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Potential mitigation of and adaptation to climate-driven changes in California's highlands through increased beaver populations

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Climate models forecast significant changes in California's temperature and precipitation patterns. Those changes are likely to affect fluvial and riparian habitat. Across the American West several researchers and civil society groups promote increased beaver (*Castor canadensis*) presence as a means to moderate such changes. This study reviews three literatures in an effort to evaluate the potential for beaver to adapt to and to mitigate anticipated changes in California's higher elevation land- and waterscapes. First, I provide a synopsis of modeled changes in temperatures and precipitation. Forecasts agree that temperatures will continue to increase, to 1.5–4.0° C by 2060; however, forecasts for precipitation are more variable in sign and among models. Second, researchers anticipate climate-driven changes in stream and riparian areas and project that snowpacks and summer flows will continue to decline, winter and spring flood magnitudes will increase, spring stream recession will likely continue to occur earlier and more quickly, and highland fires will be more extensive. Each of these changes has important implications for wildlife and public lands managers. A third focus reviews beaver natural histories and finds that where beaver dams are persistent, they may sequester sediment and create wet meadows that can moderate floods, augment early summer baseflows, sequester carbon in soils and standing biomass, decrease ecological problems posed by earlier spring stream recession, and potentially help cool early summer and post-wildfire stream temperatures. However, due in part to currently limited habitat suitability and to conflicts with other human interests, mitigation would likely be most meaningful on local rather than statewide scales.

Key words: beaver, *Castor canadensis*, climate forecasts, California highlands, hydrological changes, mitigation, wetland restoration

In California, meteorological and hydrological records indicate that the state is already experiencing changes attributable to anthropogenic climate change (Barnett et al. 2008, Pierce et al. 2008, Bonfils et al. 2008, Das et al. 2009, Hidalgo et al. 2009). As a result, the State's snowpacks are melting earlier (Kapnick and Hall 2009), and winter precipitation is falling increasingly as rain rather than snow (Hayhoe et al. 2004, Cayan et al. 2008). Several groups in the American West (King County in Washington, The Beaver Advocacy Committee in Oregon, and in California The Beaver Work Group and Martinez Beavers) are exploring increased beaver (*Castor canadensis*) presence as a way to restore fluvial and riparian habitat and increase resilience against the effects of climate change (Apple et al. 1985, Trimble and Albert 2000, Pollock et al. 2012, DeVries et al. 2012).

This article focuses on California's highlands (the Sierra Nevada and northern coastal ranges, and the Lassen, Shasta, and Trinity regions) as that is the site of most of the State's precipitation and nearly all snowfall that currently provides about one-third of all consumed water (Gasith and Resh 1999). Furthermore, because much of the land in the areas is publicly held, population expansion and damage caused by beaver works can be effectively managed. The paper reviews extant literature towards three ends. First I introduce climate models, the scenarios for future greenhouse gas (GHG) emissions they employ, and then present forecast changes in temperatures and precipitation. Next, I extend those forecasts to examine anticipated effects on fluvial and riparian form, function, and habitat that could potentially be affected by increased beaver populations. Finally, I review what is known of beaver natural history in an effort to characterize the potential adaptations and mitigations an increased beaver population could provide. California's highlands offer somewhat unique climate and geology. Findings from studies conducted east of the Pacific Rim are treated accordingly.

Climate Models and Forecast

Model ensembles and scenarios.—Following best practices established by the Intergovernmental Panel on Climate Change (IPCC) the studies reviewed here create ensemble forecasts using between 3 and 16 global circulation models (GCMs). Those models can be adjusted to provide varying spatial resolution. At their coarsest, each cell includes three degrees of longitude and three degrees of latitude, and so treats areas 160 by 330 kilometers as homogenous. Required computing power increases rapidly as resolution is increased. As a compromise researchers may use statistical resolution that compares projections made by numerous models and creates a probability distribution for more localized areas of interest. Alternatively, dynamical resolution treats the parcels surrounding the area of interest as boundary conditions and then increases resolution only for the study area. Most of the studies reviewed here have been downscaled (i.e., increased resolution) using one or both of these methods.

In order to minimize global climate response uncertainty (Costa-Cabral et al. 2013), modelers use representative CO_2 concentration pathways (RCPs)—these are referred to as scenarios. The models referenced in the following discussion employ two business-as-usual, high GHG scenarios; either the A2 scenario published in 2002 that projects atmospheric carbon equivalent to reach 800–830 ppm in the year 2100, or the more recent AR5 8.5 scenario that places CO_2 equivalent at 1250–1380 ppm in 2100.

Modelled forecasts for temperature and precipitation.—Models are more consistent in temperature forecast than those for changes in precipitation. Together, increased warming in winter and spring is already causing diminished summer streamflow across the West (Stewart et al. 2004, 2005), a phenomenon modeled to continue (Hamlet et al. 2005, Barnett et al. 2008). Diffenbaugh et al. (2015) reported that even though rainfall anomalies have not increased in California over the past two decades, warming temperatures have decreased water availability significantly, and forecast increased drought conditions as a result.

Models agree that highland temperatures will rise through the end of the century (Table 1; Pierce et al. 2013). This is the most vigorous study published at the time of writing this review. Pierce et al. (2013) employed the SRES A2 GHG scenario and employed both statistical and dynamical downscaling to forecast changes for the 2060s relative to a 1985–1994 base period.

Precipitation changes forecast by Pierce et al. (2013) and Walsh et al. (2014) are presented in Table 2. The latter used the updated and higher greenhouse gas AR5 8.5 scenario.

