Ecosystem Function, Degradation, and Restoration in Wetlands of the Sierra Nevada, California

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Abstract

The wetlands of the Sierra Nevada were formed and are maintained by a feedback between soil, plant, and hydrologic processes. Primary production of plants builds soil organic matter and plant roots bind soil, preventing erosion during flooding. In turn, soil organic matter retains water and nutrients that support plant growth, while the hydrologic regime regulates soil organic matter decomposition, plant community makeup, and plant production. The relative stability of these interacting processes has built thick meadow soils over the past several thousand years. However, modern human impacts such as livestock grazing and water extraction have decoupled the interacting processes. Removal of plants by grazers exposes soil to water erosion and reduces production, the source of soil organic matter. Erosion gully formation and direct water extraction lower the wetland water table, speeding soil organic matter decomposition, altering plant community composition, and reducing production. Gully formation and loss of soil organic matter occur rapidly but are extremely slow to reverse by natural processes alone. Wetlands that have experienced these impacts enter alternative stable states that will not quickly return to their original configurations. In these cases, ecological restoration is necessary to repair human impacts and reestablish the stabilizing feedback of soil, plant, and hydrologic processes.

This dissertation is composed of five chapters that explore wetland ecosystem function and restoration in the Sierra Nevada.

Chapter 1 is an overview of Sierra Nevada fens: groundwater-supported peat-accumulating wetlands. Underlying geology and topography exert strong control over the distribution and vegetation of these ecosystems. Groundwater chemistry is largely determined by watershed rock type and is a significant determinant of plant species composition. Wide-ranging values of pH (4.28–8.00) and dissolved cation concentrations (1.6–62.0 mg/L) span the categories of transitional poor–rich to extremely rich fens. Species richness is primarily (and negatively) correlated with altitude. Peat thickness

(15–253 cm) is constrained in smaller catchments and on steeper slopes, and is positively correlated with soil organic matter content (16–92 %).

Chapter 2 describes a field exclosure experiment testing the effects of native deer and rodent herbivory on the meadow and streamside willow vegetation of Tuolumne Meadows. Streamside willows protected from deer gained a net average 16.7 ± 7.0 cm height, 13.8 ± 11.4 % shoot frequency, and 49.2 % (20.5 – 66.9%) flowering plants, compared to control plots exposed to herbivory. Meadow plots protected from herbivory by fencing grew an additional 106 ± 66 g m^{-2} of aboveground biomass compared to control plots. Bare ground in fenced plots dropped by 3.5 ± 3.1% areal cover, and survival of two species of sedges and lodgepole pine are significantly higher in fenced plots. Sedge cover is low and bare ground is high in Tuolumne Meadows compared with similar nearby meadows, likely due to the large size and accessibility of the meadow to shepherds in the late 1800s. Native herbivory is limiting sedge survival and maintaining a high proportion of bare ground.

Chapter 3 looks at the effect of the meadow herbivory exclosure on carbon dioxide fluxes into and out of the Tuolumne Meadows ecosystem. Models for gross primary production (GPP) and ecosystem respiration (ER) were built using hourly measurements of environmental variables to fill in gaps between direct field measurements of GPP and ER carbon fluxes. The modeled summer carbon flux shows ER flux approximately double that of GPP, resulting in net ecosystem exchange (NEE) ranging from 469 to 666 g CO_2-C m^{-2} released from the meadow to the atmosphere. NEE was significantly higher in wet plots compared to dry plots. In the summer of 2014 the herbivore fencing treatment reduced NEE efflux to the air in the wet plots by 92.8 ± 58.9 g CO_2-C m^{-2} while the fencing effect on NEE was not significant in the dry plots.

Chapter 4 examines the effects of groundwater pumping on the sustainability of a mountain wetland complex in Yosemite National Park. Daily head pressure and water table declines observed at

sampling locations within 100 m of the pumping well were strongly correlated with the timing and duration of pumping. Predictive scenarios developed using a groundwater model showed that even in a dry year like 2004, distinct increases in fen water table elevation can be achieved with reductions in pumping. Site vegetation composition indicated that maintenance of a high water table during summers following low snowpack years had a more significant influence on vegetation composition than depth of water table in wet years or peat thickness.

Chapter 5 describes a field investigation of the effects of soil compaction on wetland plant growth, a field experiment to determine how the addition of wood chips affects soil compaction, and a greenhouse experiment to measure how phenolic compounds from wood chips affect wetland plant growth. Field soil compaction (MPa) was significantly negatively correlated with both wetland plant height and width, resulting in -9.8 and -11.9 cm MPa^{-1}, respectively. Experimentally amending soil reduced compaction by 0.174 MPa per 10%-by-volume addition of wood chips. In the greenhouse, a high concentration of phenolic compounds derived from bark (211 mg/L) significantly reduced wetland plant growth and triggered the production of polyphenol oxidase (PPO). However, phenol concentrations similar to field conditions (0 – 12 mg/L) did not affect plant growth or PPO production.

