RESEARCH ARTICLE

Habitat Conditions of Montane Meadows associated with Restored and Unrestored Stream Channels of California

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ABSTRACT

Mountain meadow habitats are valued for their ecological importance. They attenuate floods, improve water quality, and support high biodiversity. Many meadow habitats in the western US are degraded, and efforts are increasing to restore these montane meadow ecosystems. Rewatering projects such as pond-and-plug quickly raise the water table by blocking the existing incised stream channel and can result in the rapid recovery of wet meadow habitats. Based on the existing literature, however, it is difficult to determine realistic expectations for outcomes of restoration projects across a range of hydrogeologic conditions. We compared wetland, vegetation, soil carbon, and channel condition variables between ten randomly selected restored and ten paired unrestored montane meadows in California to provide a comparison of habitat conditions. We found that unrestored meadows had a higher proportion of wetland habitat, fewer indicators of channel instability, and greater topsoil carbon stores compared to restored meadows. Restored meadows had more herbaceous biomass within their wetland habitats, but also had more cattle exclosures. The restoration category of the meadow remained important when watershed variables were included in models. While restored meadows were highly degraded prior to project implementation, our results suggest that, in general, conditions do not improve beyond the average conditions of nearby unrestored meadows. Realistic expectations of outcomes and consequences are necessary for managers to make appropriate decisions about restoration options and whether or not to implement rewatering projects that often greatly alter the meadow landscape.

Keywords: meadow restoration, Pond-and-plug, Sierra Nevada, soil carbon, wetland determination

Montane meadows are restricted to low gradient valleys of watersheds with shallow or impermeable soils where fine sediment accumulates and water collects (Wood 1975, Weixelman et al. 2011). Shallow water tables and high densities of soil carbon and nitrogen allow for lush herbaceous vegetation growth that supports high biodiversity (Allen-Diaz 1991). Functioning stream-associated meadows also stabilize channel banks, dissipate energy from high flows, filter sediment and enhance groundwater recharge (Peterson et al. 2001, Viers et al. 2013). These ecological functions are reduced, however, when stream channels through montane meadows incise and the meadows become less connected to the hydrologic system.

Channel incision in meadows commonly results from disturbances such as longterm overgrazing by livestock, timber harvesting in the watershed, or channel modifications (Kattleman 1996, Blank et al. 2006, NFWF 2010). Down-cutting of the channel lowers the water table, reduces sediment delivery to the meadow, and reduces the hydrological connection with the meadow floodplain, resulting in more xeric plant communities and less water storage (Loheide and Gorelick 2007). Deteriorating meadows release greenhouse gases into the atmosphere (Kayranli et al. 2010, Norton et al. 2011) instead of acting as carbon sinks (Badiou et al. 2011). Attempts to quantify natural wetland conditions across landscapes suggest that a large proportion of the earth's wet meadows are disappearing or are in a degraded condition (e.g., Menke et al. 1996, Pan and Wang 2009, Nie and Li 2011).

Realization of the importance of montane meadows and their level of degradation has prompted increased efforts to restore, rehabilitate, or enhance (herein "restore") these habitats, especially in regions where water needs are great such as in the western United States. For example, the National Fish and Wildlife Foundation (NFWF) has a goal of restoring about 8,090 hectares per year of the approximately 77,660 hectares of meadow habitat in the Sierra Nevada of California (NFWF 2010, Viers et al. 2013). The primary methods now being promoted to repair highly incised stream-associated mountain meadow systems

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include "rewatering" techniques such as pond-and-plug. These projects are designed to raise water tables in meadows throughout the growing season, thereby maintaining wet meadow vegetation and increasing water storage (Loheide et al. 2009). While some rewatering projects involve minimal physical modifications within the channel, most require major land disturbance and result in novel systems. For example, the pond-and-plug technique involves excavating alluvial material from the incised channel and adjacent floodplain, and using that material to plug the incised channel. This process, repeated down the length of the project area, results in a series of ponds and plugs that can cover several acres of previous channel and meadow habitat. In the ideally redesigned channel, stream flow and sediment are redirected away from the ponds to smaller channels on the meadow surface, restoring natural meadow function. The newly occupied channels may have existed previously as alternate or abandoned channels, and the upstream and downstream transitions from untreated channels are typically secured against erosion with base-level control structures.

Pond-and-plug restoration can result in meadow habitats with greater vegetative productivity, raised water tables, increased ability to sequester carbon, and greater habitat stability (Benoit and Wilcox 1997, NFWF 2010, Loheide and Gorelick 2007, Hammersmark et al. 2008). For example, Hammersmark et al. (2008) used before and after hydrological assessments of a pond-and-plug restoration project in northeastern California to show that the restoration raised groundwater levels, increased the duration of floodplain inundation and decreased the magnitude of flood peaks. Secondary effects can include less sediment transport downstream of the project, increased biodiversity at the site, retention of pollutants, and steady release of water downstream (Peterson et al. 2001, NFWF 2010).

To date, these studies have focused on a few well-funded projects. For example, three of four published studies assessing hydrologic responses to pond-and-plug meadow restoration were conducted on Last Chance Creek in the Feather River watershed (Liang et al. 2007, Loheide and Gorelick 2007, Cornwell and Brown 2008). From this information, it is difficult to determine realistic expectations for outcomes of current or future projects across a range of geologic and hydrologic conditions (Bernhardt et al. 2005, NFWF 2010). Because most restoration projects are minimally monitored, the existing literature may portray a bias toward well-funded projects that give an overly optimistic impression of meadow restoration. In addition, post-project monitoring tends to be short-term, so while the project may show rapid success once hydrological connectivity is restored, how the restored landscape functions within the natural variability of the system over the long term is not well understood. Given the high relative cost of rewatering projects compared to other wetland restoration projects (Bernhardt et al. 2005) and the potentially large physical footprint on the landscape, we believe it is important to gain a better understanding of the range of outcomes of these techniques.

The objective of this study was to provide a comparison of habitat conditions of restored meadows that used rewatering techniques relative to each other and similar but unrestored meadows. We focused on easily measurable habitat and soil carbon variables that allowed us to sample 20 meadows in a summer. Our goals were to determine if restored meadows supported a higher proportion of wetland habitats, supported greater vegetative cover and productivity, sequestered more carbon, and had more stable stream channels compared to paired unrestored meadows. We chose these specific response variables because rewatering projects have been shown to raise meadow water tables (Hammersmark et al. 2008) and thereby increase wetland area and vegetative cover and productivity (Loheide et al. 2009). In addition, functioning wet meadows in the Sierra Nevada tend to have at least twice the soil carbon levels as hydrologically disconnected meadows (Norton et al. 2011).

