damage to soils and root structures. Hoof punctures in wet soils sever root mats that stabilize fine sediments, accelerating rates of erosion and leading to altered stream channel morphology and reduced hydrologic connectivity (Herbst et al., 2012; Knapp & Matthews, 1996). Heavy grazing can also increase soil compaction and decrease rates of water infiltration, altering water flow paths and increasing surface erosion (Hill & Mitchell-Bruker, 2010). Increased rates of streambank erosion also result in greater stream turbidity and transport of suspended sediments (Herbst et al., 2012). Livestock may further impact downstream water quality through the deposition of manure and urine; significantly higher concentrations of fecal coliform and *E. coli* have been found downstream of riparian meadows subject to season-long grazing (Myers & Kane, 2011; Myers & Whited, 2012). Removal of streamside vegetation, particularly willows and other shrubs, can also lead to higher water temperatures and increased algal growth through greater exposure to solar radiation (Herbst et al., 2012; Nusslé et al., 2015).

Altered stream bank morphology and increased rates of erosion as a result of livestock trampling can lead to loss of hydrologic connectivity and associated shifts in vegetation from hydric and mesic communities to predominantly xeric species (Dull, 1999; Herbst et al., 2012; Nusslé et al., 2015, 2017; Wolf, 2017). Reduced cover of wet meadow species exposes mineral soil which, coupled with drier surface soils, improves conditions for germination and establishment of conifers (Taylor, 1990). Heavy grazing, especially by sheep, followed by moderate to no grazing and fire suppression created conditions for widespread conifer invasion of Sierra Nevada meadows in the early to mid-1900s (Vale, 1981, 1987).

Grazing influences soil biogeochemistry in meadows through both direct and indirect pathways. Direct effects include soil shearing, trampling, soil compaction (Baccei et al., 2020), and inputs of urine and feces (Blank et al., 2006; Blank & Morgan, 2010), while indirect effects occur through grazing-induced changes in vegetation or hydrology that affect nutrient cycling (Freitas et al., 2014; Holmquist et al., 2010, 2013). In central Nevada meadows, grazing has been shown to reduce belowground allocation of carbon by plants (Morra et al., 2023c). Under carefully managed grazing, soil carbon stocks increased following meadow restoration, albeit more slowly than when grazing was excluded (Morra et al., 2023a). In addition to meadow condition, geology, and climate grazing intensity and season of grazing are likely to influence the effects of grazing on meadow biogeochemistry (Blank & Morgan, 2010; Oles et al., 2017; Roche et al., 2014), though questions remain about the interacting effects of these drivers. Further study of grazing effects on soil biogeochemistry in healthy, degraded, and restored meadows in the Sierra Nevada is needed.

Livestock grazing can affect meadow biodiversity and habitat quality for a range of taxa. The primary impacts of grazing on wildlife occur through alteration of foraging habitat and cover (Holmquist et al., 2010; Loft et al., 1987), reduction of habitat complexity (Ammon & Stacey, 1997), decreases in water quality (Herbst et al., 2012), changes in prey availability(Herbst et al., 2012), and disturbance from livestock behavior and presence (Loft et al., 1993). For meadow birds, such changes can reduce productivity (Ammon & Stacey, 1997; Valentine et al., 1988) and alter species composition, with additional pressures from increased parasitism by Brown-headed Cowbirds (Molothrus ater) in some systems (Airola, 1986; Flett & Sanders, 1987). For amphibians, light grazing appears to have limited effects on Yosemite Toad (*Anaxyrus canorus*; McIlroy et al., 2013), which is less dependent on aquatic habitats than many other amphibians. However, effects on more water-dependent species remain largely unknown. In aquatic macroinvertebrate communities, grazing tends to decrease species richness and shift species composition toward disturbance-tolerant taxa adapted to lower water quality, while reducing the abundance of species dependent on high-quality water (Herbst et al., 2012). Collectively, these changes contribute to differences in species assemblages and abundance between grazed and ungrazed meadows (Hatfield & LeBuhn, 2007; Herbst et al., 2012; Holmquist et al., 2010, 2014;

Powers et al., 2011; Schmidt et al., 2005). Grazing increases spawning habitat in meadow streams for Golden Trout (*Oncorhynchus aguabonita*), a limiting factor for population density, while simultaneously reducing other aspects of habitat quality (Knapp et al., 1998). Meadow grazing is estimated to reduce the carrying capacity for mule deer by 18%, primarily by reducing cover, forage, and habitat complexity (Kie et al., 1991; Loft et al., 1987, 1991, 1993; Loomis et al., 1991). Further study of grazing impacts on different wildlife taxa is needed, including evaluations of varying grazing intensities, the effectiveness of streamside exclosures, and wildlife response to restoration in grazed compared to ungrazed meadows.

2.3.1.2.3 Fire

Fire was employed extensively as a management tool by Indigenous groups in the Sierra Nevada to maintain meadows and reduce fuel accumulation in the surrounding uplands. However, widespread Euro-American fire suppression beginning in the early 1900s increased the mean fire return interval of upland forest from ~10 y to 378 y (Norman & Taylor, 2005; Scholl & Taylor, 2010). Increases in forest stand density following fire suppression, coupled with the end of Indigenous burning practices and the introduction of heavy grazing, created conditions for rapid encroachment of meadows by conifers (Cummings et al., 2023).

Over a century of fire suppression has also contributed to an increase in the size and severity of fires in recent decades (Miller et al., 2009; Williams et al., 2023). Warming temperatures and periods of aridity have also been linked to extreme fire behavior (Gutierrez et al., 2021; Jain et al., 2022). Anecdotal evidence suggests that large wet meadows offer valuable refuge for wildlife (Jager et al., 2021) and may alter fire behavior. Studies have shown that large riparian zones and beaver-dammed riparian corridors remain relatively unaffected by fire and may act as natural fuel breaks (Fairfax & Whittle, 2020; Kobziar & McBride, 2006). It is reasonable to assume that Sierra Nevada wet meadows may play a similar role; however, the impact of wet meadows on fire behavior and the conditions under which they may mediate fire behavior or provide refugia have not been tested. Concepts of fire spread in riparian forests (e.g., those presented in Pettit & Naiman, 2007) are often applied to wet meadows without consideration for differences in fire behavior between meadows and riparian forest.

Life history traits that allow meadow and riparian vegetation to recover quickly after floods also facilitate rapid recovery following fire (Dwire & Kauffman, 2003; Kaczynski & Cooper, 2015; Willard et al., 1995). Decreased rates of evapotranspiration in the surrounding uplands due to vegetation loss and type conversions following fire—particularly high severity fires—may also result in elevated water tables in hydrologically connected meadows, favoring the growth of hydric and mesic species and expansion of meadow area (Wood, 1975). In the Illilouette Creek Basin in Yosemite National Park, meadow area increased by 200% four decades after the end

of fire suppression (Boisramé et al., 2017a; Boisramé et al., 2017b). In other areas, meadows lost to conifer encroachment have reverted back to meadow vegetation following fire (DeBenedetti & Parsons, 1979). Rapid rates of vegetative recovery in meadows relative to the surrounding uplands, particularly following high-severity fires, likely enhance the ecological value of meadows for wildlife during the post-fire period, though changes in patterns of use have not been studied.

Meadows that have been encroached by conifers or have large channel incisions and xeric vegetation communities are more likely to burn (Van De Water & North, 2010) and, anecdotally, many have burned in recent high-severity fires. Under drought conditions, peat can also burn—sometimes down to mineral soil—potentially resetting ecological trajectories of small fens and patches of wet meadows. Palaeoecological evidence suggests that peat formation may resume post fire if hydrologic conditions remain unchanged. However, the time required for ecosystem recovery and the impact of frequent, high-severity fires remains unknown (Anderson & Smith, 1994; Koehler & Andrson, 1994). Further, recovery trajectories in hydrologically disturbed meadows are not likely to mirror those of meadows with resilient hydric plant communities.

Most wildlife species inhabiting the Sierra are adapted to the historical fire regime. However, the impacts of fire on wildlife vary depending on each species' ecology and behavior. For example, some species rely on meadows during the breeding season and then move to upland forests during the non-breeding season. The endangered Yosemite Toad is one such species and, as a result, may be more susceptible to direct mortality during forest fires than other amphibian species (Liang & Stohlgren, 2011). Several species of macroinvertebrates, such as leafhoppers and Lepidoptera, lay their eggs in meadow litter, increasing their vulnerability to fire (Holmquist & Schmidt-Gengenbach, 2020). While most birds can escape direct fire, they often rely on meadows during the post-breeding period and fall migration. These periods frequently coincide with heavy wildfire smoke, which is known to negatively affect avian health and movement (Overton et al., 2022; Sanderfoot et al., 2022). Further, fire severity modifies wildlife response to fire: moderate-severity fire can increase floral richness and positively affect pollinators, whereas high-severity fire tends to decrease pollinator abundance (Tarbill et al., 2023). More studies are needed to quantify wildlife use of meadows under both burned and unburned conditions (Kelt et al., 2013), particularly as fires in the Sierra are projected to increase in severity and extent.

Increased rates of sediment transport following wildfire can also impact meadows, either by depositing pulses of sediment or increasing channel erosion in areas that have experienced loss of stabilizing vegetation (Leonard et al., 2017). Restoration activities that capture post-fire sediment flows may be effective in aggrading incised channels or preventing post-fire stream channel erosion (Long & Davis, 2016; Sevier et al., 2024). However, studies from other regions demonstrate that rates of sediment

erosion and deposition following wildfire depend on fire severity, topography, soil type, vegetation, and precipitation patterns in the first years following a fire (Arkle & Pilliod, 2010; Scott & Van Wyk, 1990; Verkaik et al., 2013). Ultimately, predicting the location and timing of post-fire sedimentation can be challenging, and uncertainty remains about the reliable use of post-fire sediment for channel aggradation (Sevier et al., 2024; Wilcox, 2023).

A notable consequence of meadow disturbance and fire suppression has been the widespread encroachment of coniferous trees—especially *Pinus contorta*—into meadows. Conifer encroachment results in decreased soil moisture and reduced cover and richness of meadow species (Boisramé et al., 2017; Halpern et al., 2010; Haugo et al., 2011; Haugo & Halpern, 2010). While the presence of conifers in meadows is considered a natural phenomenon, meadow stratigraphy suggests that widespread encroachment was historically rare (Wood, 1975). Rates of encroachment in Sierra Nevada meadows have accelerated since the 1920s, coincident with the reduction of grazing following periods of heavy grazing, fire suppression, and warming climate conditions (Lubetkin et al., 2017; Millar et al., 2004; Vale, 1987). In some areas of the Sierra Nevada, conifer encroachment is now nearly ubiquitous in meadows up to 10,000 feet (3,000 m) in elevation (Lubetkin et al., 2017).

2.3.1.2.4 Invasive Species

Several invasive wildlife species have been introduced to Sierra meadow streams either directly or indirectly by humans. The most impactful are non-native trout and other salmonids, which now occupy the majority of lakes and ponds that were historically fishless (Bahls, 1992; Ryan et al., 2014). Through direct predation, these fish have contributed to the decline and listing of the mountain yellow-legged frog (*Rana muscosa*; Knapp et al., 2003; Knapp & Matthews, 2000; Ryan et al., 2014), Sierra Nevada yellow-legged frog (*Rana sierrae*; Halstead et al., 2023; Knapp et al., 2016; Ryan et al., 2014), and Cascades Frog (*Rana cascadae*; Cole & North, 2014). Fish may also impact bat activity by reducing the availability of macroinvertebrate prey (Gruenstein et al., 2021). Non-native bullfrogs (*Lithobates catesbeianus*) and signal crayfish (*Pacifastacus leniusculus*) have likewise expanded in the Sierra Nevada, primarily due to changes in hydrology (Light, 2003) and climate (Nelson & Piovia-Scott, 2022). Both are known predators of aquatic species, including the western pond turtle (*Actinemys marmorata*), a species under review for listing (Woodruff et al., 2025).

While the stocking of fish in the 1920s is frequently cited as the main cause of amphibian decline (Drost & Fellers, 1996), the emergence of chytrid fungus (*Batrachochytrium dendrobatidis*) in North America in the 1990s caused mass die-offs of the remaining amphibian populations in the Sierra (Ouellet et al., 2005; Vredenburg et al., 2010). Although chytrid remains prevalent in the environment, some species have shown signs of developing tolerance to low levels of the fungus (Knapp et al., 2024).

There is little research on the effects of invasive plant and animal species on birds in Sierra Nevada meadows, with the exception of the Brown-headed Cowbird. In the last century, Brown-headed Cowbirds have expanded their range into the Sierra and occur at densities far above levels observed prior to the onset of European cattle grazing (Rothstein et al., 1980). Cowbirds strongly prefer meadows as breeding habitat in the Sierra and are associated with areas used by livestock (Verner & Ritter, 1983). They are known to parasitize many meadow species including some of conservation concern, namely Willow Flycatcher and Yellow Warbler (Flett & Sanders, 1987; Verner & Ritter, 1983). Parasitism can lead to reductions in reproductive success of meadow host species (Airola, 1986; Valentine et al., 1988) and has been implicated in the decline of other riparian birds in California (Kus, 1999). The effects of restoration on Brown-headed Cowbird parasitism rates have not been studied in Sierra Nevada meadows.

Invasive plants have altered vegetation community composition in many Sierra Nevada meadows. The California Invasive Plant Council (Cal-IPC) suggests that climate change is likely to increase the vulnerability of Sierra Nevada meadows to invasive plants (California Invasive Plant Council, 2019), which could impact wildlife habitat through alteration of vegetation community composition and structure. However, little is known about the effects of invasive plants—including thistles, grasses, and forbs—on wildlife communities in meadows. Studying wildlife communities in meadows where invasions have occurred could increase understanding of this potential vulnerability and help prioritize eradication efforts.

2.3.2: Climate Change

2.3.2.1 Expected Climate Change in the Sierra Nevada

The Sierra Nevada region has already begun to experience the impacts of climate change including increasing temperatures, prolonged drought, extreme precipitation events, and declining snowpack (Khan et al., 2026). Under current emissions scenarios, climate models predict average warming of >9 °F (>5 °C) across the region by the end of the century. Under lower emissions scenarios, where greenhouse gas emissions are stabilized by midcentury, warming may be limited to ~4 °F (2.2 °C). However, even this more moderate scenario is predicted to yield substantial changes for the region (Khan et al., 2026).

Precipitation trends vary by model, but the central and southern Sierra are generally expected to experience overall declines in precipitation while the northern and eastern Sierra Nevada region may see modest increases (10-30%) relative to historic values (Khan et al., 2026). Warming temperatures will increase the fraction of precipitation that falls as rain rather than snow across the region, resulting in earlier snowmelt, decreased summer streamflow, and reduced groundwater recharge (Ficklin et al., 2012; Khan et al., 2026; Null et al., 2010). Snowpack declines of 20-90%

are predicted across the region, with only the highest peaks expected to maintain snowpack by the end of the century. Climate change is also likely to increase the risk of extreme precipitation events in the Sierra Nevada, which, combined with an increased fraction of precipitation falling as rain, could increase runoff from extreme storm scenarios by 200-400% by the end of the century (Huang & Swain, 2022).

2.3.2.2 Impacts of Climate Change on Meadow Ecosystem Function

2.3.2.2.1 Hydrology

Climate change is expected to fundamentally alter the hydrology of the Sierra Nevada with consequences for the ecological function and stability of wet meadows. Specifically, warming temperatures coupled with changes in the timing, form, and amount of precipitation are expected to impact rates of spring snowmelt, timing of peak runoff, groundwater recharge, and late season flows (Khan et al., 2026). By mid-century, ~60% of subwatersheds across the Sierra Nevada region are expected to experience snowmelt decreases greater than 50% due to increased temperatures. Under current emissions scenarios, by the end of the century, almost 90% of watersheds are expected to see similar declines (Ficklin et al. 2012). As a result of earlier snowmelt and less precipitation falling as snow, peak streamflow is predicted to occur 1-2 months earlier across the region by the end of the century (Ficklin et al., 2012; Null et al., 2010; Stewart, 2013; Young et al., 2009). The largest decrease in snowmelt driven streamflow is likely to occur in mid-elevation watersheds (5,000–10,000 feet; 1,500–2,500 m) along the western Sierra Nevada that rely on snowpack (Ficklin et al., 2012; Knowles & Cayan, 2004; Young et al., 2009). Higher elevation watersheds, particularly those in the southeastern Sierra Nevada, may experience smaller decreases in snowmelt driven streamflow and smaller changes in runoff timing under current climate predictions by the end of the century (Ficklin et al., 2012; Null et al., 2010). However, Ficklin et al. (2012) also predicted that these watersheds would be the most sensitive to climate change and may experience similar changes if temperatures warm beyond predicted values or increases continue into the future. Models suggest that lower elevation watersheds that are less reliant on snowpack and those with deep soil moisture storage (e.g., watersheds in the northern and northeastern portion of the Sierra Nevada region) may be more resilient to changes in runoff timing than snowmelt dependent watersheds, though decreases in mean annual flow are still likely to occur (Null et al., 2010).

