Historic alteration and potential for restoration of vegetation and soil processes in Tuolumne Meadows

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Project Summary

Decades of intense sheep grazing during the middle to late 1800's caused novel and threshold-crossing impacts to Sierra Nevada meadows. In many steeply sloping meadows erosion gullies formed when livestock eliminated the soil-binding, flood-resistant sod of native sedges. However, in more level landscapes, such as Tuolumne Meadows, the primary effect of intense grazing was to shift the vegetation community from perennial sedges to tap-rooted herbs and annuals, which produce lower carbon-content soils. A century after the cessation of grazing, native herbivory may be preventing the recovery of the perennial sedge community. Previous research has focused mainly on the hydrologic and vegetation effects of erosion gullies in meadows, with very little work examining the consequences of altered vegetation and herbivory on soil carbon dynamics. Even less attention has been devoted to evaluating the potential for directed restoration projects to reverse the long term trends created by grazing impacts and reestablish a stable and functioning meadow ecosystem. This research project investigated the interaction of present-day native herbivores with the vegetation of Tuolumne Meadows in Yosemite National Park to:

1. Evaluate the effect of current native herbivory on sedge and lodgepole pine seedling survival in a meadow herbivore-exclosure experiment.
2. Measure the effect of deer herbivory on streamside willow height growth and catkin production in a stream-side herbivore-exclosure experiment.
3. Quantify the meadow ecosystem CO_2 flux to create a carbon budget for control plots and herbivory-exclosures in Tuolumne Meadows, and control plots in reference meadows.

Introduction

Meadows cover less than 3% of the Sierra Nevada land area (Fryjoff-Hung & Viers 2012), but they are disproportionately important for bird (Van Riper & Van Wagtendonk 2006), insect (Simonson *et al.* 2001; Hatfield & LeBuhn 2007), amphibian (Morton & Pereyra 2010; Liang & Stohlgren 2011), mammal (Grenfell & Brody 1986) and plant biodiversity and habitat (Jones 2011). In addition to their biotic and ecological significance, mountain meadows can attenuate flood peaks (Hammersmark 2008), store and transform carbon and nitrogen (Norton *et al.* 2011), and retain shallow groundwater and soil water (Loheide *et al.* 2008). For millennia, mountain meadows throughout the Sierra Nevada have accumulated mineral sediment and organic carbon (Wood 1975) , which have been used to reconstruct prehistoric climate and vegetation (Anderson & Smith 1994). This record of accumulated carbon and sediment is evidence that relatively stable meadow hydrologic and biogeomorphic processes occurred over the past several thousand years (Benedict 1982; Ratliff 1985). Frequent and/or large soil disturbance events would have destroyed the integrity of this accumulated history.

The abundant natural resources in mountain meadows have made them focal areas for human use and impact. The most widespread direct human impact to Sierra meadows has been livestock grazing. Starting in the 1850's and lasting into the 20th century, large flocks of sheep and cattle were summered in Sierra Nevada meadows (Kinney 1996). For example, in 1870 LeConte reported, "the Tuolumne Meadows are celebrated for their fine pasturage. Some 12,000 to 15,000 sheep are now pastured here. They are divided into flocks of about 2,500 to 3,000" (LeConte 1870). John Muir, in his

first summer in the Sierra in 1869, tended a flock similar to those described by LeConte (Muir 1911). Unregulated grazing persisted for nearly a half-century, even following the formation of Yosemite National Park (YNP) and other federal jurisdictions. The YNP Superintendent's report of 1898 documented that he ejected from parklands 214,050 head of sheep and hundreds of cattle and horses (Ernst 1949). The cessation of sheep and cattle grazing did not occur until 1905.

Grazing impacted the vegetation and soils as livestock ate the most palatable plants, decreasing or destroying populations of sedges, rushes and other long-lived clonal plants with high root-to-shoot ratios (DeBenedetti 1980). While partial recovery has occurred in some meadows, the vegetation composition of many meadows remains altered (Ratliff 1985; Bartolome, Erman & Schwarz 1990; Dull 1999; Allen-Diaz 2004; Cooper, Chimner & Wolf 2005), with unvegetated patches, and reduced plant production. A study in the southern Sierra Nevada (Odion, Dudley & D'Antonio 1988) found that 50-80% of grazed meadows now dominated by dry meadow plants were formerly wet meadows, and are in need of restoration. Meadow soils are high in organic matter, but the present vegetation composition of annual plants and broadleaf herbs in many meadows does not generate sufficient below-ground productivity to have formed these soils. The lower productivity of the alter plant community fails to keep pace with the decomposition rate of highly organic soils, resulting in a net loss of soil carbon.

In flat-lying meadows, such as Tuolumne Meadows in Yosemite National Park, grazing-induced changes have created a higher proportion of bare ground and lower cover of clonal monocots (Ballenger & Acree 2009) as compared to nearby, but smaller, less-accessible, and likely less-grazed meadows. A shift to a sparser herbaceous and annual-dominated vegetation is likely to result in reduced soil organic matter input. In ecosystems where densely-rooted perennial and clonal monocots are dominant, their high root-to-shoot ratios form meadow soils with large soil organic carbon pools (Rasse, Rumpel & Dignac 2005; De Deyn, Cornelissen & Bardgett 2008). In addition, the species of perennial monocots that appear to be underrepresented in Tuolumne Meadows, such as *Carex scopulorum* and *Carex subnigricans*, are C3 plants, whereas some of the species that are currently abundant, like *Muhlenbergia filiformis,* are C4. Experimental evidence indicates that organic matter derived from C4 plants decomposes much faster than that from C3 species (Wynn & Bird 2007).

Soil organic matter plays a key role in retaining soil water (Hudson 1994; Saxton & Rawls 2006) and increasing soil cation exchange capacity (van Erp, Houba & van Beusichem 2001). Vegetation changes that result in an annual net-loss of soil carbon can cause a concurrent loss in water holding capacity and nutrient availability. This can set up a feedback of degradation where the loss of soil water and nutrients limits vegetation growth and ground cover, exposing more soil organic matter to drier, more oxygenated conditions, resulting in greater decomposition. The generally sparse vegetation cover exposing significant bare ground and specifically the lack sedges in Tuolumne Meadows is resulting in a loss of soil organic matter and water-holding capacity. If this continues the meadow could become too dry to restore to the original wetland sedge dominated community.