Prior to restoration, the randomly selected restored meadows were in a highly degraded condition in which the channels were deeply incised and water tables were below historical conditions. Seven of ten had post-project monitoring reports, and six of them reported overall success citing raised water table elevation, increased wet meadow vegetation after treatment, increased faunal activity by species that prefer wetland flora, or elevated water tables at downstream treatment sites. One project found minimal change in groundwater levels and little vegetative response up to six years after treatment. While most of these restoration projects were deemed successful compared to pre-project conditions, we specifically wanted to know how they compared to nearby unrestored but otherwise comparable meadows. Based on the positive findings of published studies on rewatering projects and because the majority of montane meadows in our California study area are in a degraded condition (Menke et al. 1996, Norton et al. 2011), we predicted that the ten restored meadows would score higher, or at least similarly, on our measured metrics than their unrestored meadow counterparts.

Methods

Experimental Design

In 2010 we reviewed and compiled available information about completed montane meadow restoration projects in California. We developed a database of over 120 projects, which we subset by restoration technique, land ownership, and project age. Of the 37 rewatering projects on United States Forest Service (USFS) land that were completed at least three years prior to our 2011 field study, we randomly selected ten (seven pond-and-plug and three channel

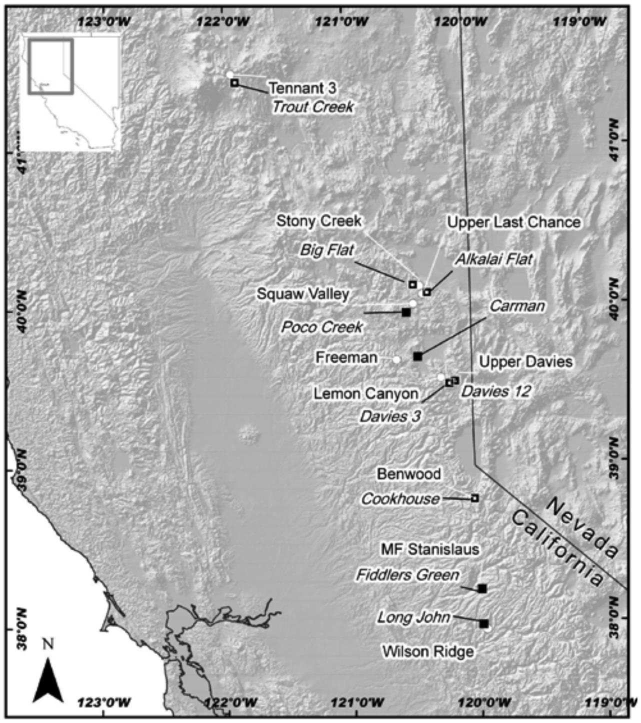

Figure 1. Locations of sampled montane meadows, California, USA. Black squares represent restored meadows and white circles representing unrestored meadow pairs. Black squares with white dot represent meadows with pond-and-plug restoration.

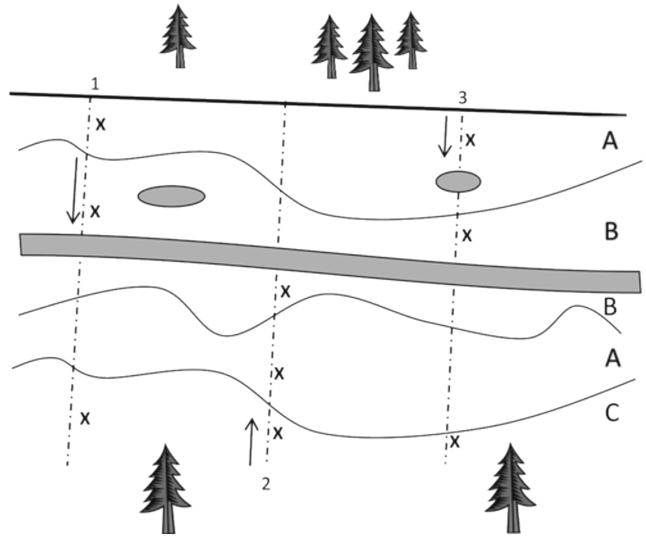

Figure 2. General orientation of baseline and transects (dotted lines) in a hypothetical project area. Arrows represent the direction of survey along a transect, alpha characters represent different plant communities, X represent plots, and shaded polygons represent water features including ponds and the stream channel.

restructuring) and paired them with nearby untreated reference meadows (Figure 1). Channel restructuring projects focused on techniques such as creek realignment and placement of base-level control structures, including use of rip-rap in older projects. We used the USFS, Region 5 Sierra Nevada 2011 meadow layer to identify a paired meadow within a 5 km radius of each of the treated meadows and attempted to match meadow size, slope, elevation, and watershed area (ESRI ArcMap 10.0; Table 1). While habitat condition was not considered when selecting pairs, we chose sites also on USFS lands with similar land management histories as the restored sites. These "reference" meadows, therefore, were not chosen to represent target conditions, but to represent realistic conditions given existing land use disturbances. If two or more meadows were identified, one was randomly selected to be the reference meadow. If none were identified, we expanded the radius to 10 km and conducted the exercise again. One sampled pair (UD) was identified in the field after three GIS-identified options proved not to be suitable pairs.

Once the 20 study meadows were selected, we systematically delineated meadow habitat types as wetland or upland, measured herbaceous cover and biomass, and collected soil carbon samples at sample plots along transects in the meadows. We also noted presence or absence of cattle activity (animals or scat) within the meadow. We established a baseline along the length of each meadow parallel to the channel and two to four transects across each meadow perpendicular to the baseline (Figure 2). Meadows with baseline lengths over 500 m were split into four transects; those between 200–500 m were split into three transects, and those less than 200 m were divided into two transects. Specific transect locations were determined by dividing the baseline into equal sections by the number of transects, then using a random number to locate the transect intercept.