Changes in snowmelt timing not only affect surface water flows but also subsurface processes including groundwater recharge, soil water storage, and evapotranspiration. Working in a granitic watershed in the central Sierra Nevada, Ciruzzi & Lowry (2017) found that a 10% reduction in snowpack could result in an order-of-magnitude decrease in aquifer recharge from a high elevation meadow over the course of the growing season. However, Drexler et al. (2013) noted that sensitivity of groundwater recharge to climate varied across the region and speculated that

differences in hydrogeology may drive the response of groundwater to changes in climate. Specifically, they postulated that deep aquifers and high rates of hydraulic conductivity, common in the northern and northeastern Sierra Nevada regions, may build resilience against climate change-induced reductions in groundwater recharge because they are able to store more water with long residence times (Drexler et al., 2013). In the southern Sierra Nevada, strong correlations between rainfall and annual groundwater recharge suggest short residence time in the unsaturated zone of granitic watersheds with shallow soil and greater susceptibility to climate change induced variability (Meadows & Hagedorn, 2022); however, more studies are needed to determine the impacts of hydrogeology on groundwater recharge in meadows across the region under climate change.

Advances in runoff timing and decreased groundwater recharge are likely to increase the period of summer low flows and stream temperatures. Water temperatures and dissolved oxygen concentrations in wet meadow streams are driven by air temperatures and cold water contributions from snowmelt and groundwater (Ficklin et al., 2013). Stream temperatures across the region are expected to increase by up to 10 °F (5.5 °C) relative to historic conditions by the end of the century, with the highest predicted temperatures and lowest dissolved oxygen concentrations predicted to occur in low elevation subbasins of the southern and central Sierra Nevada. In ~7% of these subbasins, summer dissolved oxygen levels may drop below the lower limit to maintain aquatic ecosystems (Ficklin et al., 2013).

Significant increases in both interannual and intraseasonal variability of precipitation will lead to even more pronounced contrasts between the brief, wet winters and long, dry summers characteristic of the Sierra Nevada's Mediterranean climate. Extreme precipitation events and rapid transitions between dry and wet conditions are also expected to intensify, increasing the risk of flooding, erosion, and rapid sediment transport (Das et al., 2011; Huang & Swain, 2022; Swain et al., 2018). Increased frequency, intensity, and size of wildfires may further contribute to erosion and sediment transport in Sierra Nevada watersheds under climate change (Badik et al., 2022; Olsen et al., 2021; Safford et al., 2022). The ability of meadows to attenuate high flow events and capture sediment may increase the resilience of watersheds and confer protection to rural communities. The flood mitigation potential of Sierra Nevada meadows, particularly under climate change, has not been adequately studied, though it likely depends on meadow condition along with topographic and geologic features.

Lee et al., (2015a) modeled the impact of climate change on montane wetlands in the Pacific Northwest and found a general decrease in meadow hydroperiod and increased probability of drying, with the largest changes occurring in wetlands with intermediate hydroperiods, including wet meadows. By 2080, they predict widespread conversion of intermediate hydroperiod wetlands to ephemeral wetlands

with altered ecosystem function and reduced habitat value (Lee et al., 2015). Similar analyses in the Sierra Nevada region may help prioritize meadows for restoration or conservation based on predicted climate change impacts.

2.3.2.2.2 Vegetation

Earlier declines in groundwater elevations, resulting from earlier peak runoff, lower stream flows, and reduced groundwater recharge may decouple the availability of shallow groundwater from critical phenological stages of meadow vegetation. Higher rates of evapotranspiration under elevated temperatures could further accelerate the decline in groundwater levels during the growing season (Loheide et al., 2009). Moisture deficits during the growth and reproductive phases may lead to shifts in vegetative communities from hydric and mesic to more xeric species, even in the absence of geomorphic channel incision (Loheide et al., 2009). This transition to dominance of xeric species with lower root biomass may increase susceptibility to erosion and further reductions in groundwater, initiating self-reinforcing feedbacks that lead to meadow degradation (Fig. 2.2).

Historically, periods of conifer encroachment have been correlated with climatic windows of low precipitation, high temperatures, and low rates of interannual variability(Lubetkin et al., 2017; Millar et al., 2004). Layers of thick sod and thatch that prevent seed establishment may be decreased during warm-dry periods, allowing conifers to germinate and establish roots when competition is limited (Lubetkin et al., 2017; Millar et al., 2004). This relationship suggests that meadows may be more vulnerable to conifer encroachment under future climate conditions, and some models predict meadows will fully convert to forest by the end of the century (Lubetkin et al., 2017). However, increases in fire frequency, and the associated impacts on upland vegetation and watershed hydrology, may also decrease seed supply of encroaching conifers and increase meadow wetness. More research is needed to determine how differences in meadow condition, upland vegetation, and hydrogeomorphology are likely to influence the meadow persistence under climate change.

Increased temperatures and declining snowpack are also likely to impact phenology with direct impacts on vegetation community composition and species interactions. In the Rocky Mountains, Dunne et al. (2003) found that flowering of meadow species advanced by 11 days for every 4 °F (2.2 °C) increase in spring soil temperature or two week advance of snowmelt, with high elevation and early flowering species displaying the highest degree of sensitivity. Albano et al. (2019) found that meadow vegetation was highly sensitive to April 1 snow water equivalent, which varied with climate and watershed subsurface water storage capacity. High elevation meadows with high precipitation but limited catchment subsurface storage showed the greatest sensitivities, while lower elevation meadows in basins with more basalt or metamorphic parent material showed the lowest degree of sensitivity (Albano et al., 2019).

2.3.2.2.3 Biogeochemistry

Few field-based, peer-reviewed studies have tested the impacts of climate change on biogeochemical functions in Sierra Nevada meadows. Evidence from meadows in the Qinghai-Tibetan plateau suggests that changes in precipitation patterns may impact carbon fluxes in meadows more than increasing temperatures; specifically, drier conditions are likely to lead to lower rates of carbon sequestration while wetter conditions may enhance carbon sequestration (Zhang et al., 2022). Some studies suggest that meadow productivity could increase under climate change if sufficient moisture is available to meet higher evaporative demand (He et al., 2024; Jiang et al., 2024). However, warmer temperatures may also shift vegetation composition from sedges and rushes towards grasses and forbs, with implications for belowground carbon allocation (Peng et al., 2017).

In the Sierra Nevada, changes in precipitation that impact vegetative productivity and are also likely to impact carbon sequestration and persistence. Arnold et al., (2014, 2015) found that drought conditions resulted in decreased vegetative productivity and increased carbon losses from soil respiration in Sierra Nevada meadows. Morra et al. (2023b) found that vegetative productivity was a stronger driver of mineral associated carbon formation and persistence than climate across meadows in the Sierra Nevada and central Great Basin. Drought-induced reductions in primary productivity could result in increased carbon losses, decreased allocations of carbon to the mineral associated fraction, and destabilization of carbon previously preserved through mineral association (Morra et al., 2023b). However, while changes in precipitation and vegetative productivity may impact the persistence of mineral associated carbon, laboratory studies suggest that it may be relatively resistant to warming. Bagcilar et al. (2024) conducted a warming experiment using Sierra Nevada meadow soils and found that mineral associated carbon destabilized at only one of five sites and only under extreme incubation conditions (40 °C for 17+ days). Soong et al. (2021) found that warming-induced losses of soil carbon in a conifer forest were primarily from unprotected particulate organic matter. These results suggest that restoration activities that increase hydrologic connectivity and vegetative productivity in meadows yield increased rates of carbon sequestration and mineral associated carbon formation (Bagcilar et al., 2024; Reed et al., 2022) and that this mineral associated carbon may be persistent under a changing climate conditions. However, degraded meadows and those more hydrologically susceptible to changing precipitation patterns may see increased carbon losses.

2.3.2.2.4 Biodiversity and Conservation of Special Status Species

Several studies have examined the potential impacts of climate change on Sierra Nevada meadow birds (Stralberg et al. 2014, Tingley et al. 2009, Siegel et al. 2014, Schofield et al. 2022). Siegel et al. (2014) assessed climate vulnerability across Sierra Nevada birds and identified three meadow species as moderately vulnerable: Spotted Sandpiper (*Actitis macularius*), Swainson's Thrush (*Catharus ustulatus*), and

Great-gray Owl (*Strix nebulosa*). Stralberg et al. (2014) predicted that entire bird communities would likely shift relatively short distances upslope, resulting in relatively little change in community composition. However, this prediction warrants further evaluation as meadow bird communities vary considerably with elevation. Upslope expansion of species such as Song Sparrow (*Melospiza melodia*), for example, into meadows occupied by the related but smaller Lincoln's Sparrow (*Melospiza lincolnii*) could create novel competition and displacement (Cicero, 1997). Such broad-scale analyses may not accurately capture the nuances of ecosystem change and potential impacts on wildlife, underscoring the need for better understanding of climate impacts and productivity.

Willow Flycatcher is a species that has experienced severe range contraction in the 21st century and is now largely confined to the northern and eastern Sierra (Harris et al. 1987, Siegel et al. 2006, Matthewson 2012, Loffland et al. 2014). Schofield et al., (2023) found April 1 snow water equivalent, along with mean maximum and minimum monthly temperatures, to be important predictors for the species, with climate change likely resulting in fewer favorable meadows for this species. The limited dispersal distance and infrequency with which Willow Flycatchers colonize new meadows may further increase the vulnerability of this species and represent barriers to climate change adaptation (Matthewson et al. 2010).

Climate change may also result in phenological mismatches that could be detrimental for migratory birds whose annual cycles are tightly timed (e.g., the regionally-declining Rufous Hummingbird (*Selasphorus rufus*); Burnett, 2020; English et al., 2021; Mayor et al., 2017). Little is known about the diet of meadow birds and how climate change may impact the abundance and phenology of prey. One study in Yosemite National Park found that birds derived >50% of their diet from aquatic food webs, with this proportion increasing in dry years (Jackson et al. 2020). Willow Flycatchers were also found to feed nestlings a diet of primarily aquatic insects (Dietrich 2022). Better understanding of life histories, diets, and climate sensitivities of meadow dependent birds could inform conservation planning to increase benefits and reduce vulnerabilities.

Amphibians in the Sierra Nevada also exhibit strong sensitivities to changes in precipitation and temperature because of their reliance on aquatic habitats. Snowpack plays a particularly important role. Higher snowpack is associated with increased reproduction due to greater spring water availability and reduced drying of small ponds in late summer (Brown et al., 2012; Lacan et al., 2008). Greater availability of water in late summer may be especially critical for species that remain in aquatic life stages for one to three years before metamorphosing (Halstead et al., 2023). Deeper pools formed by high snowpack also improve survival of overwintering eggs and tadpoles by reducing freezing risk (Bradford, 1983; Sherman & Morton, 1993). At the same time, high snowpack can be linked to longer winters, during which

frogs must survive on fat reserves, leading to poor body condition or starvation (Pope & Matthews, 2002). Snowpack may also influence colonization dynamics; April snowpack has been found to either increase or decrease colonization probability, depending on the species (Halstead et al., 2023). In short, a decrease in snowpack due to climate change (Lee et al., 2015) would likely result in a decrease in amphibian reproduction and survival, further decreasing these at-risk populations.

Temperature effects are less well studied, but warming is known to affect the timing of reproduction (Anderson, James, 1967), distribution (Bedwell et al., 2021), and habitat selection of amphibians (Rose et al., 2023). Late spring frosts following early breeding can also increase egg mortality (Sadinski et al., 2020). Precipitation and temperature also interact with disease dynamics. For example, chytrid fungus (*Batrachochytrium dendrobatidis*), an important driver of amphibian declines in the Sierra Nevada, is mediated by temperature and is most virulent in cold and humid conditions but may display an adaptive response to climate change that could threaten amphibian populations (Voyles et al., 2012).

Climate change threatens fishes of the Sierra Nevada through increased stream temperatures, higher peak flows, earlier peak flows, and extended periods of low flows (Jager et al., 1999). Stream temperatures on west-slope Sierra streams are predicted to increase by 2.8 °F (1.6 °C) for each 3.6 °F (2 °C) rise in air temperatures, with the greatest increases occurring during spring and at mid elevations where warming is expected to shift precipitation from snow to rain (Null et al., 2013). Similarly, the greatest declines in summer stream flow and dissolved oxygen are expected to occur at mid elevations in the central and southern Sierra Nevada (Ficklin et al., 2012, 2013). The combined effects of higher stream temperatures and earlier peak flows are likely to result in an overall decrease in fish habitat. However, the nonadditive effects of the complex interactions between temperature and stream flow may also produce different outcomes for native and introduced species. Kiernan and Moyle (2012) used a long-term data set to study the impacts of environmental changes on fish communities in Martis Creek and found that the proportion of introduced species increased in years with low annual stream flow but that these species were also more susceptible to high winter and spring flow events. They predicted that native fish assemblages may be better able to persist under changing hydrologic conditions (Kiernan & Moyle, 2012), but increased predation by invasive species during periods of drought is likely to impact long-term trends (Propst et al., 2008). The impacts of climate change are also likely to differ by elevation; increases in stream temperature may benefit fish in cooler upstream reaches while reducing abundance in downstream reaches (Jager et al., 1999). This suggests headwater meadows and streams at higher elevation may provide climate refugia for some native fishes.

Studies on the impacts of climate change on meadow dependent mammals in the Sierra Nevada are limited. Some studies suggest that small mammal use of meadows may increase in areas that experience decreased meadow wetness (Cocimano et al., 2011; Kalinowski et al., 2014) with implications for predator populations (including Great Gray Owls (*Strix nebulosa*; Kalinowski et al., 2014)). High elevation small mammals have also experienced a range contraction in the 20th century, attributed primarily to climate change (Moritz et al., 2008). Similar to birds, bats obtain >50% of their nutrition from aquatic food webs, potentially increasing the vulnerability of populations with threatened aquatic resources (Jackson et al., 2020).

The effects of changing disturbance regimes because of climate change have largely not been evaluated for wildlife in Sierra Nevada meadows. The shift to a more frequent and higher severity fire regime has the potential to alter habitat both within meadows and the surrounding uplands (Siegel et al., 2019; Tarbill et al., 2023, 2024). The increase in the number of meadows that have burned in recent years provides an opportunity to evaluate effects of fire on meadow-dependent and upland species. Observations suggest most wet meadows recover quickly following fire and may support high densities of breeding birds within a couple years after fire, but these data have not yet been published.

2.3.3: Conclusion

The ability of meadows to sustain extended periods of saturated soil conditions is critical to their persistence in the face of climate change. Several studies suggest that watersheds located in the northern and northeastern portions of the Sierra Nevada region, characterized by basalt or metamorphic parent material, deep aquifers, high rates of hydraulic conductivity, and reduced reliance on snowpack, may exhibit greater resilience to climate change. In contrast, mid-elevation meadows with shallow aquifers and greater reliance on snowpack may be more vulnerable to encroachment and loss under changing climate conditions. Mid-elevation meadows are also likely to be the most susceptible to increasing temperatures and changing precipitation regimes, with the greatest changes in runoff timing, stream temperatures, and dissolved oxygen concentrations likely to occur in these areas. Prioritizing restoration and conservation of meadows with hydrogeomorphic conditions that confer resilience to climate change may help preserve ecological function and prevent habitat and biodiversity loss.

Degraded meadows, particularly those that have transitioned to alternative stable states, may experience greater loss of ecological function or conversion to upland vegetation as a result of climate change. Restoration of floodplain hydrology—particularly in more climate resilient meadows—and return to a more natural fire regime may help increase meadow resilience and habitat refugia.

2.4: Resilience and Adaptations

2.4.1: Ecological Resilience in Wet Meadows

Ecological resilience is defined as the amount of disturbance an ecosystem can withstand without undergoing changes to self-organizing processes or transitioning to an alternative stable state (Holling, 1973). Resilience in wet meadows is maintained by biotic-abiotic interactions that are themselves influenced by hydrogeomorphology, climate, and disturbance. Anthropogenic disturbances and land use change have pushed many Sierra Nevada wet meadows beyond their resilience thresholds, creating systems that are no longer capable of repair through resistance and resilience mechanisms. Climate change is expected to alter the feedback mechanisms that confer meadow stability, thereby increasing stressors to meadow resilience. Wet meadows may be particularly vulnerable to the impacts of climate change because they exist at the terrestrial-aquatic interface where even small changes in temperature and hydrology can result in significant changes to ecosystem function and habitat loss.