Native rodents (ground squirrels, voles, pocket gophers, and mountain beaver) and deer can reinforce the historic grazing-induced impact of plant community alteration. Present-day native herbivory may limit the establishment and growth of the few clonal sedge patches remaining in Tuolumne Meadows, effectively maintaining the plant community in an altered state. In addition, the

bioturbation and disturbance of the native herbivores may favor annual or short-lived seed-dispersed plants over clonal, long-lived, perennial monocots. The vegetation in this degraded state is expected to have lower cover, lower total biomass, and a lower average root-to-shoot ratio, and therefore contribute less to the soil organic carbon pool. To measure the effect native herbivory is having on the plant community and ecosystem carbon balance, we conducted an herbivory-exclosure experiment in Tuolumne Meadows and measured sedge survival and carbon gas flux in control and fenced plots.

Meandering through the broad, flat-lying Tuolumne Meadows, the Tuolumne River influence the hydrologic regime and sediment erosion/deposition processes of the meadow (Loheide *et al.* 2008). Because changes in the river water level may affect the water level in the adjacent meadow (Lowry *et al.* 2010), factors that affect the stream channel could have significant implications for the entire meadow. One such factor is streambank stability and its influence on channel width. Easily eroded streambanks result in wider channels with shallower flow that can translate into lower meadow water tables. Willows and other deep-rooted vegetation play a key role in stabilizing streambanks and resisting erosion (Micheli & Kirchner 2002). In addition, densely branching above-ground willow stems can slow flow and encourage sediment deposition, raising river water levels and building the foundation of meadow soil. Browsing pressure from ungulates such as deer can severely reduce willow population height and their ability to reproduce by seed (Peinetti, Menezes & Coughenour 2001). Therefore, we implemented an exclosure experiment on streamside willow patches along the Tuolumne River in Tuolumne Meadows to determine whether deer browsing was significantly influencing willow height and catkin production. Concurrent sedimentology experiments (not reported on here) were conducted to quantify the effects of willows on erosional and depositional processes.

These studies were initiated in 2011, and field data collection was completed in 2015. A follow-up pilot restoration project in the wet portions of Tuolumne Meadows was funded in 2015 by the California Department of Fish and Wildlife. The goal of that project will be to reestablish 9 acres of sedge-dominated meadow and quantify the effect of vegetation restoration on greenhouse gas sequestration of Tuolumne Meadows. The following is a summary of the findings for the three objectives of the 2011-2015 work.

Objective 1

- Evaluate the effect of current native rodent and deer herbivory on sedge and lodgepole pine seedling survival in a factorial herbivore-exclosure experiment.

To determine the effect of herbivory on transplanted native perennial clonal sedges (*Carex subnigricans* and *Carex scopulorum*) and lodgepole pine (*Pinus contorta*) seedlings, we implemented a factorial field experiment. The experiment excluded small mammals and deer from treatment plots. A total of 20 fenced treatment plots and 20 unfenced control plots were installed in Tuolumne Meadows in 2011. Ten each of the treatment and control plots were located in dry and wet hydrologic settings to account for variable moisture conditions in the meadow. Exclosures were constructed from galvanized wire mesh with holes sized to eliminate voles and gophers. The fences were 30 cm tall, included roofs, and extended below ground 30 cm deep into hand dug, backfilled trenches. Each plot was 2m by 2m square in area. Because birds were observed perching on the corner posts of the fences, identical corner posts

were installed at the control plots to equalize any unintended effects of birds. In addition, all measurements within plots were made >20 cm in from the plot edge to reduce edge effects associated with the fence or researcher trampling of the perimeter immediately around the outside the plots.

The high organic matter content of the soil in Tuolumne Meadows indicates that clonal plants with high below-ground productivity were critical to soil formation. It is suspected that plants such as the two *Carex* species, which are minor components of the current plant community, were major contributors to soil-building and were far more abundant before the period of intense grazing. The annual plants and small, taprooted broadleaf perennials that are dominant today have low root-to-shoot ratios when compared to clonal sedges, and are less significant contributors to building carbon-rich soil. To test whether current herbivory is affecting perennial sedge survival we transplanted cuttings of *Carex scopulorum* and seedlings of *Carex subnigricans* into the experimental plots in early summer 2012. Seeds of both species were collected from Tuolumne Meadows in fall of 2011 and cold/wet stratified during the winter, but only *Carex subnigricans* germinated and produced seedlings in the greenhouse. Due to the complete lack of viable *Carex scopulorum* seeds, rhizome and shoot cuttings from existing populations in Tuolumne Meadow were transplanted in early summer 2012.

These two Carex species are currently minor components of Tuolumne Meadows' vegetation, but are more abundant in reference meadows. Twelve live plants of each sedge species (*Carex scopulorum* and *Carex subnigricans*) were transplanted into each plot. Because *Carex scopulorum* is a wetland-obligate plant, this species was only planted in the 10 fenced and 10 control plots of the wet block. *Carex subnigricans*, a facultative wetland species, was planted into all plots in both the wet and dry blocks: 20 fenced and 20 control plots. Transplants were marked and their survival tracked over 3 years, from 2012 to 2015.

In addition, we investigated the influence of hydrology (the wet and dry blocks) and the role of herbivory on lodgepole pine (*Pinus contorta*) seed and seedling survival. We sowed batches of 100 pine seeds into each of the 20 fenced and 20 control plots (10 each in the wet and dry blocks). Seeds were collected from ripe lodgepole pine cones gathered around the perimeter of Tuolumne Meadows in October 2013. The cones were dried and the seeds were removed and stored in a refrigerator until early summer. In late May, 2014, each plot received a 100-seed batch, sown in a 10 cm radius circle, marked at the center for relocation. In summer 2015, all lodgepole pine seedlings within 10 cm of each center marker were counted. The number of seedlings that emerged from sown seeds was a combination of the germination rate and seed/seedling mortality from herbivory and other factors. In a greenhouse setting we determined the maximum germination rate under favorable conditions.