To locate plots, surveyors walked along the transect lines and measured the length of the different plant communities, which were determined by changes in at least one of the three most dominant plant species. A plot was randomly placed along each transect within each plant community encountered. The number of plots for each meadow was, thus, determined by the number of transects and number of new plant communities crossed by the transect lines. If a plant community was repeated along a transect, we measured the community length and assigned it the same data as the first plot (Figure 2). Area for each plant community was calculated as the product of community lengths and distances between transects for that community, and meadow area was calculated by summing the area of all communities in the meadow.

Wetland Determination

For each plant community encountered, we assessed vegetation, soils, and hydrologic characteristics to determine whether or not each community was considered a wetland following the U.S. Army Corps of Engineers (ACOE) Wetland Delineation Manual (ACOE 1987, 2010).

Table 1. Meadow characterization variables and field-measured response variables (bold titles) with treatment group summaries (mean and SE in parentheses) at the bottom. No meadow characterization variables were significantly different ($p < 0.05$) between groups (ANOVA and paired T-tests). Meadows are ordered by meadow pairs from north to south with untreated pair listed first and treated pair italicized.

Meadow[1]	Meadow area (ha)	Elevation (m)	Watershed area (ha)	Relief (m)	Meadow slope	Percent wetland	Channel[2]	Biomass	Cover	Soil C 0–10 cm	Soil C 10–20 cm
T3	3.7	1650	7781	814	1.6	51.4	0.5	6.3	3.6	8.6	5.0
TC	3.5	1474	5596	126	0.8	0	4	4.2	5.2	5.3	3.6
SC	4.9	1860	4342	279	1.1	30	0.5	6.6	8.4	9.4	7.6
BF	11.9	1740	4342	298	1.7	53.4	3.2	12	8.2	7.7	7.4
LC	25.0	1724	2700	633	1.2	31.5	4	13.9	11.1	10.7	4.3
AF	11.9	1745	2725	610	0.4	31.5	4.1	14.6	9.3	6.7	3.8
SV	19.0	1695	2837	411	0.2	100	0	16.8	10.6	12.9	5.9
PC	15.0	1670	2687	268	0.9	0	6	7.5	6.9	5.6	3.1
FM	11.0	2080	4479	169	0.3	100	0	11.4	9.4	13.4	3.9
CC	35.0	1463	3923	658	0.9	63	2.1	11.2	6.8	5.4	5.8
LM	1.0	1916	2365	747	2.0	66.2	4	10.4	8	6.1	11.9
D3	1.6	1965	1721	608	3.8	80.8	0.5	16.9	9.9	4.5	4.1
UD	2.0	1870	3394	804	6.7	68.1	0	3.8	7.5	13.2	5.7
D12	20.0	1858	3391	509	1.6	71.7	2.8	7.3	9.2	10.4	5.2
BM	2.8	2274	4103	445	1.6	100	0.4	12.8	6.2	11.1	8.0
CM	7.3	2147	1186	812	0.7	89	0.3	11.6	8.1	9	5.8
MF	1.9	1912	7565	161	3.8	100	4	9.1	10	7.4	4.5
FG	1.5	2009	4391	244	2.9	11.1	2.5	4	4.8	7.1	7.9
WR	1.9	1070	2167	69	8.9	100	0	4.1	3.8	4.6	4.4
LJ	1.9	1750	2546	170	8.2	100	0.6	15.1	11.7	8.8	9.6
Untreated	**7.3 (2.6)**	**1805 (100)**	**4173 (636)**	**453 (89)**	**2.7 (0.9)**	**74.7 (9)**	**1.4 (0.6)**	**9.5 (1.4)**	**7.9 (0.8)**	**9.7 (0.6)**	**6.1 (0.8)**
Treated	***10.9 (3.3)***	***1782 (69)***	***3250 (423)***	***430 (75)***	***2.2 (0.7)***	***50.1 (12)***	***2.6 (0.7)***	***10.4 (1.4)***	***8.0 (0.7)***	***7.1 (0.6)***	***5.6 (0.7)***

[1]T3 = Tennant 3, TC = Trout Creek, SC = Stoney Creek, BF = Big Flat, LC = Upper Last Chance, AF = Alkalai Flat, SV = Squaw Valley, PC = Poco Creek, FM = Freeman, CC = Carman Creek-Kuthson, LM = Lemon Canyon, D3 = Davies 3, UD = Upper Davies, D12 = Davies 12, BM = Benwood, CM = Cookhouse, MF = Middle Fork Stanislaus, FG = Fiddler's Green, WR = Wilson Ridge, LJ = Long John's.

[2]High scores represent worse condition (signs of channel instability or incision).

If wetland vegetation, hydric soils, and wetland hydrology were found, then a community was considered to be a wetland. If one or more conditions were missing then it was considered to be an upland community. To make the vegetation determination, we identified all plant species with > 10% of the cover in the community and assigned each plant its wetland indicator status (USFWS 1988, 1993). If more than 50% of the plants in a community were listed as facultative, facultative wetland, or obligate wetland, then the community was considered to support wetland vegetation.

The presence of wetland soils was determined by taking a 20-cm deep soil sample and evaluating the soil for hydric soil indicators (USDA Natural Resources Conservation Service (NRCS 2010). If one or more hydric indicators were present, the community was considered to support hydric soils. Hydric soils were most commonly identified using the F6 Redox Dark Surface and occasionally using the F1 Loamy Mucky Mineral indicators (NRCS 2010). We considered the community to have wetland hydrology if at least one primary or two secondary hydrology indicators were present (ACOE 1987, 2010). Common primary wetland hydrology indicators were surface drainage patterns, water marks, and saturation in the upper 12 inches of soil; common secondary indicators were presence of oxidized root channels, and water-stained leaves. Once all identified communities received a wetland determination, we used community length and width measurements to calculate the estimated percent of the total meadow area consisting of wetland and upland communities. All open water features including ponds and main channels were excluded from sampling and area calculations.

Cover

At each plot location, we estimated vegetation cover using a modified laser point frame (VanAmburg et al. 2005). We connected a laser level (Strait-Line Laser Level 120) to a tripod set at approximately 1 m high, and placed it 1 m downstream of the plot-transect intercept. We placed a 36-cm diameter hoop with ten evenly spaced marks around the tripod legs parallel to the ground and sighted the laser point directly outside each mark. Data were collected by recording the number of laser contacts as the laser beam intersected the vegetation strata down to the soil surface. The laser was then rotated to the next mark until all 10 sample points were measured. To calculate cover values for each sample, we considered the first contact with vegetation to be worth 1 and additional hits further down the strata to be worth 0.1. We did not count more than one contact with the same individual stem. Therefore, if the laser intercepted four different plants before reaching the ground, that sample would receive a numeric cover value of 1.3 and, if it did not contact any live plants, it would receive a zero. The ten sample values were averaged to determine a single vegetation cover value for each plot.