2.4.2: Adaptation Measures to Increase Resilience

Restoration efforts aimed at repairing certain ecosystem functions, often through geomorphic modification, may be able to return ecosystems to a stable state with higher ecological function and increase resilience to climate change. In recent decades, activities that aim to increase the residence time of water in wet meadows, capture sediment, and reconnect floodplain hydrology have been increasingly implemented across the Sierra Nevada region. These projects have been studied and modeled extensively, but the periods of study are often short and the results difficult to extrapolate across the region. Uncertainties remain about the long-term impacts and climate resilience of these restored ecosystems. Readoption of Indigenous practices, such as cultural fires, also offer potential to increase ecosystem resilience under climate change (Adlam et al., 2022; Boerigter et al., 2024; Hankins, 2024).

2.4.2.1 Hydrology

Geomorphic restoration techniques, including pond-and-plug, channel fill, and beaver dam analogs (BDAs), have been widely successful at increasing meadow groundwater levels and storage capacity (Fig. 2.3). Pond-and-plug and channel fill techniques have been studied the most, with increases in groundwater elevations of 2-3 feet (0.6-1 m) observed during the growing season (Hammersmark et al., 2008, 2009; Tague et al., 2008). Only one study to date has quantified the impacts of BDA restoration on groundwater levels in Sierra meadows, with immediate increases of 1 foot (0.3 m) measured and long-term increases of 7 inches (0.2 m) predicted (Sevier et al., 2024). The largest increases in groundwater consistently occur adjacent to stream channels (Sevier et al., 2024; Hammersmark et al., 2008; Tague et al., 2008),

and total groundwater storage depends on valley morphology, sediment porosity, and minimum annual depth to water table (Ciruzzi & Lowry, 2017; Essaid & Hill, 2014; Nash et al., 2018).

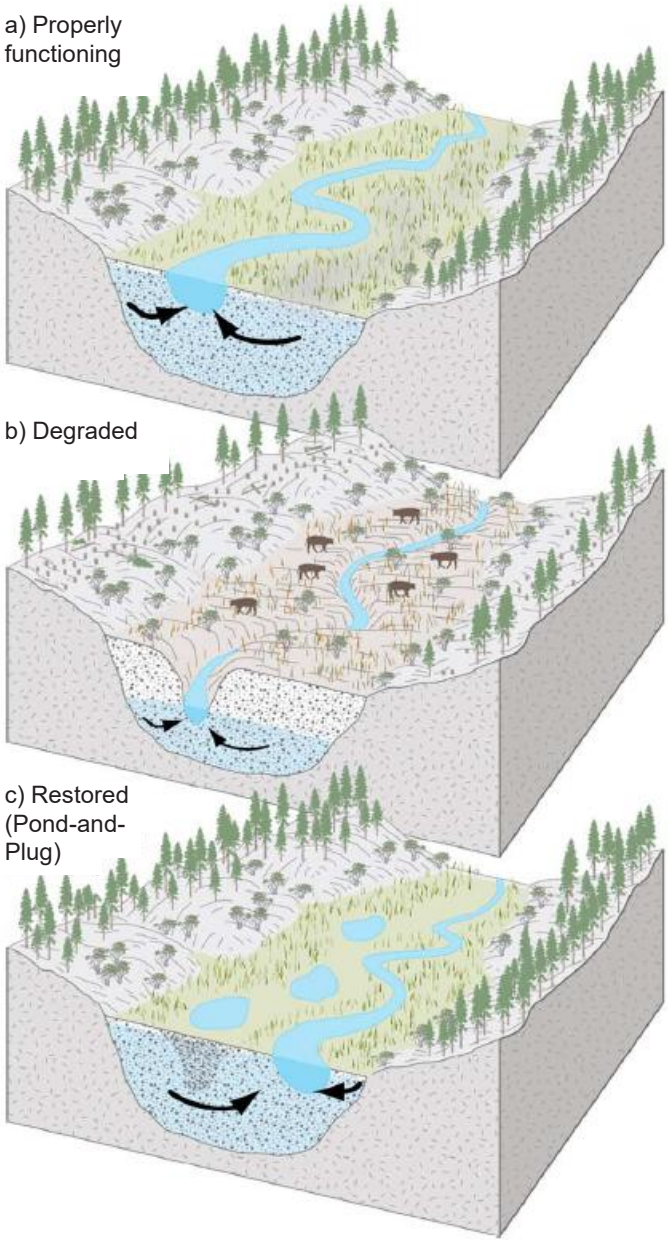
Restoration-induced reductions in channel volume are expected to flatten hydraulic gradients across valleys, slowing drainage and increasing water retention time (Loheide & Gorelick, 2007; Nash et al., 2018, 2020). Hammersmark et al. (2008) found that groundwater residence time was 16 days longer under the restored scenario of a pond-and-plug restoration project in the northeastern Sierra Nevada. Such increases in the residence time of water within wet meadows should have positive effects on stream temperatures and downstream water quality (Lucas et al., 2016; Thompson et al., 2018), though the impacts have not been quantified in Sierra meadows. Similarly, changes in residence time following restoration have not been assessed in meadows with shallower groundwater basins or granitic parent material.

Streamflow response to restoration is nuanced and strongly seasonal. Using paired gauges above and below a channel fill restoration project, Tague et al. (2008) found significantly higher streamflow below the restored reach during snowmelt recession (June–July: 11-24% increase) and significant decreases in streamflow during winter and early snowmelt (December–March). Hammersmark et al. (2008) and Ohara et al. (2014) simulated pre- and post-restoration results for meadows in the northeastern Sierra Nevada and similarly found a 10-25% decrease in the magnitude of flood peaks and sediment discharge following restoration. Both studies note, however, that the magnitude of flood peak reduction was limited by the area of the floodplain and impacted by watershed moisture levels, which may help explain why similar reductions have not been observed in smaller meadows (Essaid & Hill, 2014). Hydrogeomorphic characteristics and vegetation structure are also likely to impact the flood attenuation potential (Acreman & Holden, 2013), though this has not been explicitly studied for Sierra meadows. Further, the capacity of meadows and the surrounding watersheds to affect runoff from extreme storm scenarios predicted under climate change remains unknown.

The impact of wet meadow restoration on late summer baseflows has long been debated by restoration practitioners, land managers, and policy makers. Several studies have tried to address the question, but the impacts remain difficult to generalize and are likely influenced by interannual climate variation and watershed characteristics. Tague et al. (2008) measured no significant change in late summer baseflow between restored and unrestored reaches. Model simulations of other meadows have suggested that geomorphic restoration results in decreased baseflow within the meadow and increased late-season flow downstream of the meadow (Essaid & Hill, 2014; Hammersmark et al., 2008; Nash et al., 2018). However, these modeled decreases in streamflow within the meadow may also be linked, in part, to short simulation periods immediately following restoration when groundwater

storage is being replenished and vegetation evaporative demand is increasing (Essaid & Hill, 2014; Hammersmark et al., 2008; Loheide & Gorelick, 2007; Sevier et al., 2024). Hammersmark et al. (2008) also noted that, while baseflow ceased 16 days earlier in the restored reach, baseflow levels increased downstream, highlighting the potential impacts of sampling location on results, in addition to time following restoration. Ohara et al. (2014) conducted a long-term simulation of a watershed in the northeastern Sierra Nevada that included critical dry and wet periods. They found that the groundwater runoff component was slow to respond to restoration and >10 years were required to reach equilibrium state. Once equilibrium was achieved, baseflow increased by 10-20% in wet years and 2-5% in critical dry years (Ohara et al., 2014). Long-term monitoring and simulations that span a range of climatic conditions and watershed types are needed to better elucidate the decadal impacts of restoration on streamflow; however, any activities that restore watershed hydrologic function are likely to increase resilience to climate change.

Figure 2.3: Conceptual model of hydrologic function in pristine, degraded, and restored meadows.



In properly functioning meadows (a) meandering, shallow stream channels allow for shallow groundwater retention and surface-groundwater interactions support hydric meadow vegetation. Land use changes that result in stream channel incision (b) dewater meadows, resulting in limited groundwater storage and loss of wetland vegetation. Geomorphic restoration (c) seeks to increase groundwater storage, reconnect floodplain hydrology, and improve conditions for wetland vegetation growth. Source Loheide and Gorelick, 2005.

Beaver reintroduction is emerging as a promising strategy to enhance meadow hydrology. Though no peer-reviewed studies have assessed the hydrologic impacts of beaver in Sierra Nevada meadows, work elsewhere has shown that reintroduced beavers can increase surface water storage, raise groundwater tables, improve downstream water quality, and decrease summer stream temperatures (Dittbrenner et al., 2022; Janzen & Westbrook, 2011; Westbrook et al., 2006). As with other restoration techniques, the extent and nature of the impacts may be contingent on meadow and watershed characteristics (Fuller & Peckarsky, 2011). It is also important to note that many meadows in the Sierra Nevada may need to be rehabilitated before they can support reintroduced beaver populations.

2.4.2.2 Vegetation

Restoration projects that succeed in increasing lateral hydrologic connectivity and raising groundwater tables frequently yield rapid shifts in vegetation structure and composition (Hammersmark et al., 2008, 2009). By decreasing depth to groundwater and increasing the period of saturated and moist soil conditions, geomorphic restoration increases the suitable habitat for hydric and mesic vegetation while reducing the cover of xeric species (Hammersmark et al., 2010). Vegetation community composition and vegetation-groundwater relationships following pond-and-plug and channel fill restoration have been shown to mirror those of properly functioning meadows (Hammersmark et al., 2010; Loheide & Gorelick, 2007). As a result, aboveground vegetation biomass was 367-635 g m^{-2} higher in pond-and-plug restored meadows relative to degraded and unrestored controls over a two decade chronosequence (Reed et al., 2022). Increases in the cover and biomass of hydric and mesic species following restoration result in increased belowground carbon allocation and higher concentrations of soil organic matter (Bagcilar et al., 2024; Reed et al., 2021, 2022). Soils with high soil organic matter retain higher levels of plant available water through the growing season, maintaining conditions for productive hydric vegetative growth while also building ecosystem resilience (Akenbauer & Loheide, 2017). No studies have yet examined the impacts of beaver dam analogs and other biogenic structures on vegetation structure and composition in Sierra Nevada meadows.

Returning to a more natural fire regime in the surrounding forest has been shown to increase soil moisture and favor the growth of dense hydric species that help maintain resilient meadow vegetation communities and exclude encroaching conifers (Boisramé, et al., 2017; Lubetkin et al., 2017). In the absence of fire and restoration activities aimed at increasing soil moisture, rates of conifer encroachment into meadows are likely to increase under climate change with many meadows predicted to fully convert to forest by the end of the century (Lubetkin et al., 2017).

2.4.2.3 Biogeochemistry

Although studies remain limited, the emerging consensus is that meadow soil biogeochemistry is relatively resilient and responsive to restoration. Long-term longitudinal studies will ultimately be needed, but evidence from decadal chronosequences provides insight into the potential response of ecosystem properties and processes. Positive increases in soil carbon of 150-300 g C m^{-2} y^{-1} have been observed over the first two to three decades following restoration in both the Sierra Nevada (Reed et al., 2022) and central Great Basin (Morra et al., 2023a), despite difference in meadow condition and restoration type. These measured rates of soil carbon increase following restoration of Sierra Nevada meadows are on par with restored wetlands (Euliss et al., 2006; Knox et al., 2015) and several times higher than grassland ecosystems (Baer et al., 2002; Knops & Bradley, 2009; Matamala et al., 2008). Avoided losses of soil carbon from meadows in degraded condition (391 ± 154 g C m^{-2} y^{-1}) further contribute to the net carbon benefit of restoration.
Reed et al. (2022) found that restoration of floodplain hydrology and decreased depth to groundwater result in rapid response of aboveground biomass, while root biomass took longer to recover. Root biomass increased along with soil carbon and reached levels similar to properly functioning meadows within two decades following restoration (Reed et al., 2022). The fraction of carbon in the mineral associated fraction also increased with root biomass and soil carbon, likely driven by increases in microbial activities stimulated by higher rates of root turnover and root exudation following restoration (Bagcilar et al., 2024). Increases in the fraction of carbon in the mineral associated fraction may increase the durability of soil carbon gains in the face of climate change. See Chapter 3: Soil Age and Persistence for more information on soil carbon persistence.

Changes in soil nitrogen pools were correlated with increases in soil carbon following restoration in both Sierra Nevada (Reed et al., 2022) and central Great Basin meadows (Morra et al., 2023a). These results support other studies that suggest reestablishment of hydrologic connectivity and extended periods of saturated conditions in meadows increases nitrogen assimilation and reduces nutrient runoff (Norton et al., 2011; Sickman et al., 2003). However, the direct impacts of restoration on nutrient export have not been studied.

2.4.2.4 Biodiversity

Meadow bird response to restoration has been evaluated by two studies. Both studies found neutral to positive effects of restoration on abundance and species diversity (Campos et al., 2020; Loffland et al., 2022). Campos et al. (2020) found that 6 of 12 meadow-dependent species evaluated responded positively to restoration within the first two decades, with Yellow Warblers reaching densities found in high-quality meadow habitat a decade or more following restoration. Loffland et al. (2022) found meadow restoration stemmed losses in Willow Flycatcher density while degraded,

unrestored meadows continued to show declines. Further study is needed to evaluate different meadow restoration techniques beyond pond-and-plug and across a larger variety of meadow conditions (e.g., higher elevation meadows). There is no published literature on the response of birds to beaver dam analogs or similar techniques which have grown dramatically in application in the last decade. Nor are there any published papers on the effects of beaver modification on meadow bird communities, though one technical report linked beaver activity in meadows to increased Willow Flycatcher occupancy (Campos et al., 2019).

For many species inhabiting Sierra meadows, increasing resilience can take the form of reducing threats that drive population declines. Among management actions, the removal of non-native fish from streams, ponds, and lakes has had the greatest positive impact on amphibian populations (Halstead et al., 2023; Knapp et al., 2016; Vredenburg, 2004). Fish removal has also been shown to increase insects and the birds that forage on them in headwater systems (Clapp et al., 2025). Fish removal is widely recommended as the first step to increase colonization of amphibians and prevent extirpation of most amphibian species (Bradford, 1991; Knapp et al., 2016; Pope & Matthews, 2002), and similar recommendations have been made for other taxa such as bats (Gruenstein et al., 2021). Removing non-native fish may also increase amphibian resilience to climate change; fishless permanent ponds and lakes can serve as climate refugia in dry years, supporting colonization and stabilizing reproductive success (Halstead et al., 2023; Lacan et al., 2008). Bullfrog removal in Yosemite National Park has produced similar benefits, enabling the successful reintroduction of the threatened California red-legged frog (*Rana draytonii*; Kamoroff et al., 2020). Finally, while chytrid fungus cannot be eliminated from the environment, the reintroduction of chytrid-resistant frogs to fishless ponds has also shown promising signs of success (Knapp et al., 2024).

There is growing interest in the role of beaver in shaping meadow form, function, and climate resilience, but few studies have been conducted in the Sierra Nevada. Current understanding of beaver impacts on meadows is largely drawn from observations and research in other western riverine systems (Polvi & Wohl 2012; Bouwes et al., 2016; Dittbrenner et al., 2018, 2022; Fairfax & Small, 2018; Fairfax & Whittle, 2020), highlighting the need for Sierra-specific studies. Convincing evidence of historic beaver presence across multiple Sierra watersheds has largely resolved debates of whether beaver were native to the region (James & Lanman, 2012); however, their impacts on ecosystem function and habitat in the Sierra remain largely unstudied. The most comprehensive study of beaver in the Sierra Nevada remains one conducted in Sagehen meadow by Gard (1961). The study found similar numbers of trout in stream reaches and beaver ponds (possibly due to angler harvest) but substantially larger trout and greater numbers of non-native brown and brook trout than rainbow trout in the ponds. Paiute sculpin (*Cottus beldingii*) numbers were also significantly lower in beaver ponds than nearby stream reaches. Beaver dams were

found to be largely permeable to trout migration, especially during periods of higher flow. Additional, non-peer-reviewed studies have suggested that anthropogenic removal of beaver dams results in increased instream phosphorous concentrations (Muskopf, 2007) and that Willow Flycatcher occupancy is positively correlated with beaver dam density in the central Sierra (Campos et al., 2019).