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Chapter 1 – Fens of the Sierra Nevada, California, USA: patterns of distribution and vegetation

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SUMMARY

A broad sample of 79 montane fens in the Sierra Nevada revealed that underlying geology and topography exert strong control over the distribution and vegetation of these ecosystems. Distinct granodiorite, metamorphic, volcanic, carbonate and serpentine bedrock geology resulted in very different water chemistry, which had significant effects on the plant species found at each site. Wide-ranging values of pH (4.28–8.00) and dissolved cation concentrations (1.6–62.0 mg L^{-1}) spanned the categories of transitional poor–rich to extremely rich fens. The vegetation of a pair of fens on carbonate bedrock and two floating mat fens was markedly different from vegetation recorded any other study sites. Once these outlier fens were removed from the analyses, the environmental variables that correlated most closely with the vegetation data were pH, altitude, presence of volcanic bedrock and fen slope. The measured environmental parameters explained 9.7 % of the variability in the vegetation data. Species richness was primarily (and negatively) correlated with altitude. Peat thickness (15–253 cm) was constrained in smaller catchments and on steeper slopes, and was positively correlated with soil organic matter content (16–92 %). Of the four typical fen landforms (bedrock contact, slope, spring mound and basin), sloping fens were the most common (63 % of the 79-fen sample).

KEY WORDS: bedrock, geomorphology, peatland, species richness, water chemistry

INTRODUCTION

Peatland formation requires a specific combination of physical and biological processes that most commonly occur in low-relief tropical and boreal regions of the world. Perennial soil saturation, very low mineral soil deposition and erosion rates, and net storage of soil carbon resulting from plant production must coexist for centuries or millennia to form peat soils (Moore & Bellamy 1974).

Mountain ranges are highly variable landscapes created by glaciers, hillslope erosional processes and geological forces such as faulting and uplift. Uplift and erosion expose highly variable bedrock types so that water (surface and groundwater) flowing through mountain systems acquires different chemical characteristics depending on the local lithology. Water chemistry profoundly influences peatland vegetation (Cooper & Andrus 1994, Lemly & Cooper 2011). Steep mountain topography also promotes drainage and, thus, rapid drying of soils, high soil erosion rates on slopes and high mineral sediment deposition rates in valleys and basins (Patterson & Cooper 2007). Therefore, suitable conditions for peatland formation are of limited occurrence in mountain landscapes (Cooper *et al.* 2012). For example, peatlands occupy 1.0 % of the land surface area in the Beartooth Mountains of WY, USA (Heidel & Rodemaker 2008), 1.0 % of the San Juan Mountains in Colorado, USA (Chimner *et al.* 2010), 2.5 % of the Snowy Mountains in New South Wales, Australia (Hope *et al.* 2012) and 0.4 % of the uplands of Galicia, Spain (Pontevedra-Pombal *et al.* 2006). Preliminary measurements in the Sierra Nevada, from Sequoia and Kings Canyon National Parks (California, USA) indicate that peatlands cover approximately 0.2 % of the land area (Hopkinson *et al.* 2013).

The distinctive characteristics of mountains include large altitudinal and climatic ranges, complex migratory pathways for biota, large floras with diverse biogeographical connections and histories (Weber 2003, Cooper *et al.* 2012), and high species and community-level biodiversity (Bedford & Godwin 2003). As a small areal component of the landscape, mountain peatlands support a

disproportionate diversity of plant species (Jones 2011, Sekulová *et al.* 2013) and provide important habitat for insects (Holmquist *et al.* 2011) and many other organisms (Bedford & Godwin 2003). In addition to their importance for flora and fauna, many mountain peatlands have accumulated organic carbon for millennia (Wood 1975), allowing prehistoric climate and vegetation to be reconstructed (Anderson & Smith 1994). While the quantity of stored carbon in some mountain peatlands is minor with respect to the global carbon budget, the preserved record of climate and vegetation over the past several thousand years is invaluable. Because of their relative scarcity, their value for biodiversity and wildlife, and their importance as records of past ecological conditions, mountain peatlands have become priority research and conservation targets for land management organizations around the world (Bragg *et al.* 2003, Michael Succow Foundation 2014, Wetlands International 2014) and in the western USA (Chadde *et al.* 1998, Sikes *et al.* 2013). Mountain peatlands exist within a highly variable physical template, making them diverse and challenging to understand. Specifically, it is unclear what physical factors control mountain peatland distribution and plant biodiversity.