Biomass

At each plot location, a 20-cm diameter hoop was placed on the ground approximately 1 m upstream of the plot-transect intercept. All herbaceous vegetation was clipped to 1 cm above the ground surface and sealed in a labeled plastic bag. The biomass samples were later dried at 60°C for approximately 24 hours and then weighed using a precision balance (Denver Instruments® SI-4001, d = 0.1 g).

Soil Carbon

After removing the biomass sample, the area where the biomass sample was taken was cleared to mineral soil and a 5-cm diameter, 20-cm deep soil core was taken following the USFS Forest Inventory Act Forest Health Monitoring protocol for soils (O'Neill et al. 2005). The core sampler contained two sections, which allowed easy splitting of the core into 0–10 cm and 10–20 cm depth sections of known volume (81 cm^3). In addition to the single cores taken at each plot, we took a second paired sample (0–10, 10–20, 25–35, and 35–45 cm depths) from the plot closest to the active stream channel on the middle transect. The paired cores were sent to the USFS Rocky Mountain Research Station (RMRS) laboratory and analyzed using a multi-carbon analyzer (LECO model RC-412) to determine total organic and inorganic carbon (O'Neill et al. 2005).

The remaining samples were processed at the Humboldt State University's Natural Resources Soils Laboratory. Percent soil organic matter (% SOM) was determined using the loss on ignition (LOI) method as outlined in the USDA Natural Resource Conservation Service, Soil Survey Laboratory Methods Manual (NRCS 2004). To translate % SOM to percent organic carbon (POC), we assumed that organic matter contains 58% organic carbon (Bisutti et al. 2004, NRCS 2011). To assess the accuracy of the LOI method, we compared our results with those obtained by the carbon analyzer at the RMRS for the paired soil cores. A regression of the carbon estimates from the 0–10 cm and 10–20 cm soil depths determined that the LOI estimates were correlated with the carbon analyzer estimates with an R^2 of 0.73 for the 0–10 cm depth and 0.85 for the 10–20 depth.

Channel Condition

The rapid assessment approach of this project precluded us from calculating quantitative incision ratios and slope stability factors typical of detailed survey techniques to compute channel stability. Instead, we noted features that indicated channel instability while conducting the transect survey and walking primary channels through each meadow. These indicators included any features of potential erosional concern such as headcuts and knickpoints, undercut and failing banks, and gullied or incised channels. Using the number of unstable features counted per 1 km of meadow baseline length, we scored each meadow from 0 as most stable to 5 as most unstable. Because it is difficult to quantify severity of erosional features in such a short site visit, we consider this ranking method to provide only a qualitative assessment of channel stability.

Environmental Variables

Several landscape-scale attributes were characterized using ArcMap (ESRI, ArcMap ver. 10.1) with USGS 10-m digital elevation models as base maps. Watershed area upstream of the meadow was determined by digitizing the watershed perimeter above the meadow and calculating the area of the polygon. Meadow slope was determined by calculating the average of three longitudinal profile lines parallel to stream flow using the interpolate line tool (ArcMap 3D Analyst). Meadow elevation was obtained at the downstream edge of each meadow. Watershed relief was determined by subtracting the meadow elevation from that of the highest point in the watershed. Mean annual precipitation for each meadow was calculated from daily precipitation values for years 1999–2011 obtained from NASA's DAYMET website (http://daymet.ornl.gov/).

Statistical Analysis

We first compared channel condition and proportion of meadow habitat delineated as wetland between the restored and paired unrestored meadow groups ([Treatment]) with paired two-tailed t-tests. Then, because we expected that wetland determination (wetland or upland) likely affects the other response variables, we summarized plot-level data (herbaceous biomass [Biomass], vegetation cover [Cover], and POC in the top 10 cm [Soil Carbon 0_10cm] and 10–20 cm [Soil Carbon 10_20cm]) for each meadow by whether it occurred in a wetland or upland habitat. Values for each plot were weighted by the proportion of area that they represented within the wetland or upland habitat types of each meadow. We then included wetland determination ([Wetland]) with Treatment in blocked analyses of variances (ANOVAs) with meadow pairs as blocks. To determine if response variables were sensitive to timing of restoration, we ran linear regressions on each response variable with the number of years since project completion as the predictor for the ten restored meadows.

In addition to whether or not a meadow was restored, several landscape-scale variables are known to influence meadow characteristics (Germanoski and Miller 2004, Trowbridge et al. 2011). To assess the relative influence of Treatment, watershed factors (Watershed Area, Relief, and Precipitation) and meadow-level factors (Meadow Area, Meadow Slope, and Elevation) that may influence the response variables, we fit generalized linear models (GLMs) to the data and used multi-model inference based on information-theoretic approaches (Burnham and Anderson 2002). We developed a global watershed-level model and a global meadow-level model (including Treatment) then conducted a variable reduction exercise using Akaike's Information Criterion with a second-order bias correction (AICc) to remove unimportant predictor variables from each global model (Anderson 2008). We dropped each variable from the model, and if AICc scores were improved (reduced), we eliminated the variable from the model. We then combined the reduced models and conducted another variable reduction exercise to obtain a "best" model or models (if within two AICc units of the best model) for each response variable. We ran a null model (intercept only) with each response variable as a reference for assessing model importance (Anderson 2008). AICc-based model probabilities, or "Akaike weights", were calculated for every model in the final candidate set (Anderson 2008). Model-averaged parameter estimates were obtained from the weighted average of parameter estimates from each of the candidate models, with a value of zero assigned for models in which the parameter being estimated does not appear (Anderson 2008, Lukacs et al. 2010). Analyses were conducted in R 3.0.1. Functions available in MuMIn library (Version 0.12.2, available via http://r-forge.r-project.org/projects/mumin/) were used to determine parameter importance estimates. All continuous predictors were z-transformed to facilitate comparisons between effect sizes.

Table 2. Model-averaged parameter estimates and approximate 95% confidence intervals from candidate models assessing relationships of meadow-averaged response variables to environmental predictors and treatment (restored or unrestored). Confidence intervals that do not span zero tend to be significant and are highlighted with an asterisk. Only parameters in the top models (within 2 AICc units of the best model) are included. "Null" means that the null model without predictors yielded the minimum AICc score.