Table 1.—Forecast increases in mean seasonal temperature (°C) of highland regions of California for the period 2060–2069 when compared to the relative historic base period of 1985–1994. The model used the high CO_2 scenario (SRES – A2; from Pierce et al. 2013).

	Highland Region of California			
Season	Sierra Nevada	Shasta Region	North Coast	Central and South Coast
Winter	1.5–2.1	1.7	1.5–2.2	1.8
Spring	2.0–3.0	1.9	1.4–2.0	2.1
Summer	3.0–4.0	2.9	2.0	2.3

Table 2.—Percent changes in seasonal precipitation forecast to occur in the highland regions of California under high CO_2 scenarios (data interpreted from Piece et al 2013, Walsh et al. 2014; N= north, S=south).

	Season		
Highland Region	Winter	Spring	Summer
Northern California[a]	0 ⇔ + 10	-10 ⇔ -20 N ⇔ S	- 30 ⇔ - 10 N ⇔ S
Southern California[a]	0 ⇔ - 10 N ⇔ S	- 30 ⇔ - 40 N ⇔ S	0 ⇔ +10
Shasta Region[b]	+ 9	- 11	- 29
North Coast[b]	+ 7 ⇔ - 2 N ⇔ S	- 10 ⇔ - 18 N ⇔ S	- 32 ⇔ - 13 N ⇔ S
Sierra Nevada[b]	- 5	- 11 ⇔ - 19 N ⇔ S	- 23 ⇔ + 59 N ⇔ S
Central and South Coast[b]	+ 1 ⇔ - 5 N ⇔ S	- 19	- 13 ⇔ +50 N ⇔ S

[a]Forecast under the AR5 8.5 high CO_2 scenario for 2070–2100 compared to the relative historic base period of 1970–2000 without downscaling (from Walsh et al. 2014).
[b]Forecast percent increase in mean seasonal temperature by highland region for the 2060s compared to the relative historic base period of 1985–1994. The model uses the high CO_2 scenario (SRES – A2) and statistical and dynamical downscaling (from Pierce et al. 2013; N= north, S=south)

That group forecast changes for the period 2070–2100 relative to the historic base period 1970–2000. Though not downscaled, these results are similar in sign to findings by Pierce et al. (2013); however, the Walsh et al. study generally forecast a greater increase in winter precipitation and a less-marked decrease in spring and summer precipitation.

Climate-driven Changes in Fluvial and Riparian Areas

These forecast changes in climatic boundary conditions will likely cause changes in several landscape aspects that beaver could potentially moderate. The following discussion reviews the extant literature on climate driven changes to stream flow timing and magnitude, channel morphology, stream temperatures, fire regimes, and meadows above 1,200 meters in elevation.

Snow to rain.—California's snowpacks provide about one-third of the water consumed in that state while also supplying stream flows that are critically important to dry-season habitats. Several studies have sought to quantify the magnitude of snow water equivalent (SWE) loss. Modeling by Cayan et al. (2008) suggested that the greatest diminution of snowpack will occur at elevations below 1,300 meters. Using the SRES A2 high emissions scenario (830 ppm), the modelers used data from the 1990s as a base period. The model forecast that SWE on April 1 (historically the beginning of spring melt) will decline by 37–42% by mid-century and 70–80% by 2100, thereby decreasing spring spate and summer streamflow.

A study by Das et al. (2011) suggested that warmer winters and springs will increase evapotranspiration and that sublimation may further diminish snowpacks and spring runoff. Using an ensemble of 16 GCMs, assuming a 3°C temperature increase and holding precipitation constant, they forecast that these in situ losses of snowpack would decrease April–September flows in the northern and southern Sierra Nevada by 1.8 and 3.6%, respectively, and October–March flows by 2.1% and 3.1%. Illustrating the effects of model variability, Costa-Cabral et al. (2012) ran a similar simulation and reported no relation between temperature and sublimation-evapotranspiration due to earlier snowmelt-runoff.

Beyond a diminution of this natural water reservoir, shifts from snow to increased rain suggest two related sets of problems: increased flooding and issues related to earlier snowmelt recession (Kapnick and Hall 2009). Each of these processes in turn has direct and indirect effects on ecological and human systems.

Flooding.—Hydrographic records indicate that flood magnitudes in California have increased since the 1920s. In a national study Peterson et al. (2013) found that decadal high flow magnitudes have increased at average decadal rates of 9% in northern California, 8% in the southern Sierra Nevada, and 3% on the central coast and the central Sierra Nevada. Several investigators examined increased flood magnitude under higher GHG accumulation. Cayan and Riddle (1992) reported that in California the largest floods are associated with winter-spring circulation over the central and eastern Pacific, and are specifically caused by atmospheric rivers (see also Ralph et al. 2006, Neiman et al. 2007). Again, atmospheric conditions over the Pacific are influenced by numerous factors and model ensemble results are not in strong agreement on forecast conditions. As discussed above, however, models strongly agree on the sign and trend of temperatures in the region and uniformly forecast warming. As a result, storms will be warmer and will produce less snow and more rain (Knowles et al. 2006, Das et al. 2009), producing greater flood magnitudes, particularly during rain-on-snow events.

Several other teams have modeled future flood characteristics. Das et al. (2011) used three GCMs calibrated through precasting (forecasting past flooding given historic climatic parameters) and then input results through a variable infiltration capacity hydrologic model. All three models forecast significant increases in flood magnitudes. While one model forecast decreased flood frequency, two found increased frequency. In 2012, Wehner reported that adding elevation data to a coordinated eight regional model ensemble significantly improved its precast performance. The newly parameterized ensemble compared conditions for North America in the period 2038–2070 to a 1968–1999 base period, and forecast a 5–10% increase in winter, a 10–20% decrease in spring precipitation, a 0–5% increase in winter, and a 0–15% decrease in spring maximum daily precipitation (i.e., flood magnitude).