In order to test for the maximum expected germination and emergence of seedlings, a well-mixed random sample of 216 seeds were sown indoors (also in late May 2014) in 72 cells filled with moist peat moss. Each cell received 3 seeds and seedling emergence was recorded for each cell (to ensure no double counting or under counting) at least weekly for 140 days. By day 140, nearly 70% of the lodgepole pine seeds had germinated and seedlings developed, and the rate of emergence had slowed significantly, suggesting an asymptotic approach to a maximum value (Figure 1). All figures and text from here forward will refer to the planted propagules of *Carex scopulorum* (rhizomes), *Carex subnigricans* (seedlings), and *Pinus contorta* (seeds) as seedlings.
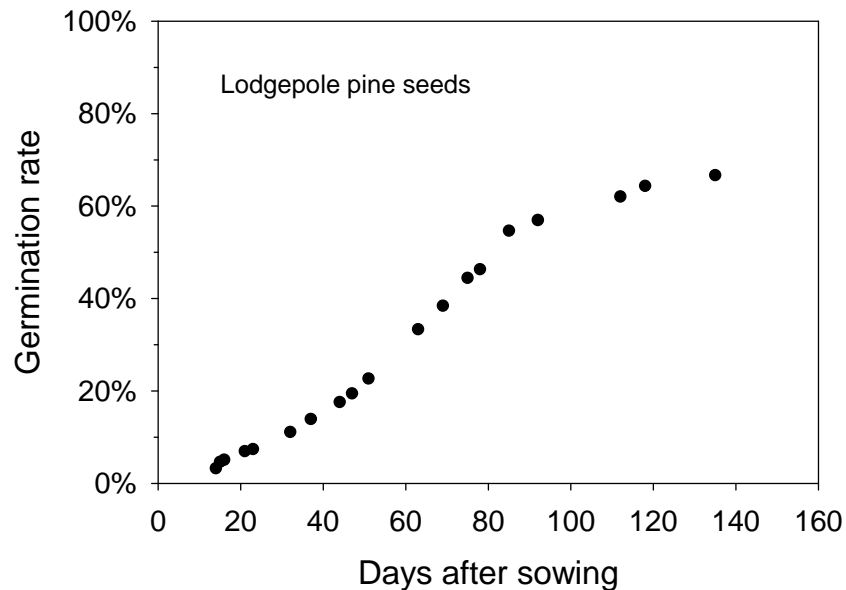
Figure 1. The proportion of *Pinus contorta* seeds that germinated in a greenhouse setting approached 70% by 140 days after sowing.

An analysis of variance (ANOVA) indicated that significantly more *Carex* survived for 3 years, and *Pinus contorta* for 1 year, when protected from herbivory (Figure 2). *Carex subnigricans* survived significantly better in the wet block of plots than in the dry block (Figure 3), but the hydrologic difference between the two blocks did not significantly affect *Pinus contorta* germination and/or survival. *Carex scopulorum* was only planted in the wet block and so is not included in the hydrologic test. Because hydrology affected *C. subnigricans* seedling survival, we tested for interacting effects of water table depth (the block) and herbivory (the treatment). The ANOVA indicated that there was no significant interaction; the effect of the treatment was similar in each block (Figure 4). Because there was a significant effect of the block (hydrology) on *C. subnigricans*, but no interaction between the block and treatment, the ANOVA to evaluate the effect of the herbivory included both block and treatment terms, but not their interaction. Because the other two species were either not planted in both blocks, or the block had no significant effects, the ANOVAs only include a term for the herbivory treatment. P-values reported on the figures are results from the ANOVAs and can be interpreted as the probability that the 2 samples being compared (control vs. fenced or dry vs. wet) were drawn from the same population.
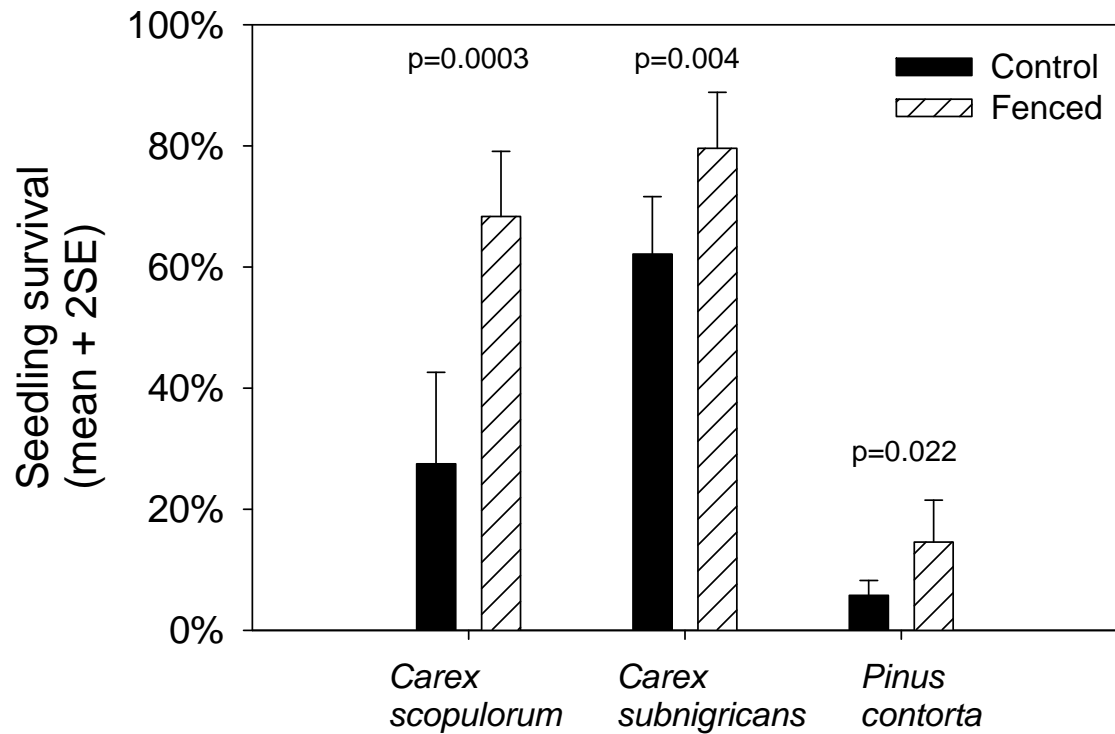
Figure 2. Seedlings of *Carex scoculorum, C. subnigricans,* and *Pinus contorta* survived significantly better in fenced plots than seedlings in control plots. The 2 *Carex* species were live-plant transplants and the data shown are the survival rates 3 years after transplanting. *Pinus contorta* was sown directly into the plots in 100-seed groups, and the data shown indicate the combined processes of germination and survival after 1 year. The germination rate of *P. contorta* seeds in a greenhouse setting was approximately 70% (see Figure 1**Error! Reference source not found.**).
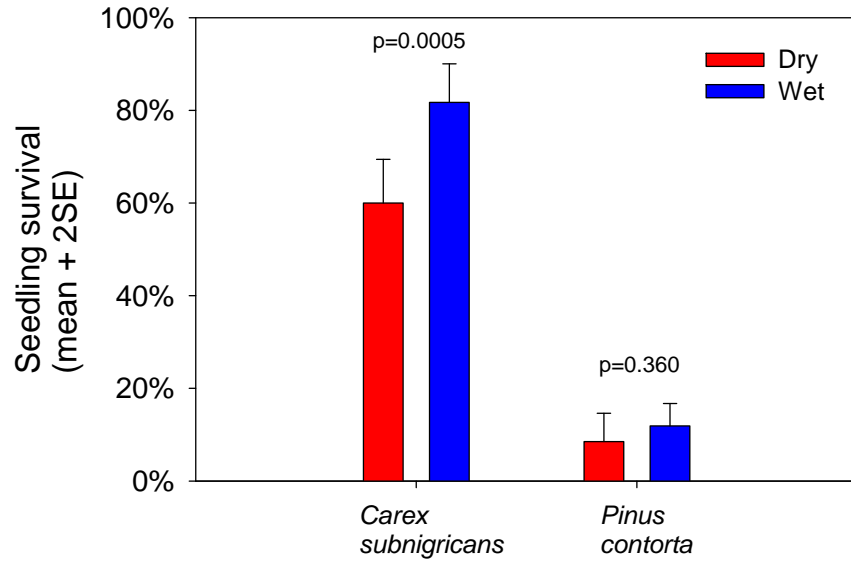
Figure 3. Seedlings of *Carex subnigricans* in wet plots had significantly higher survival rates than seedlings in dry plots, while *Pinus contorta* survival was not significantly affected by plot wetness. The *C. subnigricans* were live-plant transplants and the data shown are the survival rates 3 years after transplanting. *Pinus contorta* was directly sown into the plots in 100-seed groups, and the data shown indicate the combined processes of germination and survival after 1 year. The germination rate of *P. contorta* seeds in a greenhouse setting was approximately 70% (see **Error! Reference source not found.**).
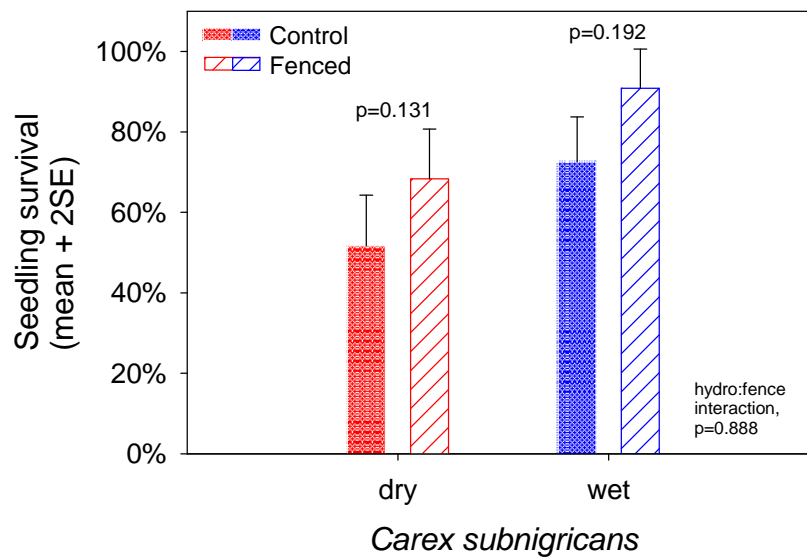