Response	Parameter	Estimate	95% CIs	
			Lower	Upper
Percent wetland	Slope	13.44	–0.17	27.05
	Elevation*	14.93	0.87	28.99
Channel condition	Treatment*	0.80	0.08	1.51
	Precipitation	–0.25	–0.63	–0.13
Biomass	Watershed area	–1.71	–3.57	0.15
Cover	Null	n/a	n/a	n/a
Soil C 0–10 cm	Treatment*	–2.60	–4.87	–0.33
	Elevation	0.98	–0.25	2.21
	Watershed area	0.88	–0.35	2.12
Soil C 10–20 cm	Null	n/a	n/a	n/a

Results

Measured response variables for each meadow are summarized in Table 1. Of the meadow-level response variables, Channel Condition was affected by Treatment in paired T-tests ($T = 2.2$, $p = 0.04$). Untreated meadows had fewer indicators of channel degradation than restored meadows (Figure 3). For example, we encountered a mean of 0.5

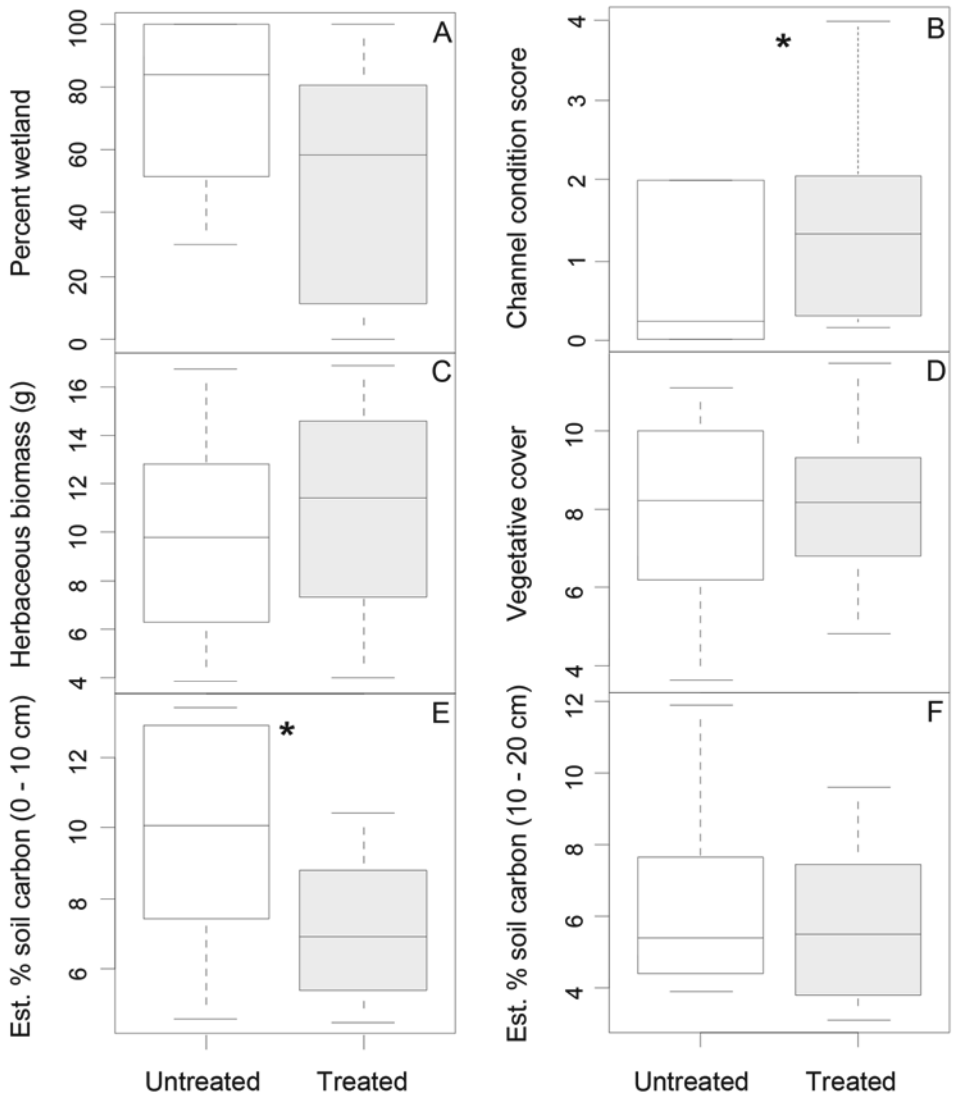

Figure 3. Box plots showing the differences between treated and untreated meadows in (A) the percent of the meadow considered wetland, (B) indicators of degradation such as knickpoints and headcuts, (C) herbaceous biomass, (D) vegetative cover, (E) estimated percent soil carbon in the top 10 cm of soil, and (F) estimated percent soil carbon at 10–20 cm deep. The solid line within each box represents the median, the bottom and top borders indicate the 25th and 75th percentiles, the whiskers below and above each box mark the 10th and 90th percentiles, and dots indicate points outside the 10th and 90th percentiles. An asterisk indicates statistically significant differences at the $p < 0.05$ level.

(SE = 0.2, range = 0–1.8) headcuts per 1,000 m of stream channel at the unrestored meadows compared to a mean of 2.2 (range = 0–4.0) at the restored meadows. Channel Condition remained most correlated with Treatment in the modeling exercise that included environmental parameters (Table 2). Percent wetland showed a trend ($T = 1.9$, $p = 0.08$) in the paired T-tests with untreated meadows having proportionately more wetland habitat (mean = 75%, SE = 9, range = 30–100%) than treated meadows (mean = 50%, SE = 12, range = 0–100%). When environmental parameters were assessed, Wetland was correlated with Meadow Slope and Elevation (Table 2) with steeper and higher elevation meadows tending to support a higher percentage of wetland habitats.