2.4.3: Conclusion

Restoration of ecosystem function in meadows ultimately depends on restoring the self-reinforcing feedbacks between vegetation, hydrology, and geomorphic processes. While different methods exist for restoring ecological processes in meadows, the effects of some methods (e.g., pond-and-plug) have been studied more than others. Pond-and-plug and channel fill restoration have been shown to improve hydrologic function, stem soil carbon losses, sequester new soil carbon, shift vegetation community composition toward wetland species, increase vegetation biomass, and improve habitat conditions. More work is needed to quantify the ecological impacts of BDAs and other biogenic structures on wet meadows in the Sierra Nevada. Similarly, the long-term impacts and projected stability of restoration projects under extreme climate events remain unknown. Increased understanding of the impacts of watershed and hydrogeomorphic characteristics on restoration outcomes coupled with watershed-scale projections of climate change impacts could help prioritize and improve restoration efforts.

2.5: Gaps in Knowledge and Policy Recommendations

This synthesis outlines the current state of knowledge of Sierra Nevada meadow formation and function, along with the inherent vulnerabilities and resilience that shape their response to anthropogenic disturbance, restoration, and climate change. While important gaps in knowledge are noted throughout the synthesis, we highlight a few here that are of particular relevance to understanding meadow function and importance, determining meadow resilience under climate change, and the capacity of wet meadows to serve as nature-based climate solutions. We also highlight policy recommendations that will facilitate effective conservation and contribute to the long-term resilience of these ecosystems.

Key Gaps in Knowledge

1. What are the characteristics of high functioning meadows? Most research in Sierra Nevada wet meadows to date has been focused on measuring the impacts of restoration. However, understanding the characteristics of relatively healthy or high functioning meadows is critical to measuring their value to ecosystem services including biodiversity, hydrology, and carbon sequestration. It also provides a benchmark by which to measure restoration

success and the impacts of climate change. Better understanding of the processes and mechanisms that drive ecosystem function may also help prioritize and improve restoration practices.

2. What are the ecological costs of meadow degradation? Similar to understanding the characteristics and importance of relatively healthy meadows, better understanding of the conditions and processes in degraded meadows is essential to quantify the net loss of ecosystem services as a result of degradation. Studies in degraded meadows also serve as a baseline against which to measure the benefits of restoration.
3. What confers resilience in Sierra Nevada wet meadows? Is ecological resilience an innate characteristic driven by hydrogeomorphic characteristics? Or can resilience be created by restoring conditions for stabilizing biogeomorphic feedbacks to occur? What are the links between watershed health and meadow resilience? And how do land use practices (e.g., grazing) affect the vulnerability or resilience of meadows to stressors, including climate change? In order to effectively steward and conserve meadows in an era of climate change, better understanding of the drivers and limits to meadow resilience are needed.
4. How do different meadow restoration techniques confer resilience and how compatible are they with changing climate conditions? Low-tech, process-based restoration techniques (e.g., BDAs) are increasingly being implemented in meadows across the Sierra Nevada. However, most studies of the effects of restoration on ecosystem services have been conducted in meadows restored using channel fill or pond-and-plug restoration techniques. More studies that include other restoration techniques are needed. Assessments of the stability of different restoration techniques under different climate scenarios could also help inform effective restoration under climate change.
5. What are the effects of Indigenous land management practices on ecosystem services and resilience in meadows? Historic and anecdotal evidence support the benefits of Indigenous land management practices (e.g., cultural burning, selective harvesting, and riparian pruning) to ecosystem function and meadow persistence. Integration of western and Indigenous science to measure the benefits of Indigenous land management could help improve restoration and stewardship practices and may contribute to changing policy.

Policy Recommendations

1. Support pathways for conservation of fens and wet meadows where ecosystem function and biodiversity have not been compromised or can be easily repaired through conservation. While restoration of degraded ecosystems is important for increasing habitat and improving ecosystem function, studies in wet meadows and other ecosystems suggest that ecosystem function in restored sites lags behind pristine or undegraded counterparts, even two

decades after restoration. Conserving properly functioning ecosystems and restoring those that have experienced minimal loss of function but are at risk of further degradation should be a priority to maximize ecological benefits.

2. Invest in market-based structures that incentivize carbon sequestration and ecologically sound management. Actions that lead to increased rates of carbon sequestration also tend to improve habitat and ecological resilience in Sierra Nevada wet meadows, a condition that is not universally true for all ecosystems. Carbon stored belowground in wet meadows is also more resilient to wildfire than aboveground carbon stocks and persistent for thousands of years. Market-based structures could provide incentives for management activities that increase soil carbon sequestration, enhance ecosystem resilience, and improve habitat value.
3. Reconsider grazing management in wet meadows and fens. Grazing is the most common land use practice in Sierra Nevada wet meadows. Yet, there is evidence that grazing can negatively impact a number of the ecosystem services that meadows provide. Standards for evaluating grazing impacts in meadows should be modified to address the full range of ecosystem services. This will allow better assessment of grazing suitability and the development of grazing strategies compatible with conserving ecological services. Investment in staffing to manage public lands and market-based structures to incentivize ecologically sound management on private lands would improve outcomes.
4. Support long-term stewardship. Currently, there is a disconnect between the need for long-term stewardship, particularly under climate change, and funding cycles that tend to be short term. Longer grant cycles or dedicated long-term funding streams, possibly coupled with market-based structures, could allow for adaptive management, stewardship, and long-term investment in watershed restoration necessary to ensure project sustainability under climate change.
5. Invest in long-term monitoring networks. Increased understanding of ecosystem function in hydrologically functioning, degraded, and restored meadows is critical to guiding land management and habitat preservation under climate change. However, interannual climate variability, and the associated impacts on ecosystem function, challenge the utility of short-term studies and monitoring efforts. A network of long-term monitoring sites would provide an avenue to better understand the importance of wet meadows and predict their fate under climate change.

3: Soil Carbon Age and Persistence Technical Report

3.1: Introduction

Soils are the largest terrestrial reservoir of carbon, containing more than the atmosphere and biosphere combined (about 1,500 Pg C to 1 m; Jobbagy & Jackson, 2000). However, feedbacks among soils, the atmosphere, and biosphere challenge quantification of terrestrial carbon reserves and increase uncertainty. Globally, wetlands contain up to half of terrestrial soil carbon (Kayranli et al., 2010; Kumar et al., 2025) and may serve as valuable natural climate solutions, increasing the need for accurate accounting of wetland carbon stocks and fluxes, along with the persistence of carbon in these ecosystems.

The balance between photosynthesis and respiration drives rates of carbon sequestration and loss in ecosystems. Similarly, carbon is continually being added to the soil as photosynthetic carbon inputs and lost through microbial decomposition, volatilization, or aquatic export. As Janzen (2015) notes, "organic matter may best be viewed, not as a reservoir entrapped in soil, but as a stream of atoms flowing through." The length of time that carbon remains in the soil before being released back to the atmosphere is reflective of the persistence, or permanence, of a soil carbon stock. The transit time of any given carbon atom may range from minutes to millennia and, though partly random, can be influenced by factors including environmental constraints to microbial decomposition and association with mineral soil particles (Hemingway et al., 2019; Janzen, 2015; Schmidt et al., 2011). As freshwater, mineral soil wetlands with dynamic redox conditions, the long-term persistence of carbon in Sierra Nevada wet meadows may depend on the formation of mineral-associated organic matter (MAOM) and key stabilization pathways.

MOAM is carbon that is chemically and physically stabilized on the surfaces of micron-scale soil particles like silts and clays, allowing it to persist in the ecosystem for hundreds to thousands of years (Torn et al., 1997). Plants and microbes interact with mineral surfaces to stabilize and destabilize organic matter under different environmental conditions (Kleber et al., 2015). The formation and persistence of MAOM is influenced by factors including vegetative productivity (Morra et al., 2023b), soil mineralogy (Kleber et al., 2015), and shifting redox conditions (Keiluweit et al., 2015). Research suggests that MAOM may increase with soil carbon concentration following restoration in Sierra Nevada wet meadows and that the potential for carbon storage in MAOM may be higher in meadows than other ecosystems (Bagcilar et al., 2024; Sokol et al., 2022). However, slower rates of cycling for MAOM are not universally true across ecosystems (Jilling et al., 2025), and the contribution of MAOM

to carbon cycling in wetlands remains poorly understood. Further, long histories of anthropogenic disturbance that alter plant-soil-water relationships in Sierra Nevada wet meadows may impact the persistence or loss of MAOM (Jilling et al., 2025; Morra, Reed, et al., 2023; Sokol et al., 2022).

In this study we address this gap in knowledge by measuring the age and persistence of carbon in properly functioning, degraded, and restored wet meadows of the Sierra Nevada. We combined soil size fractionation (to determine the partitioning of carbon to particulate organic matter (POM) and MAOM pools) with radiocarbon dating (to measure the mean age and transit time of carbon) and analyses of the concentrations of reactive metals (to assess controls on carbon transit times). We hypothesized that (1) properly functioning meadows would have intermediate transit times that increase with soil depth and high concentrations of carbon in both MAOM and less protected POM. In degraded meadows, we predicted that (2) decreased vegetative carbon inputs combined with high rates of microbial decomposition would lead to the loss of old, previously protected carbon, resulting in increased transit time and a decrease in the amount of carbon in MAOM. Additionally, we hypothesized that (3) restoration of floodplain hydrology would increase allocation of carbon to MAOM and increase the transit time of soil carbon relative to degraded meadows. Finally, (4) we predicted that soil mineralogy would impact MAOM formation and the transit time of carbon in meadows of all conditions.

3.2: Methods

3.2.1: Site description

To assess the partitioning of carbon into MAOM and POM pools, the carbon persistence, and controls on carbon persistence in wet meadows, we analyzed archived soils from 19 sites located in the northern and northeastern portions of the Sierra Nevada. Meadows spanned a range of conditions. Following the model of meadow ecosystem function presented by Lodeide et al. (2009), we defined meadows with incised stream channels <3 feet (1 m) as "mildly degraded" and sites with >3 feet (1 m) of stream incision as "degraded." "Properly functioning" meadows are sites with connected floodplain hydrology and stable stream banks that promote saturated soils early in the growing season and shallow water tables into peak productivity (Gonzalez & Smith, 2020; Loheide et al., 2009). "Restored" meadows are sites that have experienced geomorphic restoration to fill incised stream channels and reestablish lateral hydrologic connectivity. All "restored" sites in this study were restored between 1995 and 2010 by Plumas Corporation using the pond-and-plug restoration technique (Table 1). Restored meadows were selected based on soil parent material, vegetation community, and climate with the objective of controlling for soil forming factors while letting time since restoration vary (Jenny, 1941). In this way, they represent a chronosequence of secondary succession as described in more detail in Reed et al. (2022).

Table 3.1: Site locations, characteristics, and sampling information.

Meadow:	Bear Trap	Big Flat	Coyote Flat	Deer
Lattitude & Longitude	39.6420, -120.5004	40.1489, -120.4597	40.1114, -120.4187	39.4288, -120.6507
Elevation (ft.)	7,149	5,711	5,583	6,184
Dominant Vegetation Type	Carex sp. Juncus sp. Pinus contorta	Carex sp. Juncus sp.	Artemesia sp.	Carex sp. Juncus sp.
Parent Material	V/G	V	V	M
Condition	D	R - 22 y	D	MD
Max Depth Sampled	0.75 m	0.45 m	0.45 m	0.75 m
MAOM/POM	X	X	X	X
^{14}C & Fe/Al Analysis		X	X	

Table 3.1: Site locations, characteristics, and sampling information. (Continued)

Meadow:	Dixie	East Creek	Freeman	Loney
Lattitude & Longitude	39.9348, -120.3335	40.2434, -120.9024	39.6751, -120.6046	39.4207, -120.6549
Elevation (ft.)	5,967	5,059	6,814	5,990
Dominant Vegetation Type	Carex sp. Juncus sp.	Forbs	Carex sp. Forbs	Carex sp. Juncus sp.
Parent Material	V	V	M	M
Condition	R - 9 y	D	MD	MD
Max Depth Sampled	0.45 m	0.75 m	0.45 m	0.475 m
MAOM/POM	X	X	X	X
^{14}C & Fe/Al Analysis	X	X		X

Table 3.1: Site locations, characteristics, and sampling information. (Continued)

Meadow:	Lower Lacey	Lower Dixie	Middle Martis	Martis Control
Lattitude & Longitude	39.4701, -120.4197	39.9389, -120.3386	39.3033, -120.1113	39.3039, -120.1073
Elevation (ft.)	6,814	5,890	5,875	5,930
Dominant Vegetation Type	Carex sp. Juncus sp.	Artemesia sp.	Aretemsia sp. Carex sp. Juncus sp.	Aretemsia sp. Carex sp. Juncus sp.
Parent Material	M	V	V	V
Condition	P	D	D	MD
Max Depth Sampled	0.45 m	0.45 m	0.75 m	0.75 m
MAOM/POM	X	X	X	Y
^{14}C & Fe/Al Analysis		X		

Table 3.1: Site locations, characteristics, and sampling information. (Continued)

Meadow:	Poco	Sardine	Upper Clarks	Upper Loney
Lattitude & Longitude	39.9695, -120.5237	39.5126, -120.1173	40.1347, -120.5065	39.4289, -120.6511
Elevation (ft.)	5,390	6,055	5,565	6,185
Dominant Vegetation Type	Carex sp. Juncus sp.	Artemesia sp. Forbs	Carex sp. Juncus sp.	Carex sp. Juncus sp.
Parent Material	V	V	V	M
Condition	R - 6 y	D	R - 15 y	P
Max Depth Sampled	0.45 m	0.45 m	0.45 m	0.75 m
MAOM/POM	X	X	X	X
^{14}C & Fe/Al Analysis	X		X	X

Table 3.1: Site locations, characteristics, and sampling information. (Continued)

Meadow:	Upper Lacey	Van Norden	Wilson
Lattitude & Longitude	39.4534, -120.4324	39.3148, -120.3636	38.8245, -120.2561
Elevation (ft.)	6,885	6,780	6,614
Dominant Vegetation Type	Carex sp. Juncus sp.	Carex sp. Juncus sp.	Carex sp. Forbs
Parent Material	M	V/G	G
Condition	P	D	D
Max Depth Sampled	0.45 m	0.45 m	0.75 m
MAOM/POM	X	X	X
^{14}C & Fe/Al Analysis			

Parent material: V = volcanic, M = metamorphic, G = granite. Condition: P = properly functioning, MD = mildly degraded, D = degraded, R = restored (along with the age of restoration). Blank cells in the last column indicate samples not analyzed for ^{14}C & Fe/Al Concentrations. Depths are measured from the soil surface.

Soils from all 19 meadows were fractionated by soil size and analyzed for carbon concentration to assess the fraction of carbon in either the POM or MAOM pool. At each site, six previously sampled points within each meadow were randomly selected for analysis. At each point, we analyzed soils at the surface (0-15 cm) and from 30-45 cm. For points sampled deeper than 45 cm, we analyzed an additional sample at the 60-75 cm depth. A subset of eight meadows (3 points per meadow) were selected for radiocarbon dating and analysis of iron and aluminum concentrations (Table 3.1).

3.2.2: Soil Carbon Fractionation and Elemental Analysis

We used soil particle size to separate soil carbon into POM and MAOM. We adapted our soil particle size fractionation method from Sanderman et al., (2011). This method has been used in other studies of Sierra Nevada meadow soil carbon fractions (Bagcilar et al., 2024; Morra et al., 2023b) and has been shown to produce results similar to other soil carbon fractionation methods (Poeplau et al., 2018).

Briefly, approximately 10 g of rock- and visible-root-free dried soil was weighed into a 50 mL centrifuge tube. Twenty mL of 3% weight by weight of sodium

hexametaphosphate was then added, and the tubes were shaken using an orbital mixer for 9 h at 180 rpm. The solution was passed through a 53 µm mesh sieve while shaking on a Vortex Genie 2 (Scientific Industries, Inc., Bohemia, NY, USA). The sand fraction was retained on top of the sieve and washed into a beaker, whereas the silt and clay fractions passed through the 53 µm sieve into another beaker. The silt and clay fractions were then diluted with 300 mL of deionized water and allowed to settle for 2 h. The fraction remaining in suspension after settling was decanted into another beaker and was considered the clay fraction; the sedimented fraction was considered the silt fraction. All fractions were oven-dried at 105 °C until constant mass was obtained. The soil carbon concentration of each soil fraction was obtained using elemental analysis. Soil fractions were finely ground and weighed into tins on a microbalance before analysis on a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Inc., Valencia, CA).