In 2013, Dominguez et al. employed an ensemble of 8 GCMs to model changes in winter precipitation for the western United States. Comparing forecasts for the period from 2038–2070 with a base period from 1968–1999, they found a 12.6% increase in the magnitude of 20-year floods and an increase of 14.4% in 50-year floods. More generally, however, the models rendered a high probability forecast for a 7.5% decrease in average winter precipitation for the Sierra Nevada and southern California, and slight increases in precipitation for northern coastal California.

Using an ensemble of 16 GCMs and a high carbon emission SRES A2 scenario Das et al. (2013) found that flood magnitudes in the western Sierra Nevada will increase regardless of trends in mean precipitation (see also Maurer et al. 2007). The investigators found that magnitudes would increase beyond current variability as early as 2035. Compared with simulated historic 50-year flood events, the ensemble forecasts progressive increases of flood magnitude of 30–90% in the northern Sierra Nevada and 50–100% in the southern Sierra Nevada by 2100.

Again employing an ensemble of 16 GCMs and both statistical and dynamical downscaling, Pierce et al. (2013) forecast changes in three day accumulation for 100-year flood events (Table 3). Though the forecasts manifest an expected degree of variability, they produced a consensus of sign regarding flood magnitude, which is forecast to increase. There is little consensus regarding trends in total annual rainfall among California's various highland regions. An increase of winter flood events will increase the geomorphic dynamism of stream channels on a decadal scale.

Table 3.—Forecast changes in maximum three-day precipitation events in California's highland regions for the period 2060–2069 when compared to the base period of 1985–1994 (data interpreted from Pierce et al. 2013).

Highland Region	Current Accumulation (mm)	Forecast Accumulation (mm)	Increased Accumulation (mm)
Sierra Nevada	280	370	90
NE California	90	180	90
Shasta	180	300	120
North Coast	240	360	120
Central Coast	165	220	55
South Coast	160	190	30

Recession.—On an annual scale, spring spates were forecast to occur earlier and to decrease in magnitude and duration. Many species are adapted to the specific timing of the spate (Jager et al. 1999, Marchetti and Moyle 2001, Lytle and Poff 2004, Jowett et al. 2005), and exploit a typically slowly retreating moist fluvial margin (Kupferberg 1996, Freeman et al. 2001). More rapid recession will decrease riparian seeding (Shafroth et al. 1998) and nutrient loading (Rood et al. 1995, Langhans and Tockner 2006), decrease primary productivity (Acs and Kiss 1993) and arthropod abundance (Paetzold et al. 2008), decrease salmonid spawning activity (Moir et al. 2006), and weaken other trophic chains (Nakano et al. 1999, Yarnell et al. 2010). Geomorphically, rapid recession is expected to produce steeper bars and so decreased moist transitional area, increased water temperatures, and increased stranding of young amphibians (Kupferberg et al. 2008).

The corollary condition, decreased magnitude of peak spring flow, is expected to decrease the area of aquatic habitat through channel narrowing and loss of wetted side channels (Ligon et al. 1995, Van Steeter and Pitlick 1998) leading to decreases in diversity and abundance of macro-invertebrates and algal production (Peterson 1996, Jowett et al. 2005), which are important food sources for higher trophic levels. Decreased erosion and deposition will decrease lateral channel migration, decreasing channel elevation—and so habitat—variability (Parker et al. 2003, Shields et al. 2000), which may enhance riparian encroachment by woody vegetation (Lind et al. 1996, Shafroth et al. 2002). In addition, earlier melt will result in increased water temperatures, thereby favoring species adapted to warm water and diminishing cold water adapted species such as salmonids (Kupferberg 1996, Jager et al. 1999).

Stream temperatures.—Sub-alpine streams are also expected to warm as a result of atmospheric temperature shifts. Null et al. (2013) employed a regional equilibrium temperature modeling approach that incorporated mechanistic heat exchange between atmosphere and water to model changes in the Feather River as it flows west from the northern Sierra Nevada. The investigators found that at elevations below 1,000 and above 3,000 meters, stream temperatures rise about 1.5°C for each 2°C increase in mean average annual atmospheric temperature. Streams between 1,000 and 3,000 meters responded more strongly at about 1.8°C for each 2°C increase in atmospheric temperature; this is due largely to decreases in snowpack. Currently, July temperatures in the Feather River exceed 21°C in only the lower 30 km (20%) of that stream. However, Null et al. (2013) reported that with atmospheric temperature increases of 2, 4, and 6°C, that threshold is exceeded in 57%, 91%, and 99.3% of the stream, respectively. The authors also noted that the effect of increased atmospheric temperatures are moderated in that watershed through extensive basalt layers underlying the stream that produce significant hyporheic flows that help cool stream temperatures.

Fish.—For salmonids (anadromous and resident trout and salmon) these changes in temperature and flow regime pose particular problems. The upper end of the optimal temperature range for these indicator species is 19°C. The maximum sustained water temperature tolerated by anadromous salmonids is 24°C (Eaton and Scheller 1996). However, at certain stages of their life cycle—eggs and alevin—these fish require lower temperatures (Myrick and Cech 2001), and salmonids exhibit stress at sustained temperatures above 21°C (McCullough 1999, Myrick and Cech 2001). Null et al.'s (2013) forecast has much of the Feather River exceeding 21°C by 2070–2099.