The Sierra Nevada of California is one of the largest and most continuous high mountain ranges in North America. A few mountain vistas (e.g. Yosemite Valley) are world-famous icons and the majestic conifer forest vegetation has been well studied (Ratliff 1985, Barbour 1988, Fites-Kaufman *et al.* 2007). However, relatively little is known about the diversity of wetlands in the Sierra Nevada. One of the first peatlands described in the western USA is in California (Rigg 1933, Baker 1972, Erman *et al.* 1977), but there have been relatively few studies of peatlands since then (Beguin & Major 1975, Burke 1991, Bartolome *et al.* 1990, Allen-Diaz 1991).

The goal of this study is to characterize the flora, vegetation, soils, geochemistry, physical setting and landforms of representative peatlands in the Sierra Nevada, southern Cascade Range and nearby Klamath Mountains in California, focusing primarily on the Sierra Nevada. We specifically addressed the following questions: (1) are peatlands present in all regions of the study area? (2) are the

abundance, distribution and development of peatlands influenced by landscape-scale factors? and (3) how do physical site characteristics influence peatland vegetation and floristic biodiversity?

STUDY AREA

The Sierra Nevada mountain range runs north–south for 640 km in the east of the state of California, USA. The highest peak is Mount Whitney (4,421 m). To the north and north-west are the Cascade Range and the Klamath Mountains, which are regarded by earth scientists as contiguous but distinct geomorphic provinces (Figure 1). Our goal was to sample peatlands in each National Forest (NF) throughout the Sierra Nevada, with limited sampling in the National Parks (NP) and southern parts of the Cascade Range and Klamath Mountains, to cover a broad range of mountain peatland occurrences throughout California.

The dominant bedrock type varies across this large study area. Granodiorite (a quartz-rich crystalline intrusive rock similar to granite) dominates the central and southern Sierra Nevada, while volcanic rocks form the Cascade Range. Metamorphic belts are exposed in the northern Sierra Nevada and on its west- and east-facing slopes, as well as in the Klamath Mountains. Very localized exposures of carbonate metasedimentary rocks such as marble, and ultramafic metavolcanics like serpentine, occur within the metamorphic belts.

There is a strong north–south precipitation gradient (see Figure 1), with annual precipitation ranging from > 200 cm in the north and west to < 65 cm in the south and east. The climate of the Sierra Nevada is characterized by wet winters with abundant snowfall above approximately 1,600 m altitude (snowfall is 70–90 % of annual precipitation) and dry summers with only 10–30 % of annual precipitation falling between June and October (Fites-Kaufman *et al.* 2007). Therefore, peatlands must be kept saturated through the four-month growing season (July–October) by groundwater discharge with minor supplementation by direct rainfall. During the spring of each year, the melting snowpack recharges the

aquifers that supply the groundwater discharge in summer (Cooper *et al.* 2015). Because all peatlands in the Sierra Nevada must rely primarily on groundwater to remain saturated they are classified as minerotrophic peatlands, or fens (Rydin & Jeglum 2013), as opposed to ombrotrophic (rain-supported) bogs.