Figure 4. Hydrology and fencing did not interact in a significant (non-linear) way, therefore we conclude that the fencing effect was similar in both the dry and wet blocks.

Objective 2

- Measure the effect of deer herbivory on willow height growth and catkin production in a streamside herbivore-exclosure experiment.

Deer herbivory on channel bar and stream bank willows can affect hydrologic, and sediment deposition and erosive forces that influence riparian ecosystems. Willow roots are effective at holding soil in place during erosive flow events (Simon, Pollen & Langendoen 2006). In addition, their woody stems provide roughness that slows water flows and can enhance sediment deposition and accretion (Järvelä 2002, 2004). Therefore, willow presence along gravel bars and stream banks of the Tuolumne River has the potential to reduce meadow sediment erosion by preventing bank collapse. Willows may also facilitate the building of new meadow surfaces by accelerating sediment deposition and retention on gravel bars. The effectiveness of these geomorphic functions depends in part on the stature of the willows, with taller willows providing more roughness and flow resistance. In addition to directly removing willow stems, deer browsing can significantly affect production of seed, which will only develop on two-year-old stems (Kay & Chadde 1992; Case & Kauffman 1997; Peinetti *et al.* 2001).

We identified 3 stream reaches along the Tuolumne River within Tuolumne Meadows where abundant willow (*Salix planifolia*) were growing on both gravel bars and streambanks. Two other species of willow (*S. eastwoodii* and *S. lemonii*) are also common along the stream reaches, but neither is as abundant on both bars and banks as *S. planifolia*. Therefore, our study design targeted stands of *S. planifolia*, and all data were collected on this single species. All use of the term willow from here forward refers to the single species *Salix planifolia.* At one gravel bar and one bank within each reach we selected a continuous 7 m x 14 m rectangular area of approximately homogenous topography and willow cover. The rectangular area was divided in half to make two adjacent 7 m x 7 m square plots, and treatment (deer fencing) or control status was assigned randomly at each of the six reach/landform combinations (3 reaches, each with 1 bar and 1 bank). In each plot, six parallel 5m-long transects were established, 1 m apart, and leaving a 1m buffer from the plot edge. The end points of each transect were marked with rebar for relocation. Every 20 cm along each transect the vertical height-above-ground of the tallest willow stem within a 20 cm x 20 cm square, centered on the transect point, was measured. As with the herbivory plots in the meadow, the riparian plots were blocked according to hydrologic variability on the landscape. The 2 blocks for this study were plots on gravel bars and vegetated banks. Gravel bar plots were lower in elevation and we expected that they would have shallower water tables and received more frequent and intense disturbance from floods.

At the initiation of the experiment, in 2011, 30% of the transect locations within bar plots contained willows and their average maximum stem height was 12.6 cm; 63% of the stream bank plot transect locations had willows and their average maximum stem height was 31.8 cm. Over four study years, the willows in control plots (both bars and banks) lost an average height of 2.2 cm per year, and the fenced willows (bars and banks) protected from deer herbivory gained an average of 2.3 cm per

year, for a treatment effect of +4.5 cm per year (Figure 5). Over the 4-year duration experiment, gravel bar willows exposed to grazing lost 26% of their initial maximum stem height and lost 4% of their presence along transects, while streambank willows in grazed control plots lost 32% of their maximum stem height and lost 13% of their presence along the transects. Willows within the fenced treatments on bar plots gained 7.0 cm max. stem height and increased their transect presence by 10%. Fenced bank plots saw a willow height increase of 11.2 cm and a transect presence increase of 0.4%.