The forecast geomorphic changes are also expected to affect fish habitats. Mantua et al. (2010) examined the effects of expected higher winter and lower summer streamflows on anadromous salmonids in Washington State. They noted that for young Coho the two most important hydrological factors in survival are first year summer temperatures and more importantly, refuges from winter high streamflows in their second winter. Those refuges are commonly found in side channels that several studies suggested will diminish under forecast flow regimes (Ligon et al. 1995, Van Steeter and Pitlick 1998, Shields et al. 2000, Parker et al. 2003, Pollock et al. 2003).

Dam reservoir management.—Changes in precipitation, snowmelt recession, and flood regimes in highland areas pose particular problems for the management of winter and spring pool levels in California's dam system, both for flood control and for power generation (Moser et al. 2012). Das et al. (2013) observed that increased probability of larger flood events will require dams to maintain lower pools in the future to accommodate potential floods. However, should a flood not occur, dam systems will begin the dry season with pools potentially much below maximum storage. Warmer summers will increase electrical demand while summer flows into reservoirs are forecast to decrease.

Fire.—As the West warms, wildfires may become more frequent or more extensive, or both. Westerling et al. (2011) developed a three-model wildfire ensemble to forecast fire extent for California. Contrasting the optimistic SRES B1 scenario with the higher A2 emission pathway against a 1970s base period they found only moderate differences between the two scenarios and for year 2020 forecast an increase of statewide area burned at 10–20%. For 2050 and 2085 the B1 scenario forecast increases of only about 5% for each interval. However, the A2 scenario yields increases up to 38% in 2050 and 40–70% in 2085. While these increases seem somewhat moderate, a closer look at sub-regions of California yields more meaningful results. All models forecast little or no increase in area burned south of Monterey, Kings, Tulare, and Inyo counties, the Central Valley, and the mountains of the central coast. However, across the forested areas of the Sierra, all of northern California including the coastal mountains north of Marin County, the area burned is forecast to increase by 100–300%.

Increased fire extent suggests increased sediment mobilization and stream temperatures. Ice et al. (2004) reported that stream sedimentation and nutrient mobilization (with the exception of phosphorus which may volatilize) increase with fire severity (temperature and duration) and landscape gradient. They concluded that, "Long-term erosion rates in fire prone landscapes may be higher than often believed, and post-fire sediment pulses can have both positive [increased downstream channel complexity in later years] and negative effects" (Ice et al. 2004:20). The latter are related to the mobilization of fine gained sediment that can degrade spawning areas and alter trophic chains. Regarding stream temperature changes, Brown and Krygier (1970) studied two comparable streams in western Oregon, one well shaded and relatively undisturbed, the other flowed through an area that was first clear-cut then slash burned. In the second stream they observed summer temperatures rising from a mean average 13°C prior to treatment to 28°C (range 26–30°C). During the treatment summer the control stream recorded temperatures of 14–15°C. In a similar study in southwestern Oregon, Amaranthus et al. (1989) reported that small stream temperatures increased from about 14°C to 21°C following shade-removing wildfires.

High meadows.—High-elevation meadows present an additional area for consideration. A wetter climate regime beginning between 2,500 and 1,200 years BP raised water tables in high meadows that favored hydric plant communities dominated by sedges, rushes, herbs, dwarfed shrubs, and grasses (Wood 1975). Unique faunal communities subsequently adapted to live in these areas. In the later 1800s and early 1900s these meadows were widely exploited by commercial pastoralists. As a result of grazing, road grading, intentional drainage, and grass crop cultivation many meadow streams have become incised and water tables have dropped so that mesic and xeric floral communities now dominate (Loheide et al. 2009). Climate change will further stress meadow hydrologies by changing mean annual flows, shifting spring spates earlier, and produce a lengthier low-flow period (Null et al. 2011). Loheide et al. (2009) suggested that earlier and shorter snowmelt recession and reduced daily fluxes in snowmelt-related streamflows will reduce groundwater recharge. Viers et al. (2013) noted that meadows between 1,500 and 3,000 meters will be most affected, and that because northern meadows generally are at lower elevations they are more vulnerable. Beaver populations in some of these areas were also reduced in the nineteenth century (James and Lanman 2013). Central to the current discussion, meadow restoration projects on the Feather River in northeastern California are providing some of the best opportunities for research into the potential for beaver to mediate some of the aforementioned changes in California's highland waterscapes.

Beavers and Climate Change Mitigation and Adaptation in California

As the following review indicates, scientific studies are limited, first in applicability and so in number, and second in quality. Most scientific study is focused on areas of North America shaped by continental or extensive alpine glaciation, or by monsoonal or otherwise moist summer seasons, and so may not provide analogs for California's highland hydrologies. Furthermore, several widely cited studies from the western United States are somewhat anecdotal and, thus, problematic.

It is important to stress that habitat initially suitable to persistent beaver occupation is limited by certain factors (Baldwin 2013). Beaver dams are more persistent when situated in wider valleys on reaches with gradients less than 6%. Although they are generalists, beavers build more dams in areas where hardwoods grow within 30 meters of stream channels. Though cross-channel dams are most typical on 1st–4th order streams, beaver also dam side channels on larger streams. No statewide suitability study has been published. Yet, as this review suggests, some of those local benefits are potentially significant.

The following discussion addresses several processes through which beavers might moderate the climate driven changes identified in the previous section. Among these are water storage, streamflow seasonality, sediment flows and storage, nutrient flows and stocks, riparian vegetation, flood events, changes in spring stream recession, and wildfire.