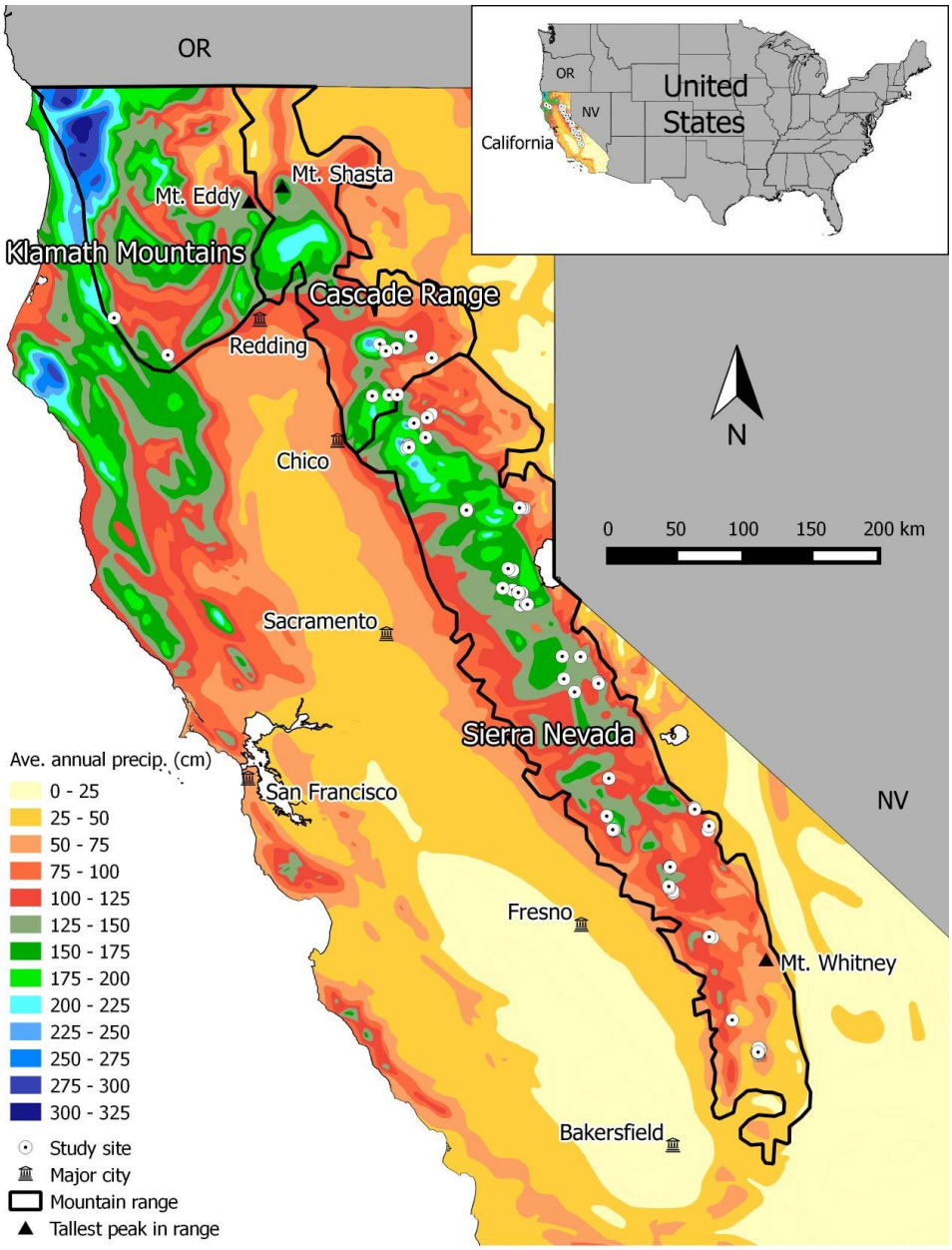

Figure 1. Locations of the 79 study fens in California. Color scale illustrates average annual precipitation (cm). The Klamath Mountains, Cascade Range, and Sierra Nevada geomorphic provinces, and each of their highest peaks, are indicated.

METHODS

Site visits

Potential fens were initially identified using natural color air photos and topographic maps. Sites for field visits were chosen to represent the range of altitudes and habitats occurring within the mountain ranges, and for ease of accessibility. A total of 79 fens were visited: 2 in the Klamath Mountains (Shasta-Trinity NF), 11 in the Cascade Range (Lassen NF and Lassen NP), and 66 in the Sierra Nevada (Plumas, Tahoe, Eldorado, Stanislaus, Inyo, Sierra, and Sequoia National Forests, and Yosemite NP (Appendix, Table 1). We delineated each fen's catchment area and determined its altitude, predominant catchment bedrock type (granodiorite, metamorphic, volcanic, carbonate or serpentine), and average annual precipitation using topographic maps and geospatial data layers (State of California 2015) in a GIS environment (QGIS Development Team 2014). All 79 sites were visited between 9 July and 21 September 2003. During the field visits we assigned each fen to a landform type, observed aspect azimuth using a compass, and measured the fen surface slope using a clinometer.

Water

In the field we measured the pH of groundwater that filled a shallow hand-dug open well. The hole was bailed and allowed to refill several times to ensure an uncontaminated sample of groundwater. Sampling groundwater (as opposed to surface water or water held in living moss tissue) has been found to yield the most consistent measurements of environmentally-controlled site pH in fens (Tahvanainen & Tuomaala 2003). We measured pH in situ using an Orion model 250A portable pH meter with combination electrode, which was calibrated daily with fresh pH standards. In each fen (not each vegetation relevé) we made one pH measurement and collected one water sample that was sealed immediately and frozen until analysis. The water samples were analyzed for electrical conductance and

concentrations of Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, HCO_3^{-}, CO_3^{2-}, Cl^{-}, SO_4^{2-}, hardness, alkalinity and total dissolved solids at the Colorado State University Soil and Water Testing Laboratory.