Soil organic carbon (SOC) in the silt and clay fractions were mass-weighted and combined to determine the concentration of carbon in the MAOM fraction, while the carbon in the sand fraction was considered representative of POM (as in Bagcilar et al., 2024). All three fractions were combined to determine bulk SOC. All carbon was assumed to be in the organic fraction because of the low to neutral pH of the soils and parent materials that typically do not contain inorganic carbon. As such, the carbon measured in the sand fraction by elemental analysis was considered to be equivalent to POM-C. Bulk soils, from the subset of samples selected for radiocarbon analysis, were analyzed for oxalate extractable iron (Fe) and aluminum (Al) at the University of California Davis Analytical Lab. The molar ratio of Fe:Al was then used to distinguish the dominant mineral phases that may be contributing to carbon stabilization.

3.2.3: Radiocarbon Analyses

Radiocarbon is a naturally occurring radioisotope (^{14}C) with a half life of 5,730 years. Depletion of ^{14}C relative to ^{12}C in organic samples is an indicator of the age of carbon and can be combined with models to estimate the mean transit time of carbon through the ecosystem. Radiocarbon analyses were conducted on dried and ground sand, silt, and clay fractions. The dried material was weighed into tin capsules (typically 100-300 µg C each) and analyzed via an Elemental Analyzer–GIS interface with an IonPlus MICADAS at the National Ocean Sciences Accelerator Mass Spectrometry facility (NOSAMS; https://www2.whoi.edu/site/nosams/). Oxalic Acid II was used as a calibration standard and a typical batch run also included secondary standards (e.g., International Atomic Energy Agency standards) and blanks along with the samples. Measurement uncertainty ranged from 70-110 years (mean: 82 years) across all samples. Radiocarbon values were corrected for mass-dependent fractionation with online $\delta^{13}C$ values, corrected to the date of collection, and reported as $\Delta^{14}C$ (‰)(Stuiver & Polach, 1977).

Model:
To estimate the transit time of soil organic matter across MAOM and POM fractions, we applied a time-dependent, steady-state radiocarbon model (Equation 1). In this context, transit time represents an estimate of how long carbon remains in a specific pool before leaving the soil system (Rhode, 1992; Sierra et al., 2017; Trumbore, 2000). We used the fractional carbon percent and radiocarbon values (expressed in absolute fraction modern) of the individual fractions to estimate the bulk soil radiocarbon value through mass balance, which was then used to constrain the model (Marín-Spiotta et al., 2008; Torn et al., 2009). Model outputs were optimized by adjusting transit times so that the modeled fraction modern values of bulk soil and the fractions matched empirical measurements (Gaudinski et al., 2000; McFarlane et al., 2013; Torn et al., 2002). Atmospheric radiocarbon inputs (F'_{atm}) were compiled from Hua et al. (2022). A single-pool structure was used to model the transit time of carbon in each soil fraction (sand, silt, and clay) individually. The transit times of the silt and clay fractions, which together make up the MAOM pool, were then combined using a weighted-average proportional to their carbon concentrations. This approach assumes (1) steady-state conditions, where carbon inputs balance losses; (2) isotopic homogeneity within each modeled pool; and (3) that carbon fixed from the atmosphere is incorporated into soil within one year. Since the net carbon flux is small relative to the total carbon stock in these ecosystems, steady state assumptions provide a reasonable first order approximation of transit times. However, given the heterogeneity of bulk SOC and individual fraction carbon concentrations, these assumptions may not be perfectly met. Therefore, the modeled transit times should be interpreted as comparative indicators of carbon transit times rather than precise estimates. The governing equation for SOM ^{14}C dynamics was adapted from Torn et al. (2009):

$$F'_{SOM(t)} = [I \times F'_{atm(t-1)} + C_{(t-1)}F'_{SOM(t-1)}(1 - k - \lambda)]/[C_{(t)}] \qquad \textbf{Equation 1}$$

where $F' = (\Delta^{14}C \times 1000^{-1}) - 1$ (or absolute fraction modern); I = inputs of carbon to a given SOM pool or fraction (g C m^{-2} y^{-1}); C = stock of carbon for the given SOM pool (g C m^{-2}); k = decomposition rate constant of the SOM pool ($year^{-1}$); F'_{atm} = the $\Delta^{14}C$ value of atmospheric CO_2; F'_{SOM} = the $\Delta^{14}C$ value of the given carbon pool; λ = radioactive decay rate of $\Delta^{14}C$ (year−1); and t = year in which calculation is being performed. Model fitting was performed in R using non-linear least squares with the nlsLM() function from the minpack.lm package.

Model performance was strong, with an average root mean square error (RMSE) of 0.014 and mean absolute error (MAE) of 0.013 across sites. The residual sum of squares (RSS) was 0.0014, compared to a total sum of squares (TSS) of 0.135, indicating low overall error and good model fit.

3.2.4: Statistical Analyses

The objective of this study was to characterize the distribution of soil carbon in MAOM and POM fractions along with the transit time of carbon in each fraction in Sierra Nevada wet meadows of different conditions. These results will be combined with data from two ongoing studies to better characterize carbon dynamics in meadows across the region. However, currently the distribution of sites within each meadow condition is unbalanced. Further, the cost of radiocarbon analysis precluded us from analyzing soils from more than three locations within each meadow. For this reason, we have chosen not to use statistical analyses for comparisons among sites and meadow condition classes. Concentrations of carbon in MAOM and POM were measured at six points within each site. A subset of three points was selected for radiocarbon dating and analyses of reactive metal concentrations. Relationships among the concentrations of carbon in the MAOM and POM fractions, bulk SOC, root biomass, and Fe and Al concentrations were assessed using plot-level measurements and statistically analyzed using general linear mixed-effects models with site as a random effect to account for the nested sampling design (nlme package in R; Pinheiro et al., 2020). Statistical significance was set a *priori* as $a = 0.05$.

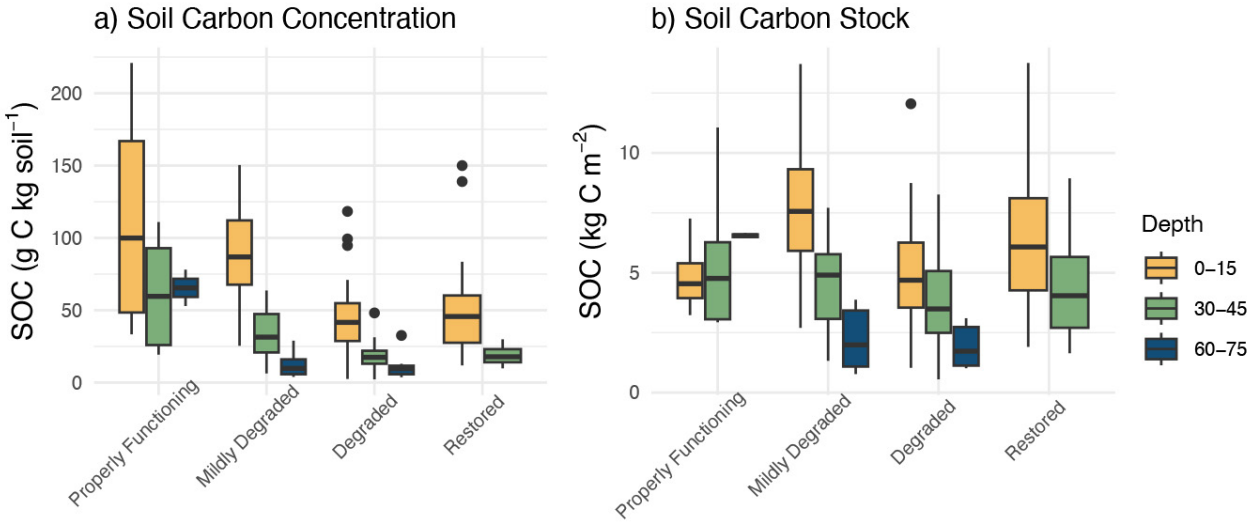
3.3: Results

3.3.1: Mineral Association and Transit Time of Carbon in Sierra Nevada Wet Meadows Across a Range of Conditions

Soil organic carbon concentration was highest in the surface (0-15 cm) mineral soil depths and declined with increasing soil depth (30-45 cm to 60-75 cm; Fig. 3.1a) in all meadows, regardless of condition. Variability of soil C concentration within meadow condition was greatest at the 0-15 cm depth and variability decreased with depth under all conditions (Fig. 3.1a). Further, variability of carbon concentration in the surface soil (0-15 cm) was greater in the properly functioning meadows than the other three meadow conditions.

Soil carbon stocks, which integrate both soil carbon concentration and soil bulk density, showed less of a consistent depth-related pattern than soil carbon concentration. Soil carbon stocks were greatest in the surface soils and declined with depth in the degraded, mildly degraded, and restored meadows. In contrast, soil carbon stocks were similar to the other conditions in the surface of the properly functioning meadows but increased with depth (Fig. 3.1b).

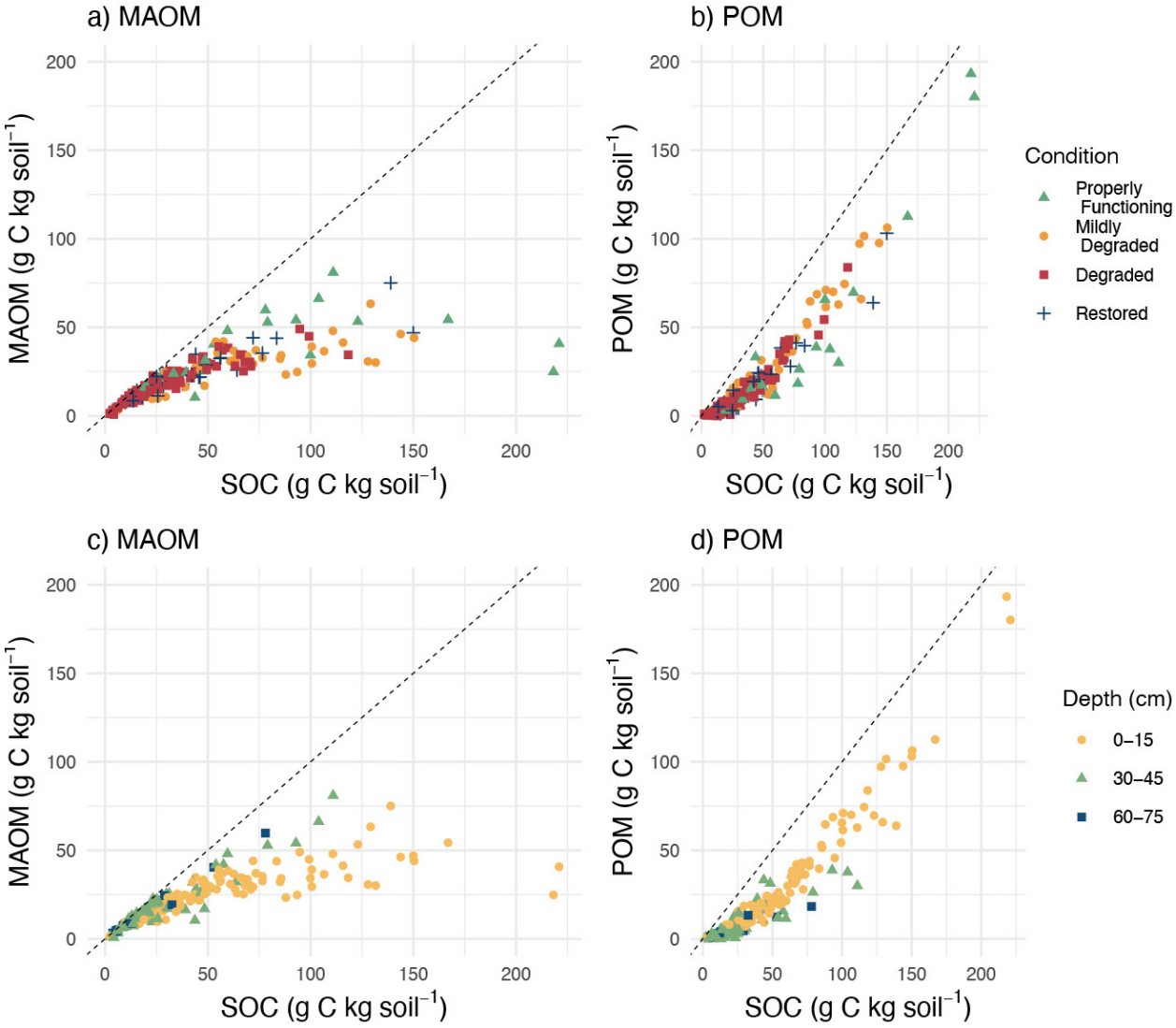
Figure 3.1: Soil organic carbon (SOC) concentration and stock by soil depth and meadow condition.



Soil depth is represented by colors and meadow condition groupings of boxes. The number of sites varied by condition (properly functioning: n = 2, mildly degraded: n = 4, degraded: n = 9, restored: n = 4). Soil was not sampled at the 60-75 cm depth in the restored meadows. Error bars reflect spatial variation in measurements within and across sites (n = 6 per site).

The concentration of carbon in both MAOM and POM increased with bulk SOC across all sites and depths (Fig. 3.2). The highest concentrations of carbon in both MAOM and POM occurred in carbon-rich soils of properly functioning, mildly degraded and restored meadows (Fig. 3.2a and 3.2b). Highly degraded meadows had lower carbon concentrations in both fractions. Carbon concentrations in both fractions also tended to be higher in surface soils (Fig. 3.2c and 3.2d). The carbon concentration in the MAOM fraction appears to saturate around 75 g C kg soil-1, above which increasing concentrations of bulk SOC did not result in increases in MAOM-C (Fig. 3.2a and 3.2c).

Figure 3.2: Relationships between mineral associated organic matter (MAOM), particulate organic matter (POM), and bulk soil organic carbon (SOC).



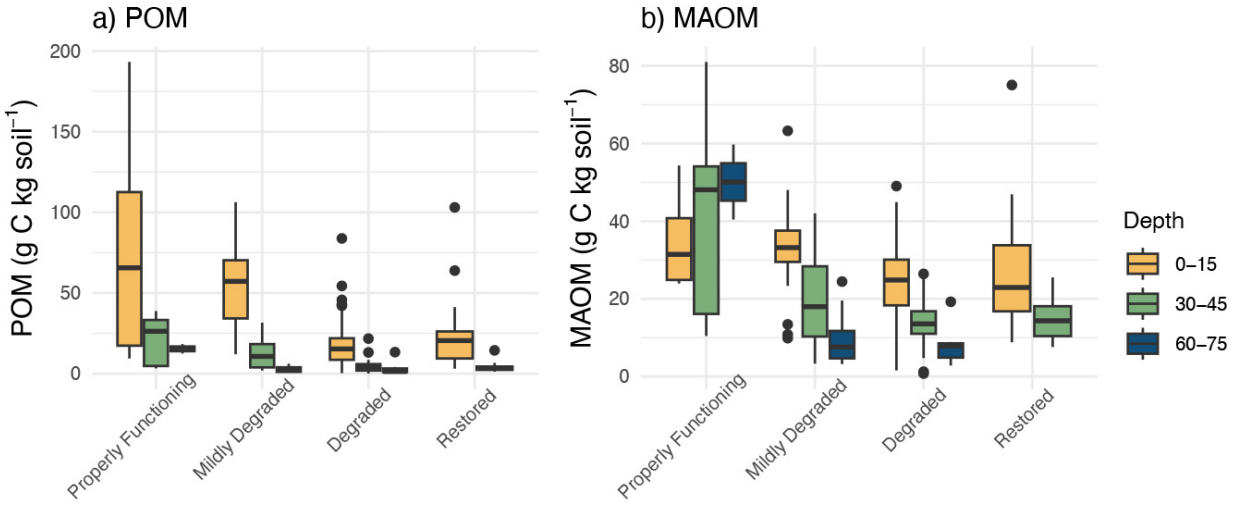
Mineral associated organic matter displayed a non-linear relationship with total SOC, while POM continued to increase with increasing SOC.

The concentration of carbon in the POM fraction was greatest in the properly functioning meadows and decreased with depth at all sites (Fig. 3.3a). Within condition classes, the highest amount of variation within POM was observed in the surface soils (0-15 cm) and the concentration of carbon within the POM fraction showed a significant positive relationship to root biomass across all depths and conditions ($p < 0.01$, t = 8.61, df = 178.21).

Carbon in the MAOM fraction was also greatest in the properly functioning meadow soils and increased with depth along with bulk SOC at that site (Fig. 3.3b). Conversely, carbon in the MAOM fraction decreased with depth in the mildly disturbed, disturbed, and restored meadows (Fig. 3.3b). There was a significant positive relationship between root biomass and the concentration of carbon in the MAOM fraction across all depths and condition classes ($p < 0.01$, t = 17.38, df = 153.99).