Water storage.—Beaver works cause water to be stored both in surface ponds and wetlands, and in subsurface or hyporheic flows. Studies indicate that the amount of storage is highly variable. Westbrook et al. (2006), for example, recorded two dams on the upper Colorado River that inundated 5.8 and 12.0 ha of the nearby flood plain, primarily by diverting streamflow onto terraces downstream from the dams. However, working in eastern Washington, Scheffer (1938) recorded average pond storage to be 86 m^3 among 22 dams in one reach of Mission Creek; in that same study the author reported a single year-old dam on Ahtanum Creek stored 2,603 m^3 and that storage expanded to 6,170 m^3 the following summer. Because beaver colonies tend to build several dams, aggregate pond storage is often more meaningful than single dam storage capacity. Studies found a wide range of colony and dam density in the West. Clearly the amount of water stored in these systems is highly variable (Table 4).

TABLE 4.—Numbers of beaver dams, or beaver colonies, per kilometer of stream channel at various locations in high mountain environments of the western United States.

Authority	Location	Average number/km
Yeager and Hill (1954)	Southern Colorado	30 active and former dams
Butler and Malanson (1994)	Rocky Mountains (Montana)	25
Bates (1963)	Wasatch Range (Utah)	24
Smith (1980)	Wyoming	1.3
Busher et al. (1983)	Eastern Sierra Nevada	0.75 to 1.5 colonies

Dams also divert surface flows to slower hyporheic flows. However, due to the impermanence of extant dams and the unpredictability of new dams, related sub-surface flows are difficult to study and quantify. In Westbrook et al.'s (2006) study the team was able to quantify dam-related hyporheic storage lost. In that case, a monitoring station 670 meters below the failed dam indicated that within a week of the breech, water levels dropped from 21 cm above to 41 cm below ground surface. While the effect is clear, in order to calculate storage one must characterize local soil water-holding capacity. Other findings are less circumstantial and are more suggestive. Studying 10 dams on first order streams in low gradient glacial valleys in Glacier National Park, Meentenmeyer and Butler (1999) reported that three dams completely diverted all streamflow to aquifers.

Several other studies provide more definitive findings. Working on Bridge Creek in central Oregon, Lowry (1993) found that the riparian water table associated with a small beaver dam closely reflected pond surface levels laterally up to 50 meters from the pond, and estimated ground water storage at 90 m^3. Working on Currant Creek in a semi-arid area in southwestern Wyoming, Apple et al. (1985) studied the effects of re-introduced beaver. They found that within two years, seven beavers had created three dam complexes that raised adjacent water tables by 0.3 to 1.0 meters. Researching a 320 meter reach of Red Canyon Creek, a second order stream in the semi-arid Wind River Range of Wyoming, Lautz et al. (2006) found that about 30% of the stream volume entered hyporheic flows above beaver dams. Those flows raised water tables as far as 50 meters to one side of the stream. Water tables reflected pond surface levels and were maintained at 20–40 cm below the pond surface. The authors also reported that various portions of the study reach alternatively gained water and lost water to hyporheic flows depending on very local conditions confounding quantifications of streamflow.

Generally water storage both in ponds and in aquifers seems to be a function of a few key factors. Low valley gradient (with accordant low stream power) and broad valley floors both allow greater storage in dams and in aquifers (Pollock 2007). Sediment pore space and depth to impermeable substrate suggests reservoir capacity. Finally, the availability of woody dam-building material controls the size, efficacy, and permanence of dams. Thus, in California the most promising areas for water storage by beaver works probably rest among high meadows on headwater streams and amid side channels on lower elevation rivers.

Emmons (2011) estimated that should all currently incised meadows in the Sierra Nevada have their groundwater storage potential restored, about 80 million additional cubic meters of water would be cached. Some portion of that storage would transfer to the atmosphere through increased evapotranspiration (Hammersmark 2008, Hoffman et al. 2013). The increased flow is not significant statewide, but local habitat benefits might be.

Extending summer flows.—Evidence for augmentation of summer flows is perhaps the weakest aspect in the scientific research into potential benefits by beavers. Numerous review articles suggest that beaver dams and ponds augment low summer baseflows; however, studies relevant to California are largely anecdotal. Peer reviewed studies from the Pacific Northwest by Finley (1937) and Scheffer (1938) both reported significant decreases and increases in baseflow following beaver removal and re-colonization, respectively. However, neither study controlled for changes in precipitation nor land cover; further, Scheffer's (1938) results are not clearly confirmed by my analysis of relevant stream gauge records (see author forthcoming for further discussion).

As research into meadow hydrologies in California has found, it is very difficult to control all variables relevant to baseflow augmentation. Studies seeking to quantify the effects of beaver are confounded by multiple uncontrollable variables: they tend not to stay where they are released, making before and after studies nearly impossible; decadal scale climate trends, land use changes, topologies specific to study sites may also alter stream flow.

Plug-and-pond meadow restoration projects in upper reaches of the Feather River in northeastern California provide a potentially useful analog regarding potential modification of baseflows by beaver colonies. There, several stream reaches were re-directed to their former shallow, sinuous, non-incised channels, and the former channels converted to series of hyporheically connected ponds (Hoffman et al. 2010). Above-and-below seepage studies on several treated reaches indicated some aquifer absorption of high flows (Tague et al. 2008) and some augmentation of baseflows, but only into July (Cawley 2011, Hill et al. 2011). Several investigators reported that even where 48.3 ha of meadow were treated, base flow was not increased in August and September (Freeman 2010, Cawley 2011, Hoffman et al. 2013). Thus, widespread meadow restoration resulting from beaver activity may help blunt floods and increase stream flow in June and into July.

Sediment flows and storage.—Because dams decrease stream velocity, their associated ponds and overbank flows may allow sediment sequestration and accumulation (Westbrook et al. 2010). Several studies characterized the variability of sedimentation related to beaver works. In Yellowstone, Persico and Meyer (2009) reported that dams on small streams more effectively sequestered sediment. Butler and Malanson (1995) noted that low-gradient streams have lower suspended and bead loads, and so sedimentation rates also decrease. Studies agree that sediment accumulation decreases with pond age while volume increases with size (Table 5).