The fence treatment had a greater effect on willow height when considering just the bank plots (mean diff = 23 cm, p = 0.003, n = 3) or the entire experiment (mean diff = 16.7cm, p = 0.0007, n = 6), than when looking only the bar plots (mean diff = 10.3, p = 0.164, n = 3). Although the fenced willows on bars and banks gained about the same height, 7.0 and 11.2 cm respectively (with the greater bank height gain driven by one fast-growing plot), the height loss was less on bars (-3.4 cm) compared to banks (-11.8 cm) in the control plots (Figure 6).

Several factors may have led to a greater height decline on the banks: 1) the bar willows started out significantly shorter, at an average height of only 12.6 cm, so had less height to lose, 2) the bar willows were closer in elevation to the river water level, so may have had less water stress, allowing them to regrow more lost height than the higher-elevation bank willows, or 3) browsing pressure may be higher on the bank, resulting in greater height loss. The difference in treatment effect on bars vs. banks was quantified by a fairly strong interaction term in the ANOVA, p = 0.076. More than 3 replications of each block:treatment type, or a longer study period, would be necessary to be certain of the interaction.
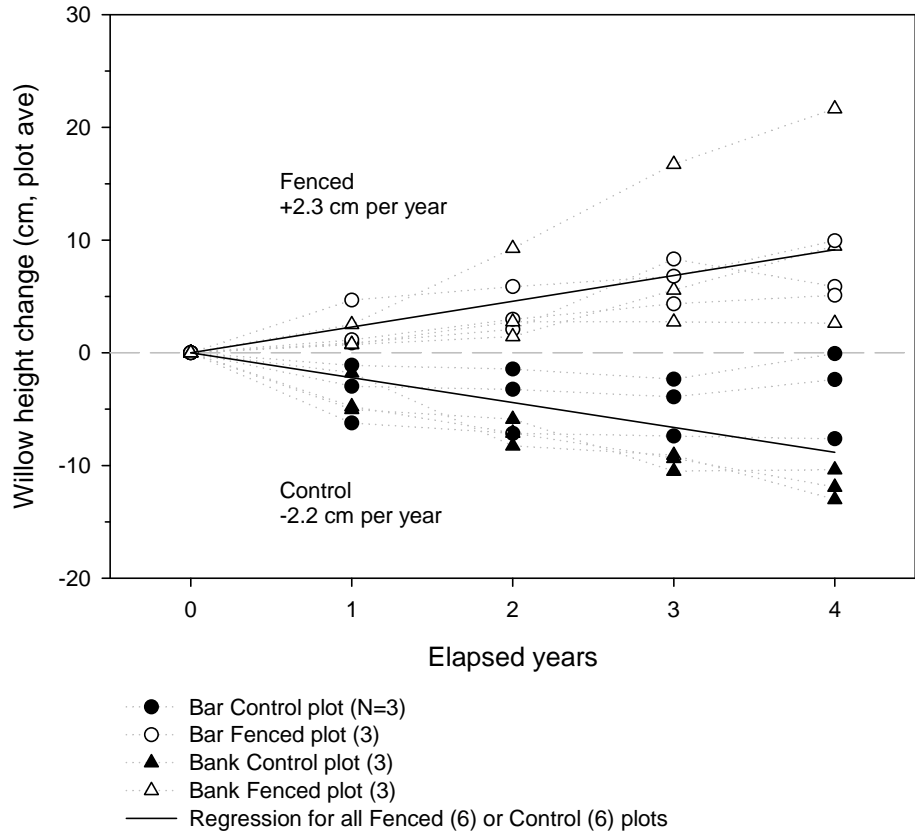
Figure 5. Change in willow height for control (black symbols) and fenced (white symbols) plots on gravel bars and banks of the Tuolumne River. Two regression lines are shown, one for all control plots, and one for fenced plots. Control plots lost and average of 2.6 cm of tallest-stem willow height per year, whereas willows in fenced plots gained an average of 2.3 cm per year.
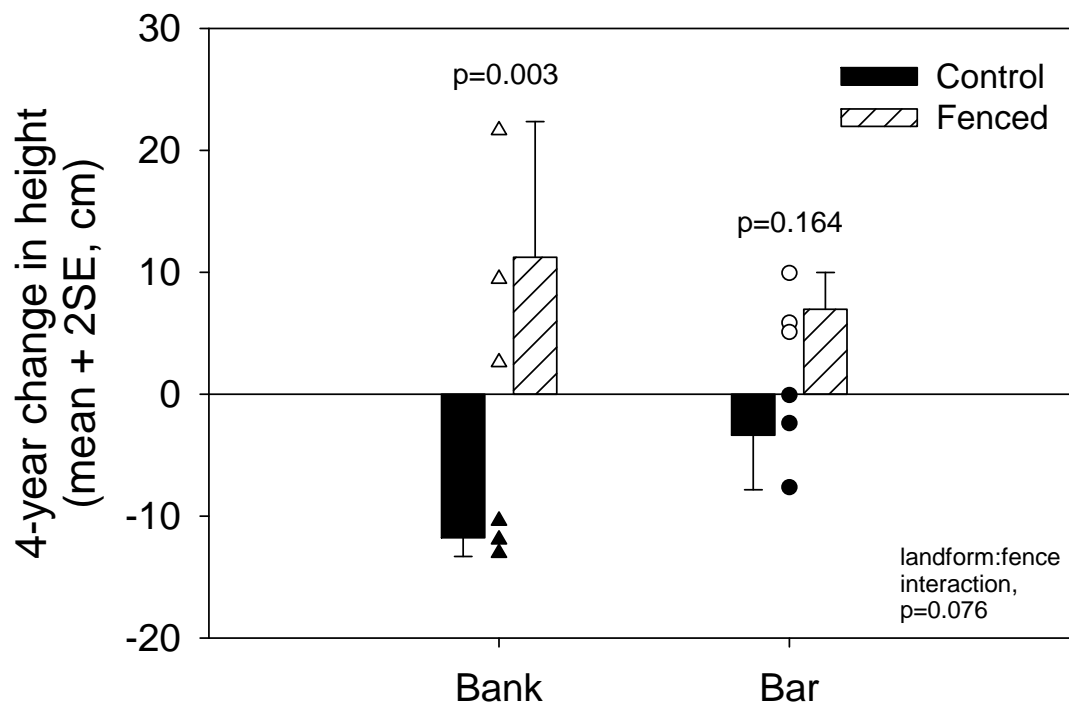
Figure 6. Greater height gains (fenced) and reductions (control) in the bank plots led to a significantly more pronounced treatment effect compared to bar plots. This interaction (different treatment effect in different landforms) was quantified by the fairly low p-value for the ANOVA interaction term.