The field data collection was spread out across an entire growing season, and we expected that water table depth measurements would not be comparable between sites measured early versus late in the summer. However, water tables were within 20 cm of the surface at all sites when visited, even during the driest period of late summer 2003. Because small differences in hydrology can affect fen functioning, it must be noted that we did not make fine-scale hydrological measurements and therefore draw no conclusion about the effect of site hydrology on the study fens.

Soils

In each fen we analyzed soils in a hand-dug pit and measured the peat thickness by pushing a steel probe vertically through the soil until rock or mineral sediment was contacted. It has been demonstrated that probing is an effective method for measuring peat thickness (Parsekian *et al.* 2012, Chimner *et al.* 2014). We collected one soil sample from 30–40 cm depth and determined percent organic matter content using loss on ignition (LOI) (Schulte & Hopkins 1996). For classifying soils as organic we used the established estimate that approximately half of the soil organic matter is organic carbon (Ball 1964, Chimner *et al.* 2014). Although we did not directly measure clay content, all soils were hand-tested in the field and none formed ribbons that would indicate clay content greater than 20 %. Therefore, we conservatively assumed that all soils contained 20 % clay. At this clay content soils require 14 % (12 + [20 * 0.1]) organic carbon, or 28 % organic matter as determined by LOI, to be considered organic soils according to the US Department of Agriculture definition of organic soils (USDA 1999). While this definition may suffice for soil taxonomic purposes, there are no scientific criteria or thresholds for organic content or organic horizon thickness that are known to influence the functioning of a site as a peatland (Driver 2010).

Vegetation

We sampled 1–7 homogenous relevés within each fen, recording a total of 290 relevés within the 79 fens. Relevés were 4–20 m^2 in area, depending upon the size of the largest plants, the smallest relevés being used for moss-dominated stands and the largest for those with shrubs and stunted trees (Mueller-Dombois & Ellenberg 1974). Within each relevé a complete list of the plant species present was made, and the percent canopy cover of each species was visually estimated by the same experienced observer.

Nomenclature for vascular plants is consistent with the Jepson Manual: Vascular Plants of California (Baldwin *et al.* 2012), and for non-vascular plants (mosses) with the Jepson California Moss eFlora (Wilson 2015) and the Flora of North America (Flora of North America Editorial Committee 2015).

Data analysis

The Shannon diversity index (Hill 1973) was calculated for each vegetation relevé but, since diversity relies on relative abundances, we could not scale up the data to calculate fen-level diversity because the percent cover data are only relevant within each relevé. Instead, we calculated fen-level species richness, which is a simple count of the total number of species present within all the relevés at a single fen. The logarithmic relationship between fen-level species richness and fen area was evaluated to determine the degree to which the species-area relationship contributes to observed species richness (Gleason 1922).

Statistical differences in water chemistry, peat thickness and species richness between fens with different categories of bedrock geology and landforms were determined using ANOVA with Tukey's HSD multiple comparison test (R Core Team 2014).

We evaluated the ability of 13 continuous environmental variables to predict peat thickness and species richness using multi-model selection. When evaluating model fit, all possible combinations of

explanatory environmental variables were ranked by AICc (Akaike's Information Criterion, corrected for small sample size) using the glmulti and AICcmodavg packages in R (R Core Team 2014). All models within two points of the minimum AICc model were exhaustively cross-validated (using the leave-one-out technique) to determine their predictive power using mean-squared-error (cv.glm routine in the "boot" R package).

Variables were then systematically removed and models cross-validated to evaluate whether simpler models would provide equivalent predictive error. For estimating peat thickness or species richness based on the measured environmental parameters, the model with the smallest number of parameters that provided equivalent predictive error to the minimum AICc model was identified as the model of choice. This was because the datasets for some fens were not complete and, under these circumstances, inclusion of more parameters in the models could influence the effective sample size by excluding the fens with missing data. Therefore, we experimented with removing parameters from the minimum AICc model to maximize sample size while including the most important predictive variables.

We used Detrended Correspondence Analysis (DCA), which is an indirect ordination technique, to identify the overall structure of the floristic gradients within the 290-relevé vegetation data set. The structure in the vegetation data was analyzed for correlations with environmental variables in a canonical correspondence analysis (CCA). Because the environmental data were collected at the fen level, each relevé within a fen was associated with the same set of environmental variables. To determine whether the observed CCA correlations between species and environmental data could have arisen by chance, we conducted Monte Carlo simulations. The environmental data were randomly reassigned to fens, the CCA was re-run 100 times, and correlations and eigenvalues were calculated for each randomized run. The observed values were compared with the Monte Carlo output to determine the probability that the observed correlation between the environmental matrix and the vegetation

data could have arisen by chance, reported as a p-value. The program PC-Ord, version 4.37, was used to perform all ordination analyses (McCune & Mefford 1999).