One or both of Treatment and Wetland were important for determining Biomass, Cover, and Soil Carbon 0–10 cm (Table 3, Figure 3). Biomass was greater in wetland habitats (mean = 12.3, SE = 1.2, range = 4.8–23.6) compared to upland habitats (mean = 8.2, SE = 1.2, range = 5.8–11.7) and we found a strong interaction effect of Treatment and Wetland with less biomass in restored upland habitats and more in restored wetland habitats compared to unrestored meadows (Table 3). Biomass was slightly greater in restored meadows than unrestored (Table 3). Because we noted cattle exclosures at 7 of 10 restored meadows compared to 1 of 10 of the unrestored meadows and cattle have been shown to reduce vegetative biomass in montane meadow systems (Roath and

Table 3. Analysis of variance for the response variables biomass (g), vegetative cover, and carbon within the top 10 cm of soil and 10–20 cm of soil. Asterisk denotes significance at α ≤ 0.05 and the direction of effect is provided for Treatment (R = restored, U = unrestored) and Wetland determination (W = wetland).

Source	df	SS[a]	MSE[b]	*F*	*P*
Biomass					
Block (=Pair)	9	118.52	13.17	0.75	0.66
Treatment (T)	1	56.50	56.50	3.22	0.09
Wetland[c] (W)	1	175.45	175.45	10.02	0.005* (W)
T X W	1	157.29	157.29	8.98	0.007*
Residuals	19	332.83	17.52	—	—
Cover					
Block (=Pair)	9	80.73	8.97	1.55	0.20
Treatment (T)	1	0.14	0.14	0.02	0.88
Wetland (W)	1	59.59	59.59	10.33	0.005*(W)
T X W	1	2.31	2.31	0.40	0.53
Residuals	19	109.63	5.77	—	—
Soil Carbon 0–10 cm					
Block (=Pair)	9	63.84	7.09	1.13	0.39
Treatment (T)	1	73.68	73.68	11.76	0.003*(U)
Wetland (W)	1	31.90	31.90	5.09	0.04*(W)
T X W	1	4.49	4.49	0.72	0.41
Residuals	19	119.00	6.26	—	—
Soil Carbon 10–20 cm					
Block (=Pair)	9	40.62	4.51	1.04	0.45
Treatment (T)	1	8.22	8.22	1.89	0.18
Wetland (W)	1	14.59	14.59	3.36	0.08
T X W	1	0.30	0.30	0.07	0.79
Residuals	19	82.54	4.34	—	—

[a]SS = sum of squares
[b]MSE = mean square error
[c]Wetland represents the wetland determination as wetland or upland as defined by the Wetland Delineation Manual (ACOE, 1987, 2010).

Krueger 1982, Flenniken et al. 2001), we conducted a post hoc GLM at the meadow scale that included a binomial variable for meadows grazed by cattle or ungrazed in addition to Treatment. The cattle predictor removed the Treatment effect ($F = 1.32$, $p = 0.32$), but was also not significant ($F = 1.96$, $p = 0.14$). Watershed area was the only important landscape-level factor for predicting Biomass with meadows in larger watersheds having greater biomass (Table 2). Cover was greater in wetland habitats (mean = 9.18, SE = 0.47, range = 5.8–11.7) compared to upland habitats (mean = 6.50, SE = 0.84, range = 0.3–10.8) but was not affected by treatment (Table 3, Figure 3) and none of the tested environmental variables were important for predicting Cover.

There was higher Soil Carbon in the top 10 cm of wetland and upland soil in untreated compared to treated meadows (Table 3), but there was no significant difference for soil 10–20 cm deep (Table 3). Treatment remained the only important predictor for Soil Carbon 0_10cm when combined with environmental predictors. Consistent with the ANOVA results, models assessing relationships with Soil Carbon 10_20 cm were poor. When the response variables from the ten restored meadows were assessed with the number of years since restoration, they showed consistent but non-significant inverse relationships with project age (Figure 4).

Discussion

We applied a natural field experiment to compare ecological indicators of meadow health in restored and unrestored montane meadows in California. Except for finding greater vegetative biomass in restored meadows, we did not find more wetland habitat, herbaceous cover, or soil carbon in restored compared to unrestored meadows. Our study design does not permit a before-and-after comparison of the specific meadow restoration projects, so we cannot quantify changes in meadow health due to project implementation; however, we provide context for completed restoration projects in relation to existing meadow conditions. While the restored meadows were all highly degraded prior to project implementation, our results suggest that, on average, conditions do not improve beyond a selection of nearby unrestored sites with similar physical characteristics and management histories but varying in degrees of degradation. These results are similar to the findings of recent summaries and meta-analyses of restoration projects world-wide (Rey Benayas et al. 2009, Bernhardt and