Some have argued that beaver-driven sediment accumulation may make significant changes in western landscapes. Working among headwater creeks in Colorado, Ives (1942:198) wrote that, "Detailed field studies indicate that water levels have been raised as much as two feet [0.6 meters], during the past 20 years, in about one-fifth of the beaver occupied area … As pond-filling proceeds at about the same rate as the elevation of water levels, but with the lag of several years, it may be assumed, from these figures, that valley floor elevation, as a result of beaver work, proceeds at a rate approximating one quarter inch per year." While the studies themselves were not included, Ives suggested that the "false senility" of streams—mature features such as meanders, oxbows, and peat bogs, all the result of low gradient—provide further evidence of valley-wide aggradation. Ives (1942) argued that beaver ponds normally transition to meadows following pond filling and that process repeats continually, as beavers move to new sites. Though somewhat anecdotal, this study is cited by 98 scholarly sources identified in Google Scholar's database.

Table 5.—Sediment accumulation rates, and volumes of sediment accumulated by younger and older, and smaller and larger beaver dams in Montana and Oregon, USA.

Authority	Location	Sedimentation Accumulation Rate (cm/yr) Younger <=> Older	Accumulated Volume of Sediment (m^3) Smaller <=> Larger
Butler and Malanson (1995)	Glacier NP Montana	27.9 <=> 2.1	
Meentenmeyer and Bulter (1999)	Glacier NP Montana	45 <=> 30	~ 9.4 <=> 267
Bigler et al. (2001)	Glacier NP Montana	43 <=> 19	
Pollock et al. (2007)	Bridge Ck Oregon	45 <=> 7.5	17 <=> 533
Westbrook et al. (2010)	Glacier NP Montana		Maximum of 750

In a more empirical study, Pollock et al. (2007) reported significant sediment deposition upstream from dams and argued that long-term occupation by beavers decreases bed slope and increases the area likely to be wetted during over-bank flows. Again, variability of landscape response to beaver activity is evidenced by the contrasting results of Meentenmeyer and Butler (1999), who reported that repeat field visits and aerial photo survey indicated that ponds seldom become meadows in Glacier National Park, Montana. Viers (2013) reported that where ponds do fill with sediment and transition to meadows, beaver works may provide important refugia for a host of native California species.

Nutrient flows and stocks.—As beaver works may slow and accumulate sediment, so too may they affect flows of nutrients. In their study of a 320 meter reach of Red Canyon Creek, a second order stream in the semi-arid Wind River Range of Wyoming, Lautz et al. (2006) reported that hyporheic exchange decreased total solute flow velocity by about 30%. Working on Currant Creek in southwestern Wyoming, Maret et al. (1987) reported that during high flows suspended solids, total phosphorous (but not ortho-phosphate), and nitrogen decreased in beaver ponds.

While decreases in suspended sediment are attributable to decreases in velocity, decreases in dissolved nutrients are due to adsorption to fine clays accumulated in the pond bottom sediments (Naiman and Melillo 1984). As a result, pond sediments tend to be very fertile. Naiman et al. (1994) measured available soil nitrogen in beaver meadows at 29.8 kg/ha compared to 6.8 kg/ha in a nearby dry forest. Other investigators reported that total organic carbon is also elevated in pond or meadow soils. Westbrook et al. (2010) analyzed the soil sequestered behind a failed dam and found relatively abundant nutrients: carbon was 24.1 g/kg of soil, total nitrogen 1.5 g/kg soil, and total phosphorous 0.9 g/kg soil (see also Klotz 1998). Naiman et al. (1986) reported that organic carbon turnover time in pond sediments was about 161 years, compared to 24 years for a nearby riffle, and that the pond's stream metabolism index of ecosystem efficiency was over five times higher for the pool than in the riffle.

Nutrient sequestration suggests that high meadows might serve as significant carbon sinks. Norton et al. (2014) suggested that southern Sierra Nevada wet meadows contain about 54.3 mg/ha of soil organic carbon, or about 12.3% of all such carbon sequestered in the Sierra Nevada. In addition, these rich soils encourage further carbon sequestration in new standing biomass.

Vegetation.—As Yeager and Hill (1954) observed under certain conditions, beavers may denude riparian vegetation and "scalp" top soils from pond edges and may also cultivate riparian deciduous and wetland herbaceous production. They may accomplish this through several processes. First, beavers increase water availability both spatially across valley bottoms through hyporheic flows, through overbank flows, and through canals excavated in order to more effectively move cut wood to the dams (Seton 1953), and temporally by providing water further into summer dry seasons. Apple et al. (1985) illustrated the effect upon riparian vegetation: three summers after beavers were re-introduced on Currant Creek in southwest Wyoming willow had colonized and grown up to 2.0 meters in height in spaces where water tables had been raised by beaver ponds to within 40 cm of the surface. In the downstream reach where aquifers were not charged by beaver ponds, willows had not recovered. On the Colorado Plateau in New Mexico, Trimble and Albert (2000:91) noted the addition of "extensive riparian habitat, especially willows" 6–14 years after re-introduction. Other authors reported that aspen, alder and cottonwood also responded well to the wetter habitats created by beavers (Ives 1942, Baker 2003).