The 13 continuous environmental variables used to model peat thickness were: altitude, fen slope, fen aspect azimuth (sine transformed: sin(azm.+ 90) + 1), soil organic matter, fen area, catchment area, average annual precipitation, soil-water pH, soil-water electrical conductivity (EC), calcium concentration (Ca), magnesium concentration (Mg), north latitude, and species richness.

These same 13 variables (with species richness substituted by peat thickness) were used to model species richness and to generate the CCA ordination. In addition, the categorical variables of catchment bedrock geology (five categories) and geomorphic landform (four categories) were converted to binary variables for use in the CCA. The five binary geology variables created were: granodiorite, metamorphic, volcanic, serpentine and carbonate. The four binary landform variables created were: (bedrock) contact, slope, (spring) mound and basin (see Results). Each fen was assigned to one geological type and one landform type, and values of unity were assigned to the corresponding binary variables (e.g. for a sloping fen in a granodiorite catchment: slope = 1, all other landform variables = 0; granodiorite = 1, all other geology variables = 0).

RESULTS

Site characteristics

Fens were found throughout the Sierra Nevada, the southern Cascade Range and southern Klamath Mountains (Figure 1). The areas of the 79 fens we visited ranged from 45 m^2 to 200,000 m^2 (median 1,713 m^2) and their altitudes ranged from 1,207 m to 3,233 m a.s.l (median 2,094 m). Fens occurred at lower altitudes in the Cascade Range, Klamath Mountains and northern Sierra Nevada than in the southern Sierra Nevada, which is the highest-altitude section of the range with relatively low annual precipitation (see Appendix, Table 1).

These fens had formed in four major geomorphic settings, namely: at geological bedrock contacts, on slopes, as spring mounds, and in basins (Figure 2). Multiple landform types can occur within a single fen site. For example, a sloping fen may be adjacent to and connected with a basin fen, and spring mounds can occur at the heads of sloping fens or within larger basin fens. When multiple landform types occurred within a single fen complex, we observed which mechanism was most important for maintaining the hydrological regime of the fen and classified it accordingly.