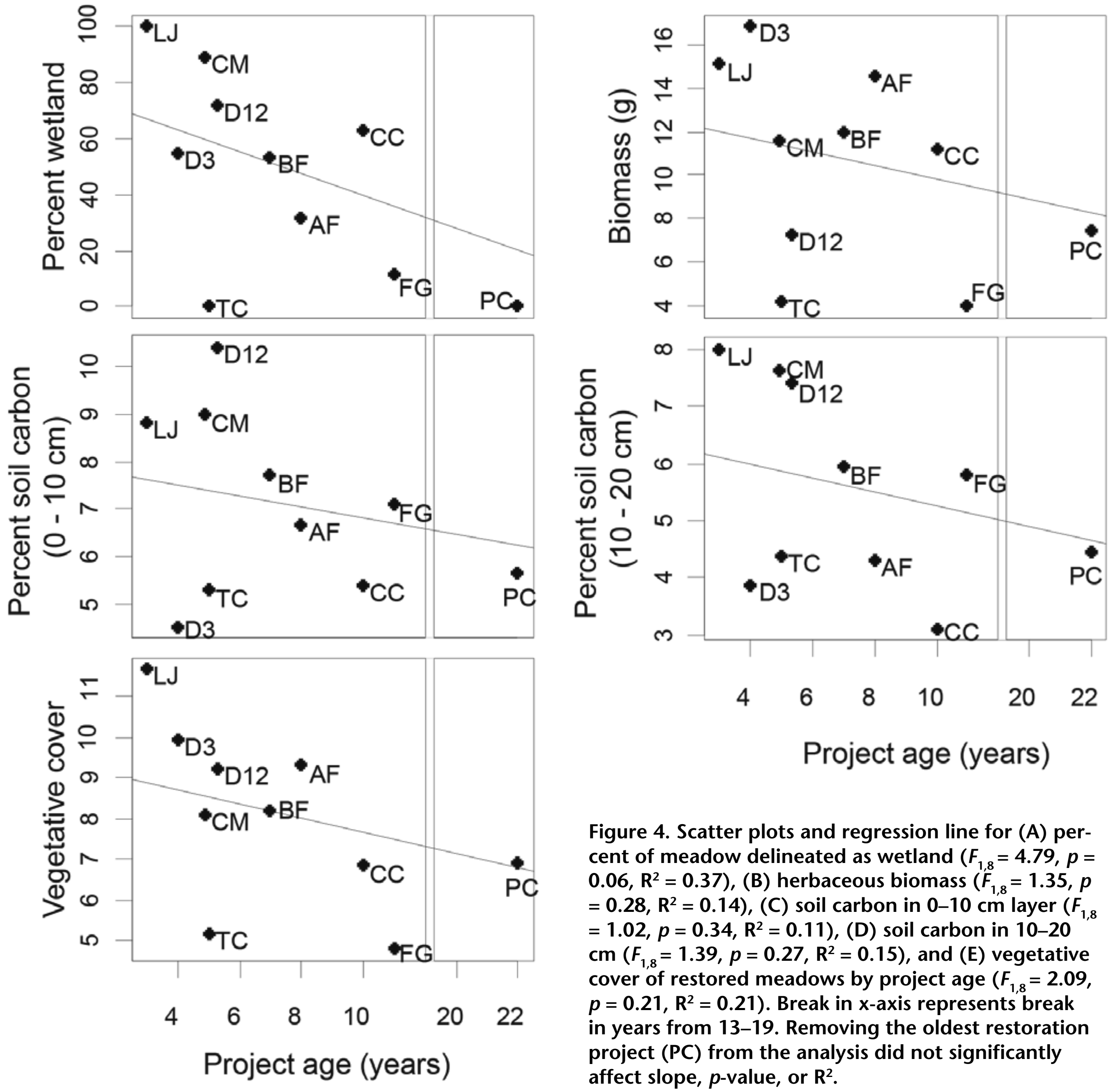

Figure 4. Scatter plots and regression line for (A) percent of meadow delineated as wetland ($F_{1,8}$ = 4.79, *p* = 0.06, R^2 = 0.37), (B) herbaceous biomass ($F_{1,8}$ = 1.35, *p* = 0.28, R^2 = 0.14), (C) soil carbon in 0–10 cm layer ($F_{1,8}$ = 1.02, *p* = 0.34, R^2 = 0.11), (D) soil carbon in 10–20 cm ($F_{1,8}$ = 1.39, *p* = 0.27, R^2 = 0.15), and (E) vegetative cover of restored meadows by project age ($F_{1,8}$ = 2.09, *p* = 0.21, R^2 = 0.21). Break in x-axis represents break in years from 13–19. Removing the oldest restoration project (PC) from the analysis did not significantly affect slope, *p*-value, or R^2.

Palmer 2011, Moreno-Mateos et al. 2012). Rey Benayas et al. (2009) determined that ecological restoration significantly improved pre-project biodiversity and ecosystem services, but that conditions remained lower in restored than reference ecosystems. Moreno-Mateos et al. (2012) found that restored wetlands had less vegetation structure and lower carbon storage than unrestored natural reference wetlands.

An alternative explanation for our results is that the restored meadows have not had enough time to develop wetland characteristics or to build soil carbon stores. Herbaceous vegetation is directly tied to the hydrologic regime and can change quickly following raising or lowering of the water table (e.g., Balcombe et al. 2005, Loheide and Gorelick 2007, Lowry et al. 2011, Purdy et al. 2012), but soil characteristics may take longer to adjust. For example, Wolf et al. (2011) found that created wetlands that were three and four years old showed less soil development than wetlands created seven and ten years prior. When we compared the response variables with project ages of the restored meadows, we found a consistent, albeit non-significant, inverse relationship between the number of years since the project and the response variables. In general, recent projects (three to five years old) had higher percentages of wetland habitat, more soil carbon and greater biomass and cover than older projects (Figure 4). We interpret this finding to suggest that restored meadows can exhibit wetland characteristics and increase soil carbon quickly after successful implementation of a rewatering project, and that the science and implementation of meadow restoration is improving and newer projects are becoming more successful. Engineers, hydrologists, ecologists, and soil scientists have joined in recent years to answer important questions about how hydrogeomorphology and ecological processes respond to different restoration techniques (e.g., Loehide and Gorelick 2007, Hammersmark et al. 2010, Lowry et al. 2011). Recent projects, however, showed high variability in measured response variables highlighting that success is not yet consistent across projects.

The inverse relationship between project age and the response variables may also mean that older projects have had more time to destabilize and revert to a more degraded condition. Typically, post-project monitoring is conducted for a few years, which is probably inadequate for projecting longterm project success. For example, at one sampled treatment meadow (BF), retreatment was required nine years after the first treatment, and seven years later we found several warning signs of channel instability in what currently appears to be a well-functioning stream-associated meadow system. A final interpretation is that older restoration projects occurred in the most degraded meadows and more recent projects occurred in less degraded meadows. However, a review of project reports does not support this explanation.

We found that biomass was greater in wetland habitats and less in upland habitats in restored meadows compared to unrestored meadows. This strong interaction effect could be because wetland habitats in restored meadows represent those areas where reconnection to the water table was successful whereas the upland habitats remain in their pre-restoration state. The finding that biomass was also greater in restored compared to unrestored meadows overall seems to be related to the exclusion of cattle from 70% of the restored meadows versus 10% of the unrestored meadows since our post hoc analysis including a cattle variable reduced the effect of Treatment to not significant.

General assessments of physical processes can be useful for predicting channel and meadow condition (Miller et al. 2011, Pilkey and Pilkey-Jarvis 2007). We found that restored meadows had more signs of head cuts, knickpoints, and channel erosion than unrestored sites. Potential reasons for instability range from failure to eliminate the cause of the degradation (on or off site), unintended flow paths through unprotected sediment including plugs, erosion at key project diversion and control points, and project designs that fail to account adequately for hydrologic, geomorphic, and ecological processes. For example, some pond-and-plug projects incorporate a pond at the top of the meadow on the pre-existing stream channel. As the stream flows into the pond, sediment carried from upstream deposits there instead of in the meadow. Sediment-poor "hungry" water (Kondolf 1997) entering the meadow will tend to erode the channel bed and banks to provide sediment to satisfy transport capacity, and the treatment reach will be sediment starved until the upstream deposit is large enough that sediment throughput is reconnected. A lack of consideration of process-based approaches to restoration has been highlighted as a major flaw in stream restoration design (Palmer 2009, Beechie et al. 2010).