Catkin production was measured in June 2014 (in the beginning of the third year of the experiment) by counting the total number catkin-producing willows within a plot, as proportion of the total number of willows. Although an imprecise measure of total seed production, this method quickly quantifies large discrepancies in potential reproductive output between treatment and control plots. Willow individuals were defined visually based on distinct clusters of radial branches emerging from a single rooted main stem. In addition, because willow flowering is a precocious, short-duration, synchronous event producing catkins on available second-year stems of reproductive plants, flowering plants are easily distinguished. However, *Salix planifolia* can reproduce clonally from rooting stems, so while most plants observed in the plots were clearly separate individuals, care was taken in dense stands to not overcount individuals. As a result, our plant count is most accurate for less dense plots where individuals were more apparent and is likely conservative for the most-dense plots. Because the fencing treatment increased size and density, our reported willow counts for these plots are probably conservative: the treatment effect on catkin production is likely to be even larger than we report here.

As with the wet/dry groups in the meadow transplant experiment, the bar/bank plots were set up as blocks so the effects of herbivory could be compared to the natural variation in environmental conditions. Bank plots had more willows overall, and more catkin-producing willow plants, than bar plots (Figure 7), but the differences between bar and bank were not statistically significant (ANOVA, p =

0.219). The interaction between the block (bar/bank) and the experimental treatment (control/fence) was investigated because the herbivory effect appeared more pronounced in the bank plots: control plots on the bank had very low numbers of catkin-producing willows even though they had more total willows than control plots on gravel bars. The result of the interaction term in the ANOVA, p = 0.076, suggests that willows may have different flowering responses to herbivory based on which landform they grow on (see above discussion of interaction in the height data for possible reasons). Because of this possible difference in herbivory impact between bar and bank plots, we included the block, treatment, and block:treatment interaction term in the ANOVA of the experimental effect. The average number of catkin-producing willows was 9.3 plants per control plot and 62.7 plants per fenced plot (ANOVA, p = 0.0005), after two full years of summer fencing. Because willows only produce catkins on stems from the previous year (Peinetti *et al.* 2001), the removal of current-year growth by deer browsing results in a 1-year lag response to browse protection. The count of catkin-producing willows was conducted in the spring of 2014, so catkins were produced from stems that grew in 2013. The first full year of browse protection in this experiment was 2012.
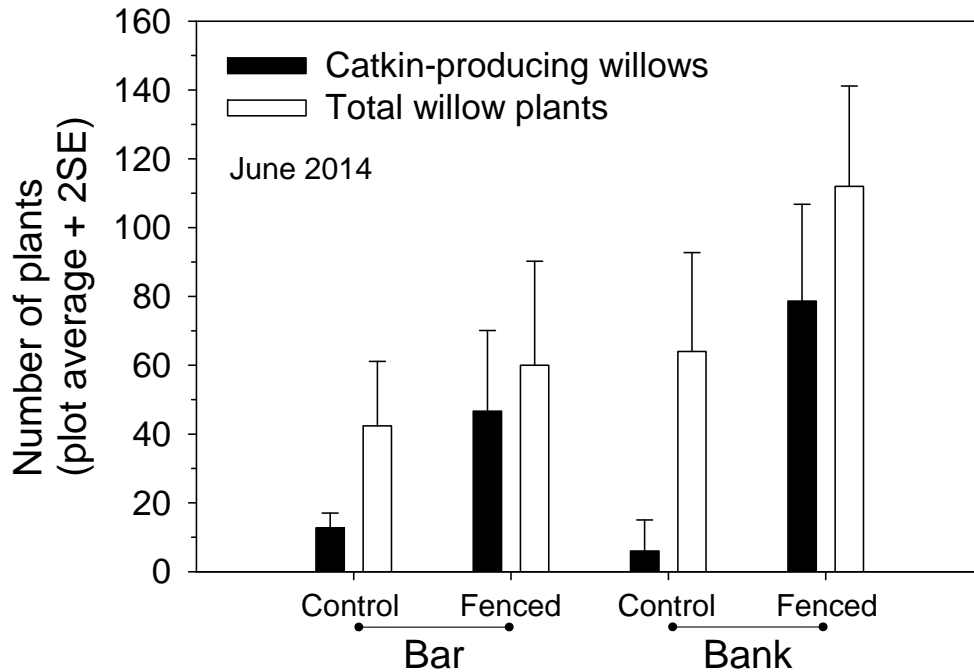

Figure 7. The number of catkin-producing willows, as compared to total willow plants, in control and fence treatment plots on both gravel bar and stream bank landforms. The fencing treatment had a much larger direct effect than the overall difference in landforms. However, as with the willow height response, the treatment and landform may have interacted, resulting in fewer catkin-willows in the bank/control and more in the bank/fenced plots as compared to their bar counterparts, despite similar patterns in total willows.

Objective 3

- Use in-situ CO_2 flux measurements to model the carbon balance of Tuolumne Meadows, including the effect of herbivory-exclosures, compared to two reference meadows.

Within the meadow herbivory exclosure field experiment we measured net ecosystem exchange (NEE) and ecosystem respiration (ER) of carbon dioxide (CO_2) using a clear plastic chamber equipped with an infrared gas analyzer (IRGA, PP Systems EGM-4). Measurements were made approximately monthly during the growing seasons of 2011-2015. Readings were taken in the 6-hour midday time span during which photosynthetically active radiation (PAR) was within 10% of its daily maximum. NEE readings were taken in full sunlight, and using shade cloth, at 70%, 40%, and 10% sunlight. ER was measured using an opaque cover (0% sunlight) to completely stop photosynthesis. ER occurs constantly and must be subtracted from NEE to arrive at a value for gross primary production (GPP). We measured soil temperature, air temperature, PAR, and soil moisture concurrently with each manual CO_2 flux reading, and also continuously (hourly) at several fixed locations using sensor/data-logger installations. Plant phenology was measured using a field time-lapse camera that took one photograph of a fixed area of meadow per day. The photos will be analyzed for "greenness", relative to a grey reference plate within the photo frame, and this will be used to create a phenology index (Richardson, Klosterman & Toomey 2013).