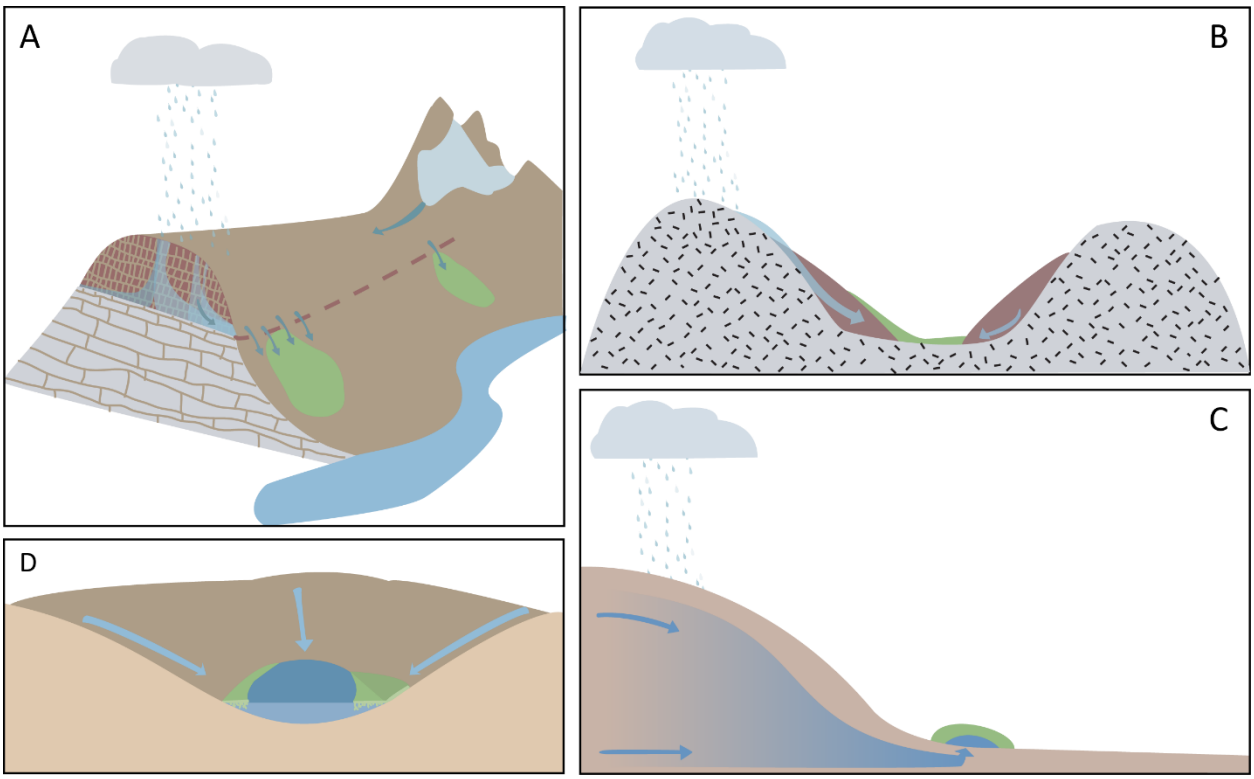

Figure 2. The four major landform types identified amongst the Sierra Nevada fens. A = bedrock contact (fed by seepage from the contact zone between an aquifer and an underlying layer of less permeable rock), B = slope, C = spring mound (formed at a groundwater discharge site), and D = basin. The arrows indicate directions of groundwater and/or surface water flow.

At bedrock contacts, more permeable rock (an aquifer) overlies less permeable rock, forcing water out of the ground along the contact zone. This often occurs where one lava flow lies on top of another, and the lower flow's upper surface has been sealed by contact with the later flow. Snowmelt water moves laterally on the impermeable surface created by the discontinuity and discharges on

hillslopes where the contact is exposed. These spring complexes may be large and produce perennial flows of water, forming fens on steep slopes that nonetheless have thick peat bodies and well-developed fen vegetation. Eleven (14 %) of the 79 studied fens were classified as bedrock contact fens.

Fifty (63 %) of the 79 study fens had formed on hillslopes where groundwater discharges to the surface from glacial moraines, talus, alluvium and hillslope-exposed bedrock fractures. Slopes range from gentle to steep (Figure 3), and although small pools may occur, large areas of open water are never present. Sloping fens require constant inflow of groundwater to maintain soil saturation because downhill drainage is relatively rapid.

Figure 3. Four fens in the study region: (top left) gently sloping fen dominated by the spike-sedge Eleocharis quinqueflora; (top right) fen with high cover of Pinus contorta and shrubs; (bottom left) steeply sloping fen with the pitcher plant Darlingtonia californica in the foreground; (bottom right) Convict Creek basin, which is the only region with limestone/marble in the Sierra Nevada, showing fen dominated by the sedge Kobresia myosuroides.

Spring mounds form at localized points of groundwater discharge that can often support only small fens. Many spring mound fens are only tens of meters in diameter, but they are morphologically and ecologically distinct. Spring mound fens may occur at locations with strong upward groundwater discharge within a sloping fen complex. Five (6 %) of the 79 fens were characterized as spring mounds with upwelling groundwater.

The remaining 13 (16 %) of the 79 fens were in basins. Basin fens probably originated as lakes or ponds that infilled with partially decomposed plant remains. They are typically flat and may enclose ponds with floating mats of peat-forming vegetation that rise and fall with the water level, thus maintaining contact between the peat and water surfaces. This fen type is widespread and includes the largest fens in the Sierra Nevada region. *Sphagnum teres* and *Sphagnum subsecundum* are common species, along with the vascular plants *Carex limosa*, *Menyanthes trifoliata*, *Carex lasiocarpa* and *Dulichium arundinaceum*.

Water chemistry

The 79 study fens spanned a broad range of water chemistry. The multi-year, multi-season, volume-adjusted field-measured pH of precipitation across a series of measurement locations spanning the north–south range of the Sierra Nevada is 5.26 (National Atmospheric Deposition Program 2014). Only the five most acidic of the 79 study fens had pH values below 5.26, indicating the predominance of groundwater processes that raise the pH of rainwater as it moves through an aquifer. Using the well-established poor–rich gradient terminology (Sjörs 1950, Cooper & Andrus 1994, Lemly & Cooper 2011), the fens in the study area ranged from transitional (intermediate between poor and rich) to extremely rich, based on their pH and cation concentrations (Figure 4). Of the 27 transitional fens, four had metamorphic bedrock, one volcanic bedrock, and 22 were in catchments dominated by granodiorite. The lowest pH value (4.3) was found at a floating mat in Willow Lake, within a volcanic bedrock

catchment. Low concentrations of dissolved ions in the Willow Lake sample, along with high *Sphagnum* cover, suggest that the acidity is generated by the moss rather than by geochemical weathering by-products. The highest pH values (7.5 and 8.0) were found at two fens in the Convict Creek basin (Figure 3), where carbonate rocks (primarily marble, and some calcareous hornfels) are exposed (Major & Bamberg 1963). High concentrations of calcium and carbonate in water at the Convict Creek sites confirms that the high pH is a result of geochemical weathering of the marble and hornfels bedrock.