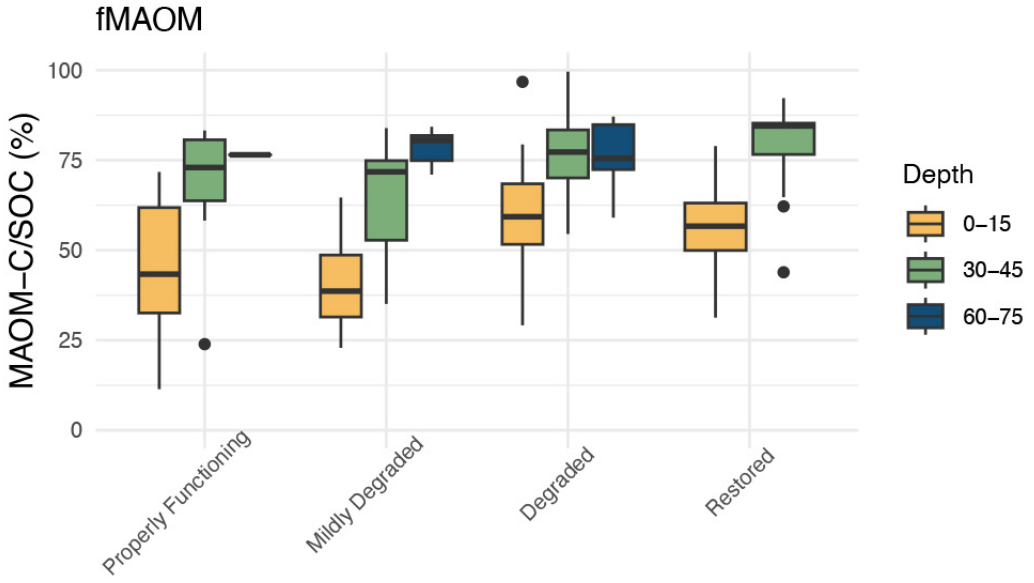
The fraction of total carbon as MAOM (fMAOM) ranged from 11.4% to 99.6% across all soil samples and was lowest in the surface soils of the properly functioning and mildly degraded meadows (Fig. 3.4). In all meadows, fMAOM increased with depth and was similar across conditions at 60-75 cm (Fig. 3.4). The fMAOM was highest in the degraded and restored meadows and only less than 50% in the surface soils of the properly functioning and mildly degraded meadows.

Figure 3.3: Concentration of carbon in the mineral associated (MAOM) and particulate organic matter (POM) fractions by depth for meadows across a range of conditions.



The number of sites varied by condition (properly functioning: n = 2, mildly degraded: n = 4, degraded: n = 9, restored: n = 4). Soil was not sampled at the 60-75 cm depth in the restored meadows. Error bars reflect spatial variation in measurements within and across sites (n = 6 per site).

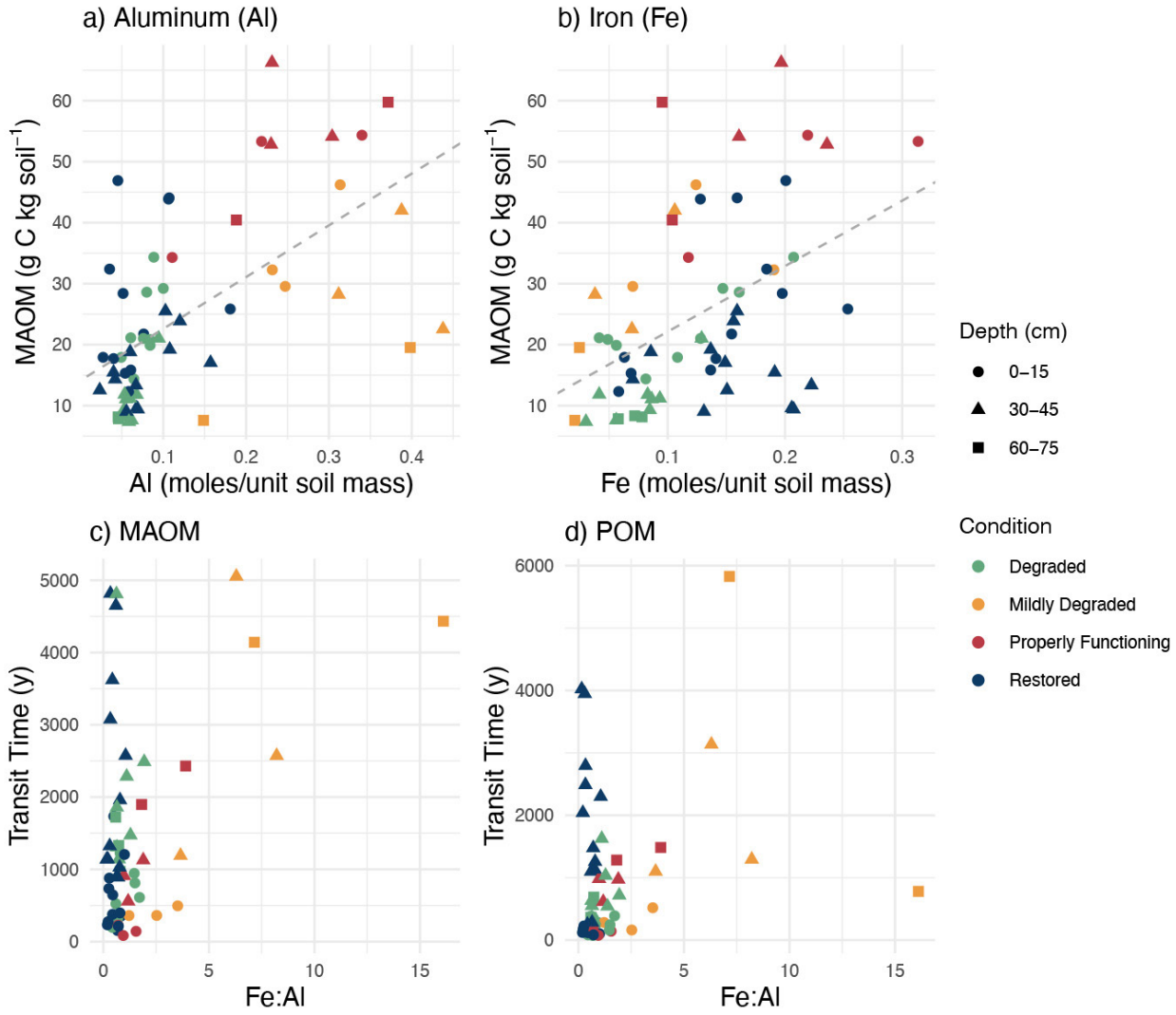
Figure 3.4: The fraction of bulk soil carbon (SOC) in the mineral associated fraction (MAOM) by soil depth across a range of meadow conditions.



The number of sites varied by condition (properly functioning: n = 2, mildly degraded: n = 4, degraded: n = 9, restored: n = 4). Soil was not sampled at the 60-75 cm depth in the restored meadows. Error bars reflect spatial variation in measurements within and across sites (n = 6 per site).

Analyses of aluminum (Al) and iron (Fe) concentrations were only conducted on the soils selected for radiocarbon analysis. However, among these meadows there were significant relationships between the concentration of C in the MAOM fraction and the moles per unit soil mass (moles/kg) of both Al and Fe (Fig. 3.5a and 3.5b). Aluminum concentrations explained 25% of the variance in bulk SOC and 35% of the variance in MAOM-C ($p < 0.01$). Iron explained 23% and 22% of the variance in bulk SOC and MAOM-C, respectively ($p < 0.01$). Combined, Fe and Al explained 45% of the variance in bulk SOC and 52% of the variance in MAOM-C ($p < 0.01$). The molar ratio of Fe:Al ranged from 0.16 -16.11 (mean = 0.77) and was greater than 1.5 only at the properly functioning and mildly degraded sites. There was a weak but significant negative relationship between the concentration of Fe and the transit time of bulk SOC ($p = 0.02$, $r^2 = 0.08$) and MAOM ($p < 0.01$, $r^2 = 0.10$). These relationships were not significant for the concentration of Al or the molar ratio of Fe:Al (Fig. 3.5c and 3.5d)

Figure 3.5: Impacts of Aluminum (Al) and Iron (Fe) on the formation of mineral associated organic matter (MAOM) and transit time of soil carbon in Sierra Nevada meadows across a range of conditions and soil depths.

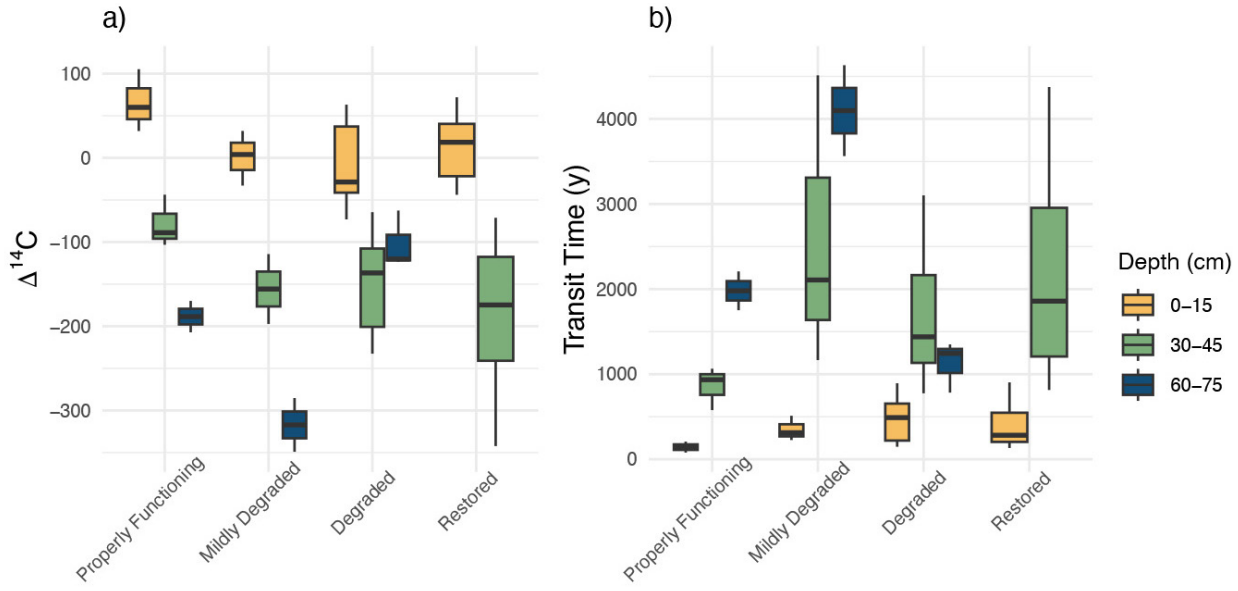


Values of $\Delta^{14}C$ were increasingly negative at deeper soil depths in all meadows. At each depth the $\Delta^{14}C$ values of the properly functioning meadow were higher than any of the disturbed or restored meadows, reflecting younger carbon in the properly functioning site, The exception to these two trends was the deepest soils in the most degraded sites. In those meadows $\Delta^{14}C$ values did not decrease from 30-45 cm to 60-75 cm depths (Fig. 3.6a).

Similar patterns existed for transit times, where the most rapid rates of carbon transit occurred in the surface soils and carbon in the properly functioning meadow had shorter transit times than other conditions at all depths, except for the degraded

meadows from 60-75 cm (Fig. 3.6b). The longest transit time (~4,000 years) was measured in the 60-75 cm depth in the mildly degraded meadow (Fig. 3.6b). Across all meadows and depths, there was a negative exponential relationship between root biomass and the transit time of carbon in both the POM (log-transformed, $p < 0.01$, t = 6.04, df = 55.94) and MAOM fractions (log-transformed $p < 0.01$, t = 3.98, df = 56.68).

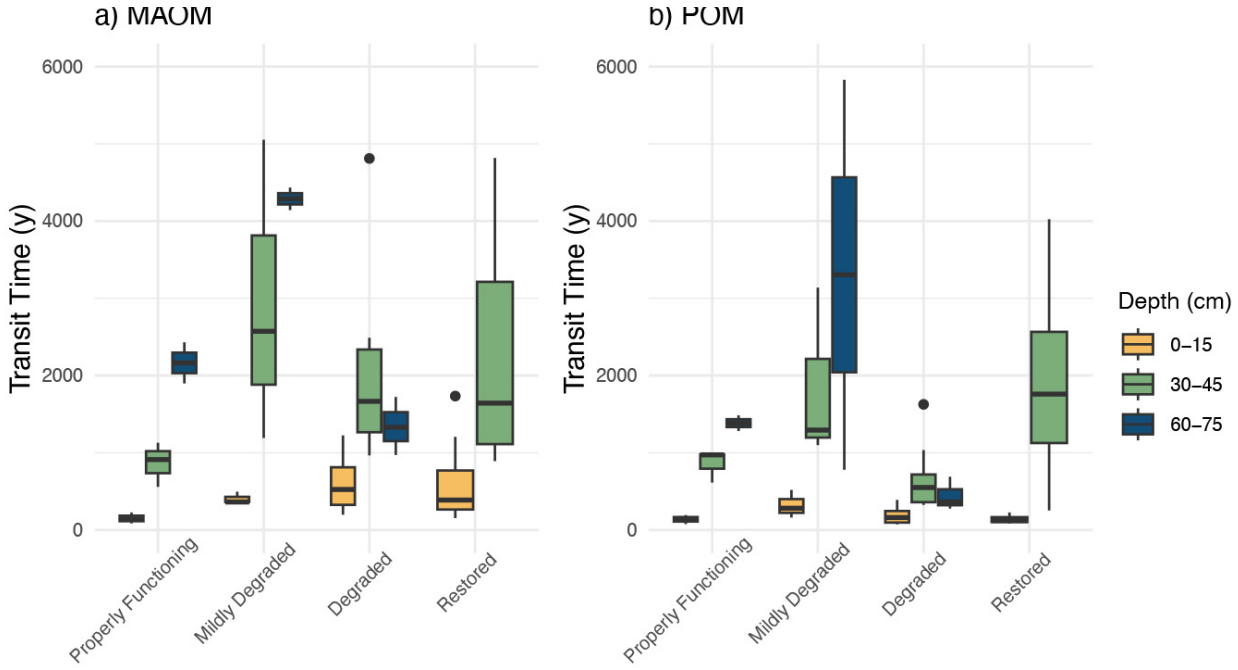
Figure 3.6: Distribution of $\Delta^{14}C$ values and transit time of bulk soil carbon by depth and meadow condition.



Lower $\Delta^{14}C$ values (a) suggest older carbon ages. The bulk soil transit time is modeled based on the $\Delta^{14}C$ values of different soil fractions. The number of sites varied by condition (properly functioning: n = 1, mildly degraded: n = 1, degraded: n = 3, restored: n = 4). Soil was not sampled at the 60-75 cm depth in the restored meadows. Error bars reflect spatial variation in measurements within and across sites (n = 3 per site).

The transit time of carbon in the MAOM and POM fractions followed similar patterns to those observed in the bulk soil. Lower variability in transit time was observed for both fractions in the properly functioning meadow than the degraded or restored meadows. In the properly functioning meadow, the transit time was similar in both the MAOM and POM fractions at 0-15 cm and 30-45 cm depths (Fig. 3.7a and 3.7b). The same was true for the 30-45 cm depths of the restored sites. In all other conditions and depths, the transit time was greater for carbon in MAOM than POM.

Figure 3.7: Transit time of carbon in the mineral associated (MAOM) and particulate organic matter (POM) pools by meadow condition and soil depth.