To create an annualized model of carbon flux in Tuolumne Meadows we will use modified published equations (Riutta *et al.* 2007) to model gross primary production (GPP) and ecosystem respiration (ER). The model for gross primary production will be a function of incoming solar photosynthetically active radiation (PAR), air temperature, and plant phenology. The model for ecosystem respiration will be a function of soil temperature, soil moisture, and plant phenology. The models will be calibrated using our field measurements of GPP, ER, and environmental parameters at the three different experimental settings: Tuolumne Meadows control plots, Tuolumne fenced plots, and reference meadow plots.

Our preliminary data from peak growing season (not annualized), indicates that the herbivore fencing treatment is increasing GPP (more negative GPP = more photosynthetic uptake of CO_2), and decreasing ER, shifting NEE towards emitting less CO_2 to the atmosphere. The reference meadows show even lower ER and more GPP, with an NEE that is near balance, possibly adding a small amount of carbon to the soil (Figure 8).
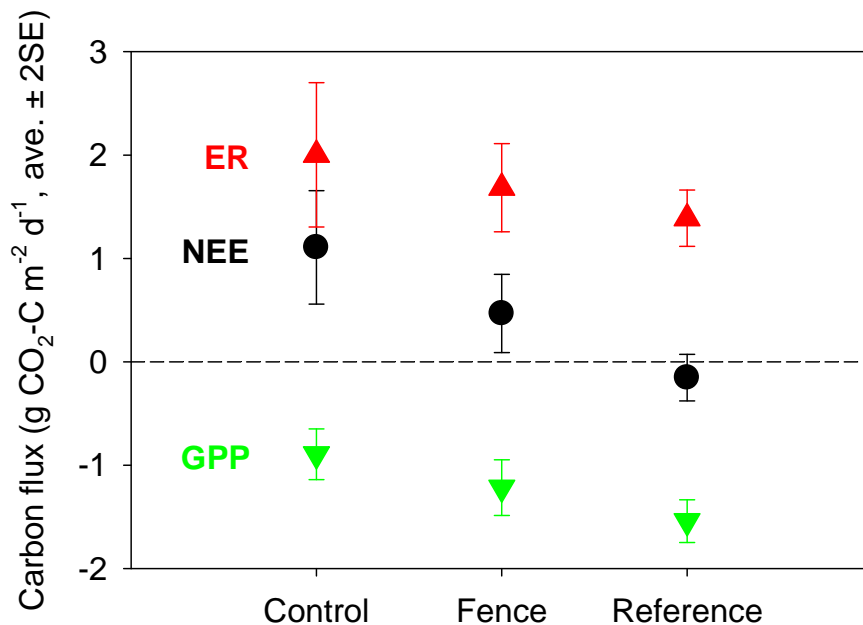
Figure 8. Ecosystem respiration (ER), net ecosystem exchange (NEE), and gross primary production (GPP) are shown for control and fenced (no herbivory) plots in Tuoloumne Meadows. Reference meadow data is shown on the right. Note that GPP is regarded as negative by convention, and more-negative GPP values indicate greater GPP.

Other researchers (Ankenbauer & Loheide II 2014) conducted a complimentary study at the same field sites investigating the influence of soil organic matter on water holding capacity and plant-available-water (PAW) through the growing season. Preliminary results from that study suggest PAW responds non-linearly to reductions in soil organic matter, with an accelerated loss of PAW at soil organic matter levels of about 8% or lower. Soil organic matter content, by mass, in Tuolumne Meadows ranges widely, from about 3 – 40% (Cooper *et al.* 2006). Almost half (30 out of 72) of the soil samples in Tuolumne were at or below 8% soil organic matter, with another 17 samples containing between 8% and 10% (Figure 9). If these preliminary results are confirmed or reinforced through further analyses, this indicates that much of Tuolumne Meadows is losing soil organic matter within a critical range where small loses cause relatively large declines in plant available water.
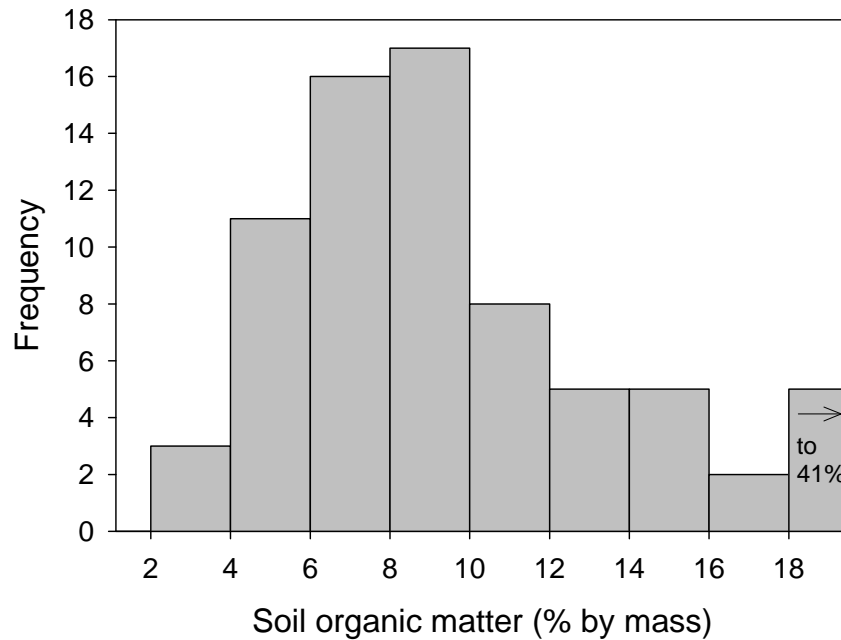
Figure 9. Histogram of the distribution of soil organic matter data in Tuolumne Meadows (from Cooper et al. 2006).