The results of several studies suggest that willows and aspen live mutualistically with beavers. Working in Rocky Mountain National Park, Baker et al. (2005) simulated the effect of beaver browse on riparian willow with and without elk browsing. With elk herbivory, willows produced fewer and longer roots and displayed a higher percentage of dead biomass. Pruning followed by elk exclusion resulted in shorter, but far more numerous shoots; total stem biomass after three years was 10 times greater without elk browsing and those plants recovered 84% of their pre-cut biomass after only two growing seasons. With browsing by elk, however, plant biomass recovery was only 6%. Thus, under certain conditions, beavers may cultivate the development of bank stabilizing willow carrs, but only where elk browsing is limited. Because elk hunting licenses constitute an important revenue source for the California Department of Fish and Wildlife, reducing populations may require further budgetary support from the State. In Yellowstone, re-introduced wolf populations effectively moved elk away from streams and allowed both willow re-growth and subsequent re-occupation of streams by native beaver populations (Ripple and Larsen 2000).

Beavers may affect other changes in riparian forests. By taking down more mature trees, either through cutting or by drowning roots, and especially of conifers, beaver works may create light gaps that allow the growth of early successional species such as alder and willow, creating a diverse ecotone at the margin of their browsing zone 30–50 meters from the edge of their ponds (Donkor and Fryxell 2000). Several investigators noted that sedges and other wetland plants often colonized the saturated margin of beaver ponds (Johnston and Naiman 1987, Pollock et al. 1998, Westbrook et al. 2010). Clearing of riparian canopies may also result in problematically warmer stream temperatures.

Flood events.—Several review articles suggested that beaver works may attenuate flood events (e.g., Parker 1986). Hillman (1986) and Ehrman and Lamberti (1992) reported evidence of this in low-gradient landscapes. Working in mountainous northern Idaho, DeVries et al. (2012) documented the hydrological effects of anthropogenic structures that emulate beaver dams and found that check dams increased the frequency of overbank flows that worked to dissipate flood crests (see also DeBano and Heede 1987). Taking a different approach, Beedle (1991) modeled flood behavior amid glacially carved valleys on Kuiu Island in southeast Alaska. His model assumed that all dams were at capacity at the time of the flood, so that much of the attenuation resulted from deflection away from channels. He found that any one dam decreased flows by only about 5 percent, but that a series of five large dams reduced the peak flow of a two-year flood event by 14 percent, and reduced the peak of a 50-year event by four percent. These are small, but potentially meaningful, changes.

Beaver dam failures figure prominently in this literature. Working in a desert environment on the Bill Williams River in Arizona, Andersen and Shafroth (2010) reported that over 50 percent of beaver dams were damaged in a relatively large flood pulse of about 60m^3/sec, and that a pulse as low as 5 m^3/sec caused significant damage. On a 32-km reach of Bridge Creek in semi-arid central Oregon, Gibson and Olden (2014) reported over a period of 17 years that no dam persisted longer than 7 years and that most breeched within two years. However, in agreement with Demmer and Beschta's earlier study (2008), the authors found that these dams did attenuate high flows through their ability to divert high flows to local terraces and by creating greater sinuosity and valley bottom heterogeneity. In Glacier National Park, Westbrook et al. (2010) also reported that extant and breeched beaver dams increased riparian drainage complexity, and also increased vegetation capable of flood attenuation. Two groups of investigators added anchoring structures and noted that anchoring significantly increased dam durability (Apple et al. 1985, Pollock et al. 2012).

In some contexts, beaver-enhanced riparian vegetation may play an important role in flood mitigation. Smith (2007) offered an extensive study on the role and capacity of willow carrs to slow flood waters, and that is particularly relevant given the ability of beavers to cultivate these thickly branched willow stands. Those investigators reported that where stem spacing is less than 30 cm, vegetative stalks up to 2 meters in height, whether flexible or rigid, are able to reduce boundary shear stress to allow sediment deposition even if over-topped. In short, thick willow stands not only protect terraces from erosion, but also trap new sediment even during flood events. This vegetative aspect of beaver ecology could, thus, attenuate anticipated increased floods and sediment mobilization in California.

Changes in spring recession and ecotones.—As discussed above, for many plant, invertebrate, and aquatic species, the recession of high spring flows produces a vital, yet transient and moving, ecotone. The altered timing and decreased availability of these wetted margins promises to stress certain species of riparian plants and invertebrates. Both intact and broken beaver dams can create similar habitat. Breeched dams expose nutrient-rich and sometimes bare soils. Because beavers typically use soil to seal leaks in dams, the structures themselves may offer moist spaces available for colonization by invertebrates or plants, or by both. Mature dams often host willow, cottonwood, and aspen samplings, young trees whose roots can help to further consolidate dams (Bigler et al. 2001).

Wildfire.—Thus far few studies have been conducted into the relationship between beavers and wildfires. In his encyclopedic *Lives of Game Animals*, Seton (1953:455) wrote that "by conserving the water supply, the Beaver keeps little brooks running all year, instead of only freshets, so the forest is helped by irrigation. …Its ponds provide valuable fireguards." However, he did not offer evidence supporting these assertions.

More careful studies offer insights into beaver-wildfire interactions. Working in areas formerly covered by continental glaciers, two studies reported rather different interactions between beaver presence and fire. In Mount Desert Island, Maine, Little et al. (2012) used aerial surveys to assess beaver response to a fire in 1947 following beaver re-introduction in 1921. Following the fire, the researchers reported that dams increased rapidly in the burnt areas, but decreased from 60 to 10 in unburned areas by 1970. They also documented a decline in dams in the burned areas from about 100 in 1980 to fewer than 40 in 1990. Interestingly, ponds in this environment were observed to become meadows.