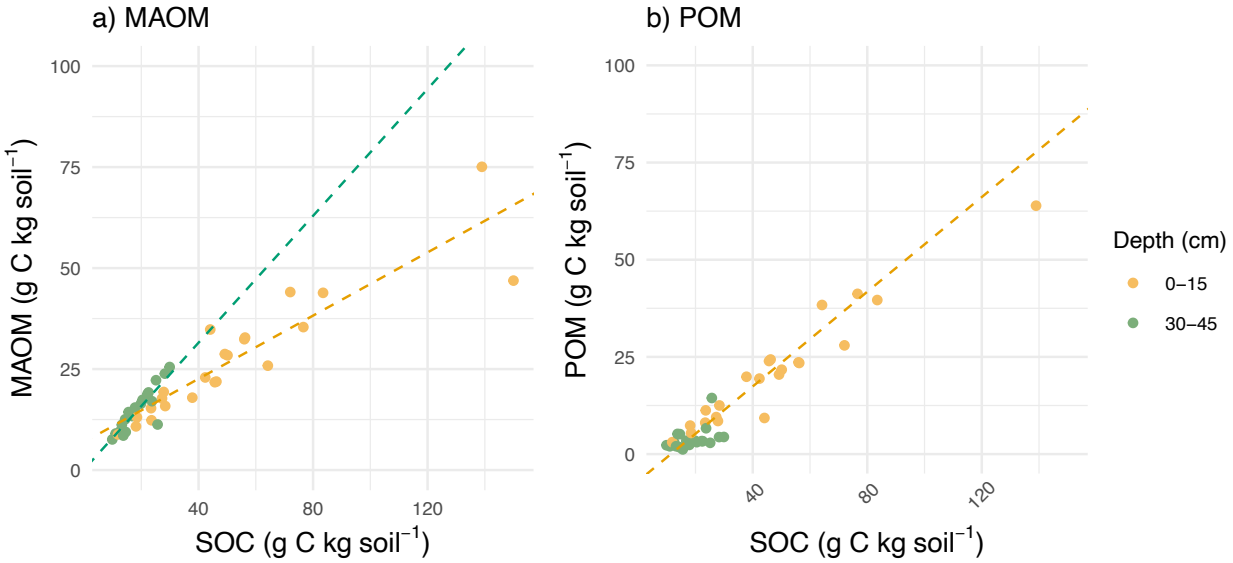


The number of sites varied by condition (properly functioning: n = 1, mildly degraded: n = 1, degraded: n = 3, restored: n = 4). Soil was not sampled at the 60-75 cm depth in the restored meadows. Error bars reflect spatial variation in measurements within and across sites (n = 3 per site).

3.3.2: Impacts of Hydrologic Restoration on Mineral Association and Transit of Carbon in Sierra Nevada Wet Meadows

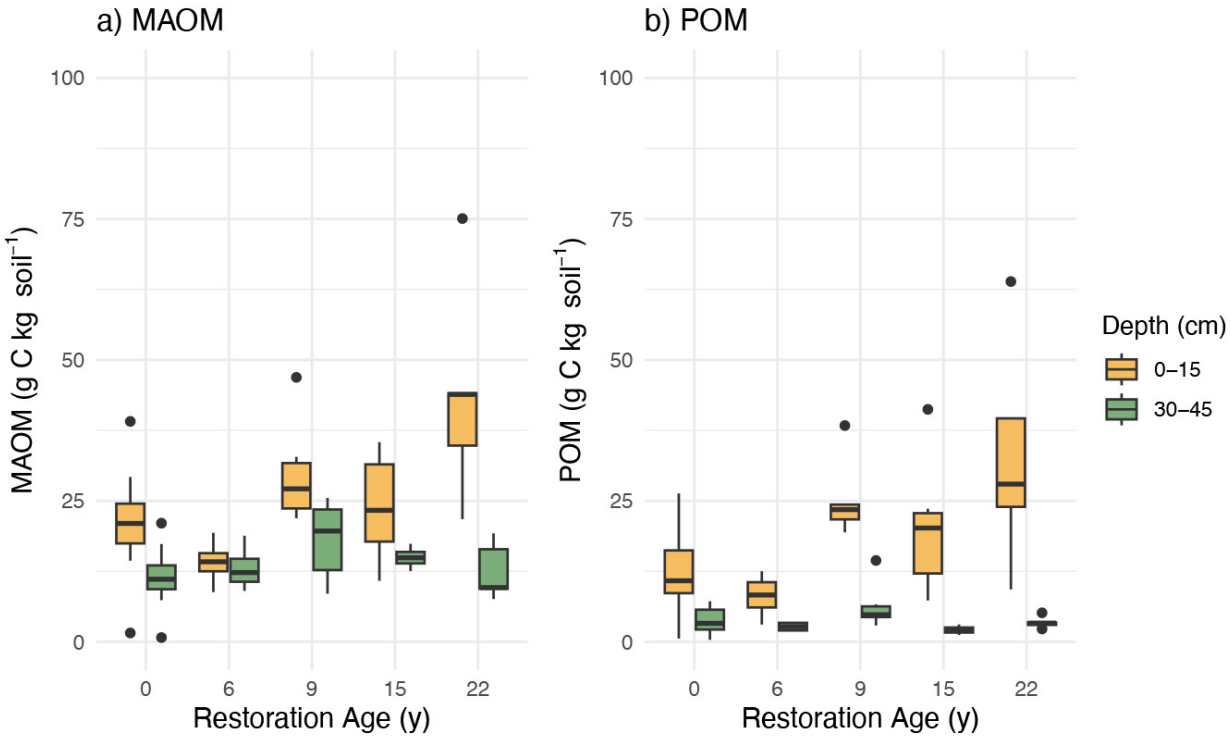
Across the chronosequence of restored meadows, the concentration of carbon in the MAOM fraction increased significantly with increases in bulk SOC from 0-15 cm ($p < 0.01$ t = 9.08, df = 21) and 30-45 cm ($p < 0.01$ t = 7.44, df = 8.39; Fig. 3.8). The fraction of bulk SOC in MAOM (fMAOM) decreased significantly with increasing bulk SOC at 0-15 cm depth ($p < 0.01$, t = 3.17, df = 20.4) but not from 30-45 cm. Correspondingly, the concentration of carbon in POM increased significantly with increases in bulk SOC at a higher rate than MAOM ($p < 0.01$, t = 16.21, df = 21; Fig. 3.8). The relationship between POM-C and bulk SOC across the chronosequence was only significant in the surface soils though.

Figure 3.8: Concentrations of carbon in the mineral associated (MAOM) and particulate organic matter (POM) fractions in relation to bulk soil carbon concentration (SOC) in meadows following hydrologic restoration.



There was more carbon in the MAOM than the POM fraction in each of the restored meadows and at both depths. The concentration of carbon in both fractions increased with time since restoration in the surface soils but not at 30-45 cm (Fig. 3.9). Using this same chronosequence, Reed et al. (2022) found that bulk SOC concentrations increased significantly in the 0-15 cm soil with time following restoration but not at the 30-45 cm depth, a result they hypothesized may have been driven by greater increases in root biomass in the shallow soil over that time period.

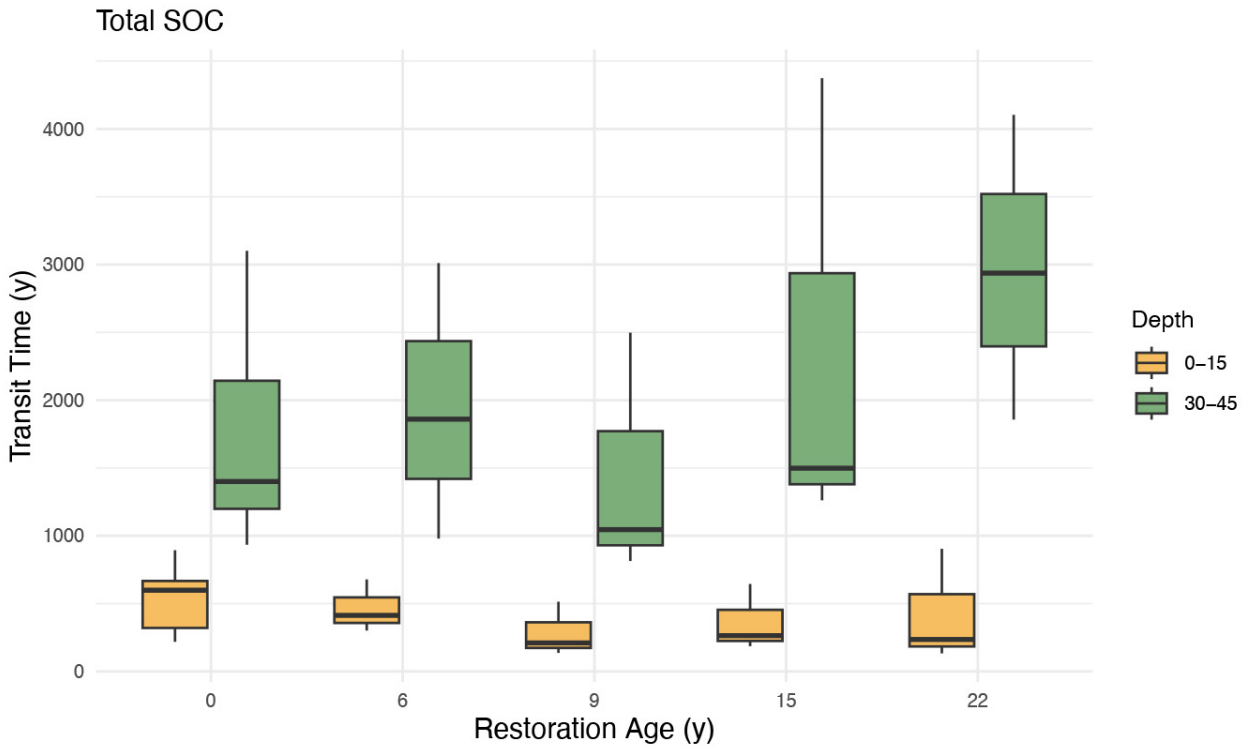
Figure 3.9: Concentrations of carbon in the mineral associated (MAOM) and particulate organic matter (POM) fractions over time across the chronosequence of restored meadows.



Error bars reflect spatial variation in measurements within and across sites (n = 3 per site).

The transit time of bulk SOC in all restored meadows was higher at 30-45 cm (mean = 2,060 years) than in the surface soils (0-15 cm: mean = 436 years; Fig. 3.10). The surface soils exhibited little variation in transit times and no patterns with age of restoration. The transit time of carbon at 30-45 cm increased with time following restoration with the oldest meadow showing a transit time of ~3,000 years. The relationship with age of restoration was not significant.

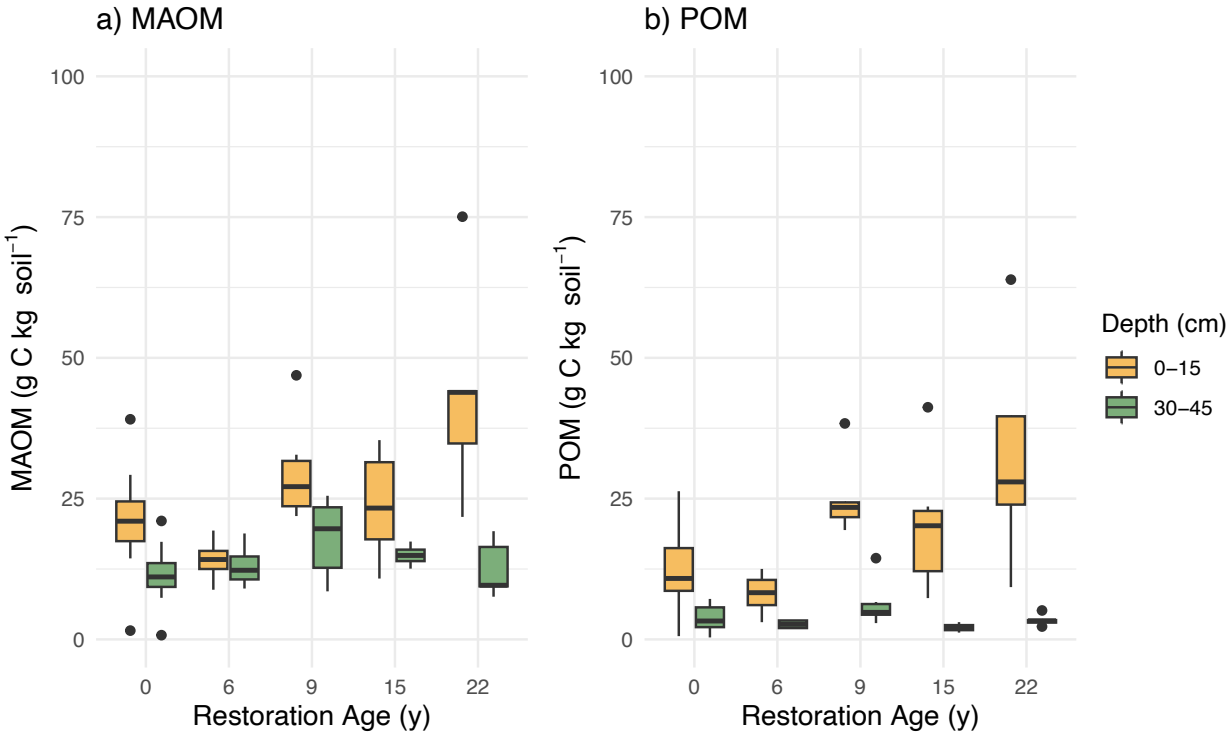
Figure 3.10: Transit time of bulk soil organic carbon in hydrologically restored meadows with different ages following restoration.



Error bars reflect spatial variation in measurements within and across sites (n = 3 per site).

The transit time of carbon in the MAOM and POM fractions followed similar patterns as the bulk soil, with longer transit times in the deeper soil. In the surface soil (0-15 cm), MAOM-C had a longer transit time (mean = 638 years) than carbon in the POM fraction (median = 160 years) but neither increased with time following restoration. At the 30-45 cm depth, the transit time of carbon in the MAOM fraction ranged from 891 years to 4,816 years (mean = 2,225 years; Fig. 3.11a). Carbon in the POM fraction generally had shorter transit times than MAOM-C at the 30-45 cm depth (mean = 1,495 years), but transit times as long as 4,023 years were measured for carbon in POM (Fig. 3.11b). The transit time of carbon in both the MAOM and POM fractions increased with time since restoration with the longest transit times measured in the oldest restored sites.

Figure 3.11: Transit time of carbon in the mineral associated (MAOM) and particulate organic matter (POM) pool in restored meadows with increasing time following restoration.



Error bars reflect spatial variation in measurements within and across sites (n = 3 per site).

3.4: Discussion

Taken together, our results indicate that soil carbon in Sierra Nevada wet meadows is abundant and persistent. Across all meadows, MAOM-C exhibited longer transit times than carbon in the POM fraction, suggesting that mineral associations stabilize organic matter. Carbon in MAOM also contains more than half of the carbon in organic matter pools—particularly at greater soil depths, with increasing time since restoration age, and in properly functioning meadows—underscoring the important role of MAOM in long-term carbon storage. Shorter transit times of carbon in the POM fraction of the surface soil may be influenced by root biomass and vegetative carbon inputs. However, at the 30-45 cm depth, the differences in transit times between POM and MAOM were less apparent, and transit times > 4,000 years were measured for carbon in both fractions.

Increasing radiocarbon age and transit time with depth were observed in all meadow conditions, except for the degraded sites at 60-75 cm. Across all sites, there was a clear shift from century-scale cycling (143-454 years) in the topsoil to millennial-

scale cycling in the 30-45 cm soil (859-2,595 years) and 60-75 cm soil (1,126-4,097 years). These findings are consistent with results from other ecosystems and reflect slower carbon cycling in subsoils as a result of strong mineral-organic associations and environmental conditions that limit microbial activity (Chabbi et al., 2009; Torn et al., 2009; Trumbore & Harden, 1997). In the surface soils, transit times in other ecosystems are generally estimated to be on the decadal scale, though transit times can exceed 100 years in wetter, anoxic zones that suppress microbial activity (Krüger et al., 2015; Leifeld et al., 2009; Trumbore & Harden, 1997).

The increase in mean transit time of carbon with depth may reflect a shift in the dominant mechanism of carbon stabilization in surface versus subsoil environments. Many studies suggest that the drivers of increased transit time in the subsoil include reduced microbial activity (due to nutrient limitation or lower oxygen availability in wet systems), physical protection via aggregation and spatial separation of decomposers and substrate, stabilization through increased mineral association, and soil environmental constraints (Fontaine et al., 2007; Salomé et al., 2010; Schrumpf et al., 2013; Taylor et al., 2002). Soils, especially those derived from basalt and andesite parent materials, typically contain a greater abundance of weathered minerals with reactive mineral surfaces at depth (e.g., allophane, imogolite, and poorly crystalline iron and aluminum oxides) that stabilize carbon through organo-mineral interactions (Lawrence et al., 2015).

3.4.1: Hypothesis 1: Properly functioning meadows have intermediate transit times that increase with soil depth, and high concentrations of carbon in both MAOM and POM

Consistent with our first hypothesis, concentrations of carbon in MAOM were higher in the properly functioning meadows relative to sites that had been altered by anthropogenic activities, including meadows in disturbed and restored conditions. Concentrations of MAOM-C in the properly functioning meadows were comparable to the highest values reported by Sokol et al. (2022) in a global synthesis of MAOM-C in grasslands and forests. The fraction of bulk SOC in MAOM (fMAOM) was not higher than other ecosystems. However, high concentration of SOC in meadows resulted in more carbon stored in the MAOM fraction than other ecosystems. High rates of belowground carbon allocation and microbial processing in properly functioning meadows may contribute to high rates of MAOM formation (Morra et al., 2023c; Reed et al., 2021; Sokol & Bradford, 2019). A higher fraction of mineral soil relative to other wetlands (Mirabito & Chambers, 2023) may also provide more reactive mineral surfaces, creating high capacity for carbon stabilization through organomineral associations (Torn et al., 1997).