Conclusions and next steps

Based on our ecological experiments, herbivory by native mammals is reducing the survival of perennial sedges and causing a greater net loss of carbon from the Tuolumne Meadows ecosystem than ungrazed test plots and reference areas. In addition, deer herbivory on streamside willows is reducing their height and seed output. Although these animals are native to Tuolumne Meadows, the plant community that they consume does not appear to be the one that formed the soil organic matter levels present throughout the meadow. Three possible explanations arise to explain the fact that the meadow soil is decomposing faster than the current plant community can form organic matter: 1) There are far more native herbivores present in the meadow than there were historically, and they are over-grazing the meadow, 2) A significant physical/environmental change has occurred that has shifted the conditions in the meadow from one that supports sedges to one that supports the current community of annuals and broadleaf plants, and/or 3) Intense sheep grazing from ~1850-1900 decimated the native plant community, and unchanged levels of native herbivory are suppressing the recovery of perennial sedges.

Although there have been studies demonstrating the "human shield" effect whereby prey species congregate near areas of human use (such as Tuolumne Meadows in the summer), this effect requires significant predator pressure (Berger 2007). Many of the largest predators are absent from the modern Sierra Nevada: wolves, grizzly bears, and wolverines have all been gone for about 100 years. The regional loss of large predators capable of killing deer may have resulted in an overall increase in deer abundance and herbivory. However, this doesn't explain why Tuolumne Meadows is so much more impacted than reference sites nearby, unless the greater number of deer congregated in certain

meadows and avoided others. Mountain lions, and to a lesser extent coyotes, are the only remaining predators within Yosemite that could kill deer. Many predators – coyotes, raptors, snakes, weasels – still hunt in the Sierra for small rodents like the ones in Tuolumne Meadows. So, although it is possible that the small rodent population in Tuolumne may be elevated due to a human shield effect, it is unlikely that the deer population is similarly affected due to relatively weak predation pressure.

There have been many local impacts to the physical environment of Tuolumne Meadows, as well as regional climate changes, which may have affected the plant community. The hypothesized shift in the Tuolumne Meadows plant community, from sedges to annuals and broadleaves, could have been caused by a hydrologic change that led to drier soil conditions. Since the nearby reference meadows in this and other studies have significantly greater sedge cover and less bare ground (Ballenger & Acree 2009), it is unlikely that the different local plant community of Tuolumne Meadows is a result of broad regional climate change that would have similarly affected nearby meadows. Because the plant community change appears to be a local effect within Tuolumne Meadows, local hydrologic impacts are more plausible explanations.

The effect of one of the most prominent impacts, the Tioga Pass Road, was investigated in 2006 (Cooper *et al.* 2006). Other than small surface water effects around culverts, the road was found to not be significantly affecting the movement of groundwater to the meadow. The main hydrologic feature of the meadow is the Tuolumne River, and changes to channel geometry and flow depth could have significant effects on water levels within the broader meadow (Loheide II & Lundquist 2009; Lowry *et al.* 2010). There have been at least two major anthropogenic impacts to the Tuolumne River channel within the meadow that could have resulting in lower water levels: direct dredging and lowering of the channel bed for road base, and sheep grazing and trampling causing bank collapse and channel widening. In 1933 "gravel for fill work and masonry construction was taken from the Tuolumne River with a dragline" (Quin 1991a) and a pool "300' square and 20' deep" replaced a former sand bar (Quin 1991b). Again in 1958, during the reconstruction of the road "great gobs of sand were being shoveled out of the Tuolumne River bed for road construction" (O'Neill 1984, p. 139).

There are no written records or studies of the effects of 19th century sheep grazing on the riparian vegetation and stream banks of the Tuolumne River (other than general statements by John Muir comparing sheep to locusts), but photographs from 1899 give an indication of the size of the Tuolumne herds (Figure 10) and show them denuding and trampling the river banks (Figure 11). The photographer, Charles E. Townsend, wrote an article describing his trip and describes Tuolumne Meadows:

"We were much surprised upon coming into the meadows to find them pasturing thousands of sheep." … "during the summer [Yosemite] is usually vigorously patrolled by the United States soldiery." … "The absence of the soldiers, on account of the war, encouraged the more adventurous sheepmen"… "Owing to the presence of the sheep, we found pasturage spare, --for ordinarily the meadows are carpeted knee-deep with flowers and grass". (Townsend 1899).

Townsend also discusses "bartering with the sheep-herders for some fresh mutton" after their exhausting climb up Mt. Lyell, so it is likely that he took the photos of the shepherds and their flocks in June 1899, and it is apparent from his article that this was his first trip to Tuolumne Meadows.

Figure 10. Unattributed photograph (probably taken by Charles E. Townsend) showing a herd of at least several hundred sheep in Tuolumne Meadows, labelled 1898 (but likely taken in June 1899). Image is from a scanned print housed at the Yosemite National Park Archives. The original negative number is YM-12, 757.

Figure 11. Photograph taken by Charles E. Townsend of shepherds and their sheep, in the background, on the banks of the Tuolumne River in Tuolumne Meadows. Willow shrubs are visible in the left foreground and background. Image is from a scanned print, labelled 1898, but probably taken in June 1899, housed at the Yosemite National Park Archives. The original negative number is RL-17, 087.

In sloping meadows across the Sierra Nevada, the effects of poorly regulated sheep and cattle grazing caused such an intense and novel impact that large erosion gullies formed where there had been only sediment accumulation for millennia (Wood 1975; Ratliff 1985; Cooper & Wolf 2006). Once initiated, gullies become self-enlarging by capturing more flow, which causes greater erosion. As gullies capture more water and it flows rapidly off-site, the adjacent meadow water table drops, drying out the soil surface and causing a shift in the plant community. Wetland sedges that prevented erosion for thousands of years, and were decimated by grazing, cannot become reestablished in dry conditions.

Therefore, the initiation of an erosion gully represents a threshold-crossing impact where degradation will continue to worsen in a series of feedbacks. The vegetation of flat-lying areas such as Tuolumne Meadows was similarly decimated. However, having almost no relief, there was no opportunity for soil erosion to form gullies. Instead, native grazing has suppressed the recovery of slow-spreading clonal sedges while a slower form of soil loss and hydrologic change has been occurring. The continued net loss of soil organic matter, and with it water-holding and nutrient-exchange capacity, is moving the entire ecosystem towards a drier condition. There may be a threshold beyond which wetland plants could no longer become established across much of Tuolumne Meadows.

Starting in 2016, Yosemite National Park and Colorado State University will embark on a 4-year pilot restoration project to determine if large areas of the wetland sedge, Carex scopulorum, can become established. A total of 9 acres of the meadow will be planted with seedlings, protected from herbivory, and monitored for greenhouse gas sequestration. The goal is to restore a native net carbon-storing plant community large enough to be resilient to herbivory.

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