Hood et al. (2007), working in Elk Island National Park in Canada, studied beaver lodge occupation in relation to prescribed fires. They reported that lodges were nearly uniformly abandoned following first burns, and completely abandoned following subsequent fires; they also reported that if the area does not burn again over the following 20–30 years, pond creation increases. The authors suggested that trembling aspen (*Populus tremuloides*) regenerates well after fire. Bailey and Whitham (2002) reported that aspen regenerated 10 times more biomass following a severe burn. However, when elk are present, browsing decreased standing aspen biomass 90-fold, and so severely limited beaver re-colonization following fires.

Wildfires can also increase sediment mobilization that can be problematic for human and wild habitats. Once stripped of vegetative cover, slopes are exposed to sheet flow and gullying. Ice et al. (2004) reported that the potential for soil mobilization increased with the severity of fires. In very intense fires soil can become mineralized and nearly impermeable, forcing any runoff to flow rapidly down-slope, entraining soil particles along the way. Beaver dams may help sequester sediment in this context as well. Christian's (2014) comparative aerial surveys of eastern Glacier National Park found that prior to a large fire upstream pond sizes were variable year to year with changes of 40% typical. Following the fire, ponds steadily decreased in size, indicating sequestration of some portion of increased sediment flows.

As noted previously, wildfires will tend to increase stream temperatures. Beaver works, through increasing residence time in ponds and through decreasing shading gallery forest canopy, may also increase stream temperatures. Where stream temperatures are very cold, this may benefit certain native species; however, in many contexts this increase in stream temperatures may be problematic to salmonids. Dams can also work, however, to cool mid-summer stream temperatures when cold spring flows diverted to aquifers re-join streams 1–3 months later (Lowry and Beschta 1994). This retention and delayed release of cooler spring water might more generally buffer increasing summer stream temperatures.

Thus, following wildfires beaver dams may help sequester sediment, very locally decrease seasonal stream temperatures, and enhance riparian revegetation. However, the persistence of beaver colonies following wildfires seems highly variable and dependent in part, upon low elk abundance and subsequent browsing.

Discussion

Recent climate models forecast decreased snowpacks and summer streamflows, earlier and shorter spring spates, increased flood magnitudes, higher stream temperatures, and increased area of wildfire amid California's highlands—all with implications for habitat alteration. Few geographically analogous studies on beavers have been published, several of those original studies are somewhat anecdotal, and their claims apparently are at times exaggerated. However, several valid studies do suggest that on some of California's headwater streams beaver dams may work to recharge aquifers, augment baseflows for several weeks into summer dry seasons, sequester sediment and nutrients, encourage restoration of meadow vegetation and willow carrs that can ameliorate some of the problematic aspects of floods and wildfires, and supplement decreasing recessional riparian ecotones.

In short, beavers cannot mitigate all of the anticipated climate related changes in California's highland hydrologies. However, as this literature review suggests, beavers potentially offer meaningful local benefits. Unlike human-engineered projects, the effects of beavers on local hydrologies and habitats are variable and uncertain, and further investigations particular to California's highlands is warranted.

Extant studies suggest experimental designs to study hydrologies and habitat changes. As before and after studies are highly problematic due to subject mobility and variable boundary conditions, a simultaneous investigation of two analogous streams or watersheds, one with and one without beavers, would obviate problems posed by inter-annual precipitation and temperature variability and avoid re-introduction issues specific to California. Ideally, study meadows would not be connected to adjacent watersheds hyporheically, thus allowing accurate quantification of the effect of beaver works on timing of flows leaving the meadow. The stream reach seepage studies conducted amid the plug-and-pond meadow restoration projects on the Feather River offer an alternative design for studying water storage and baseflow augmentation. Such studies could align with on-going efforts to restore meadowlands in California. A nascent wetland restoration grant program funded through California's carbon market and administered by the California Department of Fish and Wildlife might prove a reliable source of financial support.

Several of the studies reviewed here indicate that the ecosystem services provided by beavers are increased as colony density increases on streams and in watersheds. The extent of additive benefit is not well quantified, but a controlled study of beaver re-introduction on a watershed scale is currently under way in the Methow Valley in eastern Washington. There, the Methow Conservancy project—a partnership between Washington Department of Ecology, Washington Department of Fish and Wildlife, The US Forest Service, and the Pacific Biodiversity Institute—is engaged in a watershed scale, before-and-after study of the hydrological, geomorphic, and ecological effects of beavers. They have installed 6 flow and 32 temperature stations to monitor changes. Their experimental design calls for a three-year pre-study period prior to beaver introduction and a 3–5 year post-introduction monitoring period. The protocol has been confounded by beavers not staying or succeeding in the pre-monitored release sites. As of 2013, introduced beavers had successfully inhabited only one-third to one-half of the 45 release sites. Results thus far are also confounded by environmental variability. The strength of findings will also be subject to changing boundary conditions (wetter, drier, warmer, cooler seasons) that may coincide with re-introductions and so confuse causation. The group plans to begin publication of results as early as 2018. Due to topography, results there may be most directly applicable to California's Cascade Range and coastal ranges.

Though able to create their preferred environment to a degree, beaver persistence requires low-gradient and wide stream plains. Even when well established, they apparently are also subject to long-term drought. Persico and Meyer (2009) found in Yellowstone

National Park that beaver have been endemic throughout the Holocene; however, during two notably dry periods, from 2200–1800 and from 950–750 years BP, beavers were absent from the area. Beavers may not be able to persist into California's drier future.

Finally, though advocates often portray beavers as a very low cost means of stream restoration or climate change mitigation because they tend to interact with built infrastructure, they also require management. Publications such as the Oregon Department of Fish and Wildlife's monograph detail techniques for live-management; that activity would require resources beyond the current budgets of many wildlife or public land management agencies, but holds the potential to provide benefits beyond costs.

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