Our prediction that carbon in the POM fraction would be highest in the properly functioning meadows was supported by higher concentrations at each depth in the properly functioning meadows than other conditions. In the surface soil, the

concentration of carbon in the POM fraction (76.3 ± 71.1g kg^{-1}) was similar to values reported for wet meadows in the southern Sierra Nevada (75 g kg^{-1}; Norton et al., 2011) and alpine meadows in the Rocky Mountains (Knowles et al., 2019) but lower than organic soil wetlands (e.g., up to 4778 g kg^{-1} or 99% of bulk SOC in swamps of central Florida, USA; Mirabito & Chambers, 2023). Higher concentrations of POM in wetland and high elevation sites are commonly attributed to lower rates of biological activity under temperature and oxygen limitations (Leifeld et al., 2009; Mirabito & Chambers, 2023; Stern et al., 2007; Trumbore & Harden, 1997). However, in Sierra Nevada wet meadows, high rates of microbial decomposition have been measured in meadows across a range of conditions (Reed et al., 2021), suggesting higher concentrations of POM in properly functioning meadows may be a function of high rates of vegetative carbon inputs as much as restricted rates of microbial activity. Further, the strong relationship between root biomass and POM in the properly functioning sites demonstrates the dominant role of roots in POM formation and supports the importance of belowground carbon allocation in carbon cycling in wet meadows.

We also hypothesized that properly functioning wet meadows would have century- to millennia-scale carbon transit times that increased with depth. While rates of carbon transit did increase with depth, as expected, at each depth sampled the transit time of carbon in the properly functioning meadow was lower than the other meadow conditions. The one exception to this was the 60-75 cm depth in the degraded meadows which had a mean transit time that was roughly half that of the properly functioning meadow (degraded: 1,126 years, properly functioning: 1,980 years). We had expected that greater environmental controls on carbon cycling (particularly oxygen limitation) in properly functioning meadows would result in slower transit times at deeper depths relative to degraded meadows with more aerobic soil conditions. However, we also predicted that the influence of decomposition-limiting environmental controls on carbon transit time would be balanced by high rates of vegetative carbon inputs, resulting in intermediate mean carbon ages and transit times. Longer transit times of POM-C in the properly functioning meadow relative to the degraded meadows with aerobic soil profiles at deeper depths suggest environmental controls do impact the persistence of carbon in this pool. However, lower transit times of carbon in both the MAOM and POM pools relative to the mildly degraded and restored meadows also highlight the influence of recent photosynthate on both MAOM and POM (Morra et al., 2023b).

Radiocarbon measurements in soil represent the average age of carbon within a sample. As a result, large inputs of fresh carbon can skew this average toward younger ages and potentially obscure the presence of long-lived carbon pools. The fact that the properly functioning meadow contains the largest soil carbon stock and has been shown to be actively sequestering carbon (Reed et al., 2021) suggests

that the soil carbon pool in properly functioning meadows is highly dynamic and persistence may not be accurately represented by the age of individual carbon molecules (Dynarski et al., 2020; Janzen, 2015; Jilling et al., 2025).

3.4.2: Hypothesis 2: In degraded meadows, decreased vegetative carbon inputs will lead to the loss of previously protected carbon, decreasing the amount of carbon in MAOM and increasing the transit time.

In the bulk soil at each depth, the mildly degraded and degraded meadows had more depleted radiocarbon values and longer transit times in bulk SOC than the properly functioning meadow. These lower radiocarbon values coupled with smaller soil carbon stocks suggest a higher proportion of older carbon and the loss of soil carbon as a result of historic disturbance. Lower concentrations of carbon in the POM fraction and lower proportion of bulk SOC in POM provide further support for the idea that POM may have been readily mineralized following disconnection of floodplain hydrology. Similar results have been found in the wet meadows in the southern Sierra (Norton et al., 2011), Florida Everglades (Stern et al., 2007), and European wetlands (Krüger et al., 2015), where removal of redox limiting conditions following anthropogenic disturbance resulted in the loss of unprotected, younger POM.
The surface soils of the mildly degraded and degraded meadows had older mean radiocarbon values and longer transit times of carbon in the POM fraction than the other meadows. This may be reflective of lower rates of recent vegetative carbon inputs in these lower productivity sites (Reed et al., 2021). However, the mildly degraded meadow had some of the longest transit times of carbon in the POM fraction at the 30-45 cm and 60-75 cm depths. This site has also been shown to be a net carbon sink with high rates of belowground carbon allocation, raising questions about the mechanisms controlling POM persistence in these sites and highlighting the amount of variation in vegetative and hydrologic conditions between mildly degraded and degraded meadows (Loheide et al., 2009; Reed et al., 2021)
The transit time of carbon in MAOM was highest in the mildly degraded meadow and lower in the more degraded sites. Morra et al., (2023b) found that productivity was a leading driver of MAOM formation in Sierra Nevada and Great Basin wet meadows. Specifically, newly fixed carbon was rapidly assimilated into MAOM but destabilized within one year in the low productivity sites while higher productivity sites retained newly assimilated carbon in the MAOM fraction. Lower turnover times of MAOM in the more degraded sites, coupled with smaller carbon stocks and lower concentrations of MAOM-C, suggest that destabilization of previously preserved MAOM, in addition to POM, may be occurring at these sites.

The degraded meadows were the sites that did not follow the pattern of increasing mean carbon age and transit time with depth; surprisingly, they were almost identical at the 30-45 cm and 60-75 cm depths. One possible explanation may be that aerobic

conditions throughout the soil profile following stream channel incision facilitated increased rates of bioturbation and soil mixing. Rodent bioturbation has been shown to significantly impact carbon cycling and persistence in alpine meadows within the top 30 cm of soil (Gan et al., 2025; X. Wang et al., 2025), but less is known about the impact of rodent activity on deeper soil layers. It is also possible that the removal of environmental constraints, possibly coupled with fresh vegetative carbon inputs as the water table lowered over time, stimulated the microbial mineralization of old soil carbon (Fontaine et al., 2007, 2007).

3.4.3: Hypothesis 3: Restoration of floodplain hydrology will increase allocation of carbon to MAOM and increase the transit time of soil carbon relative to degraded meadows, but the amount of carbon in the MAOM fraction will remain lower than in properly functioning meadows.

We based this hypothesis on previous studies that showed MAOM-C increased with time following restoration (Bagcilar et al. 2024) and on the premise that MAOM would be highest in properly functioning meadows with higher rates of biological activity and greater environmental controls on carbon mineralization (Kleber et al., 2015). Consistent with the findings of Bagcilar et al. (2024), the concentrations of carbon in MAOM increased with increasing bulk SOC across the chronosequence of restored meadows at both the 0-15 cm and 30-45 cm depths. These results support findings that increased rates of biological activity and root biomass following restoration result in increased MAOM-C formation (Bagcilar et al. 2024, Morra et a. 2023b, Reed et al. 2022). However, even in the oldest restored meadow, concentration of MAOM-C remained lower than the properly functioning meadow, suggesting that, even two decades after restoration, biogeochemical function in restored meadows may not have returned to conditions found in undegraded meadows with properly functioning hydrology.

In the second part of this hypothesis, we predicted that restoration would result in longer transit times of carbon in restored meadows relative to degraded sites. Again, our results proved more nuanced than our simplistic expectation. Little change was observed in the transit time of either MAOM or POM with time following restoration in the surface soils, despite increases in the concentration of carbon in each fraction at that depth. However, at 30-45 cm, the transit time of carbon in both the MAOM and POM fractions increased with time following restoration, with some of the largest increases in transit time relative to the degraded controls observed in the POM fraction.

While these results may appear contradictory at first, we propose several potential mechanisms by which increases in soil carbon may increase transit time (more time in the soil pool) of carbon in restored meadows. Restoration of floodplain

hydrology in Sierra Nevada meadows has been shown to decrease depth to groundwater (Hammersmark et al., 2008; Tague et al., 2008), increase cover of wet meadow vegetation (Hammersmark et al., 2010; Loheide & Gorelick, 2007), and increase vegetative carbon inputs (Reed et al., 2022). Oxygen limitation in deeper soils following restoration may decrease rates of heterotrophic decomposition and increase the transit time of soil carbon (Schmidt et al., 2011). The combination of increased high-quality carbon inputs and decreased redox potential may also provide a negative priming effect that preserves older soil organic carbon. Preferential substrate utilization of high-quality root carbon inputs over lower-quality or minerally protected soil organic matter has been reported in wetlands, grasslands, and other ecosystems (Krüger et al., 2025; Kuzyakov, 2002; Kuzyakov & Bol, 2006; Wang et al., 2026). The potential for this negative priming effect may be greater under limited oxygen conditions because anaerobic microbial communities preferentially utilize soluble compounds with high nominal oxidation states commonly found in root exudates (Mueller & Megonigal, 2024). Compounds with lower nominal oxidation states that require oxygen as a terminal electron are common in soil organic matter and may be preferentially preserved under these conditions. Increases in root biomass following restoration (Reed et al., 2022) that lead to higher rates of both autotrophic and heterotrophic respiration in the rhizosphere may further deplete electron acceptors, potentially expanding the redox-driven negative priming effects and contributing to soil carbon perseveration (Mueller & Megonigal, 2024).

3.4.4: Hypothesis 4: Soil mineralogy will impact MAOM formation and the transit time of carbon in meadows of all conditions

The significant relationships between Fe and Al concentrations and MAOM-C support our hypothesis that soil mineralogy contributes to MAOM formation in wet meadow soils. However, it is interesting to note that the greatest differences in Fe and Al concentration in our study were among sites, and no clear trends with depth were observed. This likely reflects differences in parent material that arise from the complex geology of the northern Sierra Nevada. Soils developed from volcanic parent material weather to release Fe- and Al-rich oxides that stabilize organic matter through processes such as metal complexation via ligand exchange and co-precipitation (Keil & Mayer, 2014). While both Fe- and Al-oxides contribute to organic carbon stabilization, in the Sierra Nevada Al-containing short range order minerals often play a dominant role in volcanic soils (Rasmussen et al., 2005). The Fe:Al molar ratios at most sites were below 1.5, with only two exceptions, suggesting that Al-rich phases such as allophane and imogolite are more prevalent at most sites. However, the site with the longest transit times, the mildly degraded meadow, also had some of the highest concentrations of Fe and the highest ratio of Fe:Al, suggesting Fe-oxide dominance at this site.

Overall, our hypothesis was only partially supported as the positive relationship between soil mineralogy and MAOM-C did not extend to carbon transit time. While strong evidence exists for the influence of soil minerals (including Fe and Al) on the mean age and transit time of soil carbon (Kleber et al., 2015; Torn et al., 1997), questions remain about the impact of soil chemistry and degree of weathering on the strength of mineral associated carbon bonds (Mikutta et al., 2006; Trumbore, 2009). Further, seasonally dynamic redox conditions can facilitate the release and re-association of carbon by Fe-oxides, potentially reducing the relationship with mean carbon age, even as the influence on soil carbon concentration remains (Dong et al., 2023; Wang et al., 2019). More work is needed across the range to determine the role of soil mineralogy on mean carbon transit time in Sierra Nevada wet meadows.

3.4.5: Potential Impacts of climate change soil carbon partitioning and persistence

The formation of MAOM is strongly influenced by plant traits that determine the quality and quantity of carbon inputs to the soil, including root biomass, rates of root exudation, and litter chemistry (Sokol et al., 2022). In wet meadows, changes in water availability are likely to have the greatest impact in both above- and belowground vegetative productivity (Albano et al., 2019; Loheide et al., 2009), with impacts on the rate of MAOM formation and persistence of carbon in the MAOM pool (Jilling et al., 2025; Morra et al., 2023b). Long-term drought conditions that may increase under climate change are likely to result in shifts from hydric and mesic vegetation to xeric species with smaller root biomass and lower rates of belowground carbon allocation (Loheide & Gorelick, 2007; Reed et al., 2021). However, if sufficient moisture levels can be maintained, longer growing seasons under increasing temperatures could also lead to increased rates of both MAOM and POM formation (Niu et al., 2025).

4: Conclusion

Wet meadows in the Sierra Nevada contribute disproportionately to hydrologic function, biogeochemical cycling, wildlife and biodiversity, and carbon storage and persistence in the region. However, widespread degradation of wet meadows following Euro-American settlement has led to loss of ecosystem function and resilience. Climate change is likely to further the loss of ecosystem function—particularly in meadows that have been degraded or are at risk of degradation—though differences in hydrogeomorphology, geology, and climate across the region may impact the magnitude of the response to climate change. Mid-elevation meadows that are heavily reliant on snowpack may be the most sensitive to warming and precipitation changes; more studies are needed to determine the impact of changes in streamflow and groundwater on long-term meadow resilience. Efforts to better understand the drivers of ecological resilience and response to land use may help prioritize conservation and restoration efforts to maximize ecosystem benefit under changing climate conditions.

This study also demonstrates that meadow conservation and restoration may be an effective nature-based solution in the Sierra Nevada. Properly functioning meadows sequester and store large amounts of soil carbon–both as carbon associated with soil minerals and unassociated particulate organic matter—that can persist in the ecosystem for thousands of years. Degradation of hydrologic function results in the loss of soil carbon, but losses are greater from the particulate organic matter pool; mineral association confers protection to soil carbon and may buffer against the impacts of degradation and climate change. Further, our results support previous findings that large soil carbon stocks in meadows are maintained by high rates of vegetative carbon inputs and may be less sensitive to changes in environmental conditions than other wetlands and peatlands. Restoration of floodplain hydrology may further increase the durability of meadow carbon to climate change by increasing soil carbon concentrations and the transit time of carbon in the soil.

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6: Appendix A: Glossary of Terms

Aerenchymous tissue – plant tissues that have aerenchyma, or spongy tissue with air spaces that facilitate gas exchange between leaves, stems, and roots of plants.

Aerenchymous tissues are common in aquatic and wetland plants that grow soils with limited oxygen.

Alternative stable state – the idea that ecosystems can exist in multiple, distinct configurations maintained by positive feedback mechanisms and separated by thresholds or abrupt transitions between states. Stabilizing feedbacks create resistance to state shifts unless disturbances or external activities (e.g., restoration) are large enough. Ecosystems that have transitioned to alternative stable states may also have reduced or altered ecosystem function.

Basal flow – groundwater discharge that occurs from the base of an aquifer or geologic formation.

Beaver dam analogs (BDAs) – human-made structures constructed with natural materials (e.g., logs and willow branches) that are designed to mimic the function of natural beaver dams.

Channel fill – a meadow restoration technique that uses fill material, sometimes imported from offsite, to reconstruct portions of an incised stream channel.

Hydraulic conductivity – the rate of water movement through soils and rocks. Hydraulic conductivity depends on intrinsic properties of the material (e.g., pore size and texture) and degree of saturation.

Hyporheic exchange – the process of water and solutes moving between the surface of a river and the subsurface sediment, or hyporheic zone.

Lateral flow – the horizontal subsurface movement of water driven by hydraulic gradients from areas of higher hydraulic head to lower head.

Ligand exchange – a mechanism for the formation of mineral associated organic matter where hydroxyl groups in organic matter replace hydroxyl groups on mineral surfaces, forming strong bonds through inner-sphere complexation.

Mineral-associated organic matter (MAOM) – organic matter, primarily derived from microbial processing, that is chemically and physically stabilized on the surfaces of micron-scale soil particles like silts and clays.

Organomineral interactions – associations between organic matter and mineral soil particles that form through physical, chemical, and biological processes.

Particulate organic matter (POM) – partially decomposed plant materials that are assumed to be unassociated with mineral surfaces. Persistence of POM in soil depends on environmental conditions that limit microbial activity, biochemical recalcitrance, and/or physical protection in aggregates.

Pond-and-plug – a meadow restoration technique that involves intermittently plugging an incised stream channel with material excavated from borrow ponds within the meadow.

Reach (stream) – a distinct segment of a stream or river used for study, often with relatively uniform characteristics.

Restored reach – a segment of a stream or river that has experienced geomorphic alteration designed to restore ecological processes.

Subwatersheds – a smaller geographic and hydrological area within a larger watershed that drains to a specific point.

Transit time (carbon) – the average amount of time a carbon atom stays in the soil.