Through our modeling exercise with environmental covariates, we found that percent wetland habitat was positively correlated with meadow slope and elevation. In contrast, Trowbridge et al. (2011) described small and steep meadows in the Great Basin to be drier than large flatter meadows. The Sierra Nevada is less limited by water than the Great Basin and steep, high elevation meadows may have more consistent water from snowmelt and may be more protected from disturbances, such as livestock grazing and roads, that are known to increase habitat desiccation (e.g., Flenniken et al. 2001).

Severely incised systems are unlikely to be reversed simply by removing current disturbances (Schlesinger et al. 1990, Germanoski and Miller 2004). The currently favored pond-and-plug restoration technique to regain hydrologic connectivity between channels and meadows involves large amounts of excavation and fill and results in novel conditions with a series of isolated ponds and dams through the system. Aside from engineering and process-based concerns, we recommend consideration of potential indirect or unintended consequences of construction of these novel aquatic habitats. For example, while native amphibians are expected to benefit from meadow restoration (NFWF 2010), aquatic invasive species are likely to also benefit. American bullfrogs (*Lithobates catesbeinus*) and signal crayfish (*Pacifastacus lenisculus*) are associated with permanent, still water habitats such as reservoirs and borrow pits (Johnson et al. 2008, Fuller et al. 2011). We incidentally observed these invaders in created ponds at two of the restored meadows (CC and BF) with extremely high densities of both taxa at CC. Providing additional habitats for these ecologically detrimental invaders (Adams 2000, Crawford et al. 2006) should be assessed prior to implementation of a pond-and-plug project because invasions alter ecosystems and are often irreversible or extremely expensive to control (Simberloff 2003, Strayer 2010).

Assessments of the range of potential outcomes and consequences of large-scale meadow restoration projects are becoming more common prior to project implementation. However, the well-documented successes of a select group of projects may bias land managers' expectations of a meadow's potential for ecosystem recovery, carbon sequestration, and forage production. The preponderance of success in well-documented cases can foster an "if we build it, they will come" mentality that minimizes the complexity and challenges inherent in any restoration project (Palmer and Bernhardt 2006). In addition, because many of the wetland restoration projects are funded through required mitigation, there may be pressure for post-treatment results to be portrayed positively.

Our comparison of past projects to reference conditions provides one estimate of the range of project outcomes. In addition, new models are being designed to more accurately simulate the potential for change in water storage and habitat conditions following meadow restoration at a site-specific level (Hammersmark et al. 2010, Booth and Loheide 2012). A multidisciplinary process-based approach coupled with realistic expectations and application of site-specific modeling techniques will aid in appropriate decision-making about where and how to implement meadow restoration efforts.

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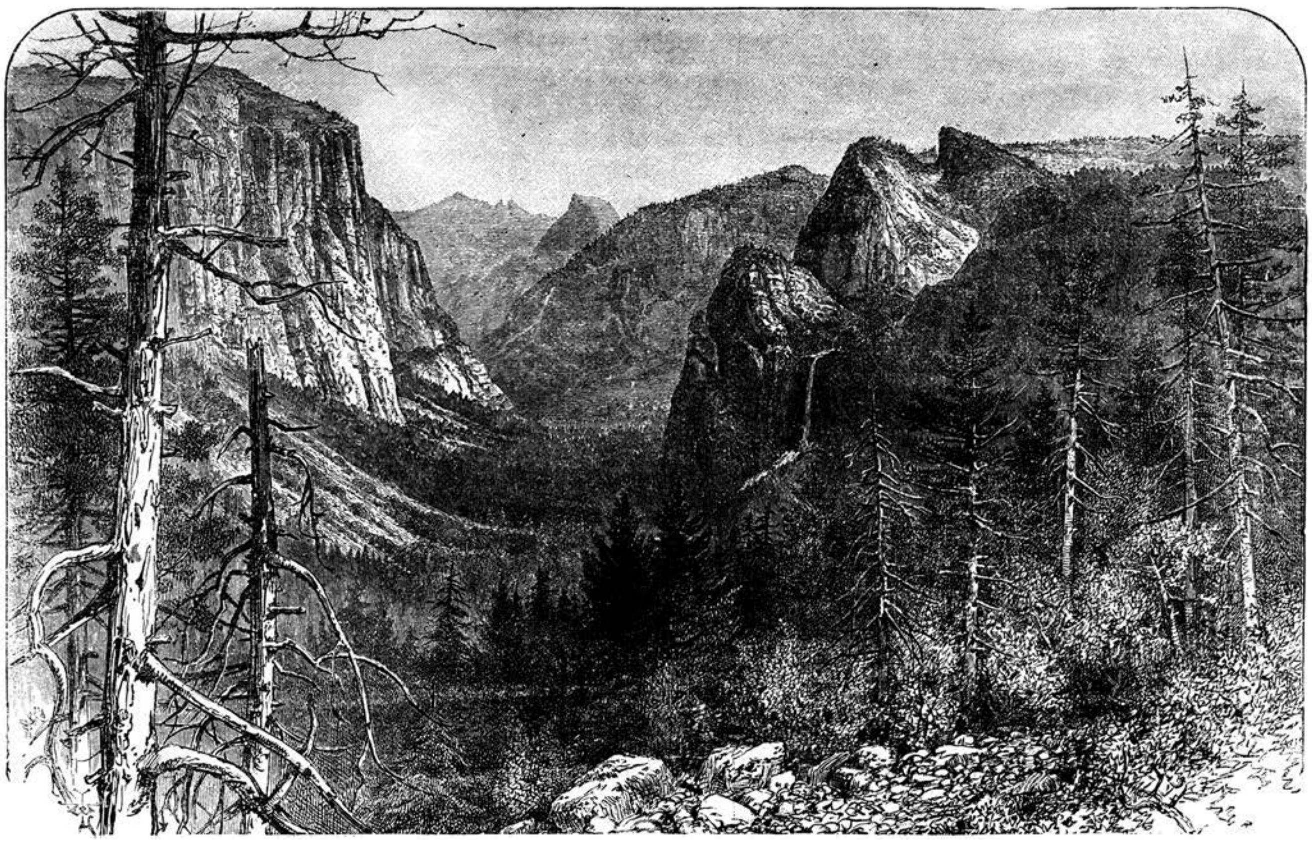

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