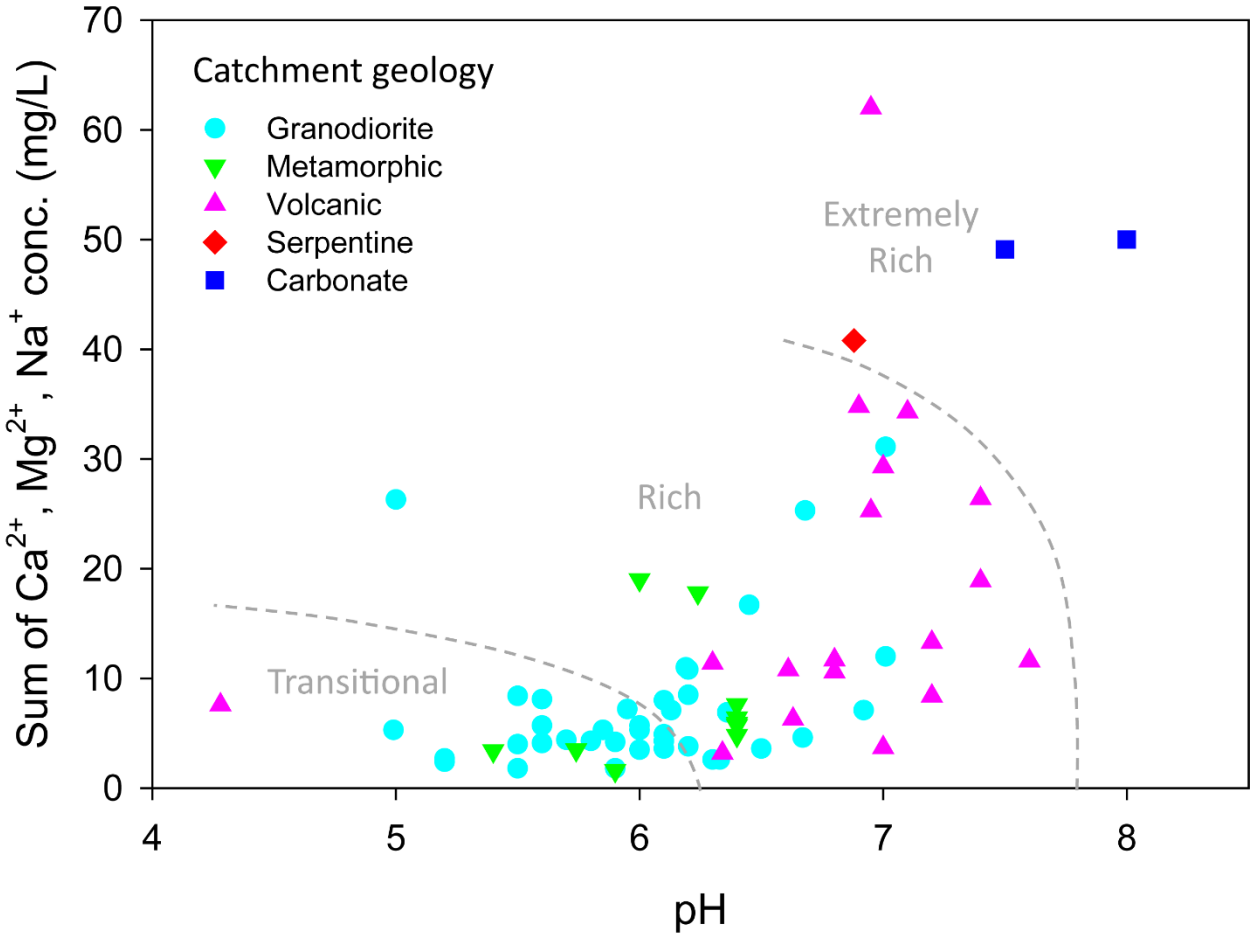

Figure 4. Classification of fens by pH and cation concentration. The bedrock geology of each fen's catchment is indicated by symbol shape and color.

Bedrock lithology strongly influenced fen water chemistry. Fens on granodiorite and undifferentiated metamorphic bedrock (metamorphics other than serpentine and carbonate marble) had significantly lower concentrations of calcium, lower EC, and were more acidic than fens on other

rock types (Figure 5). The two carbonate fens had significantly higher EC and levels of calcium, and were more basic than other fens. The one serpentine fen we visited contained groundwater with markedly elevated levels of magnesium.

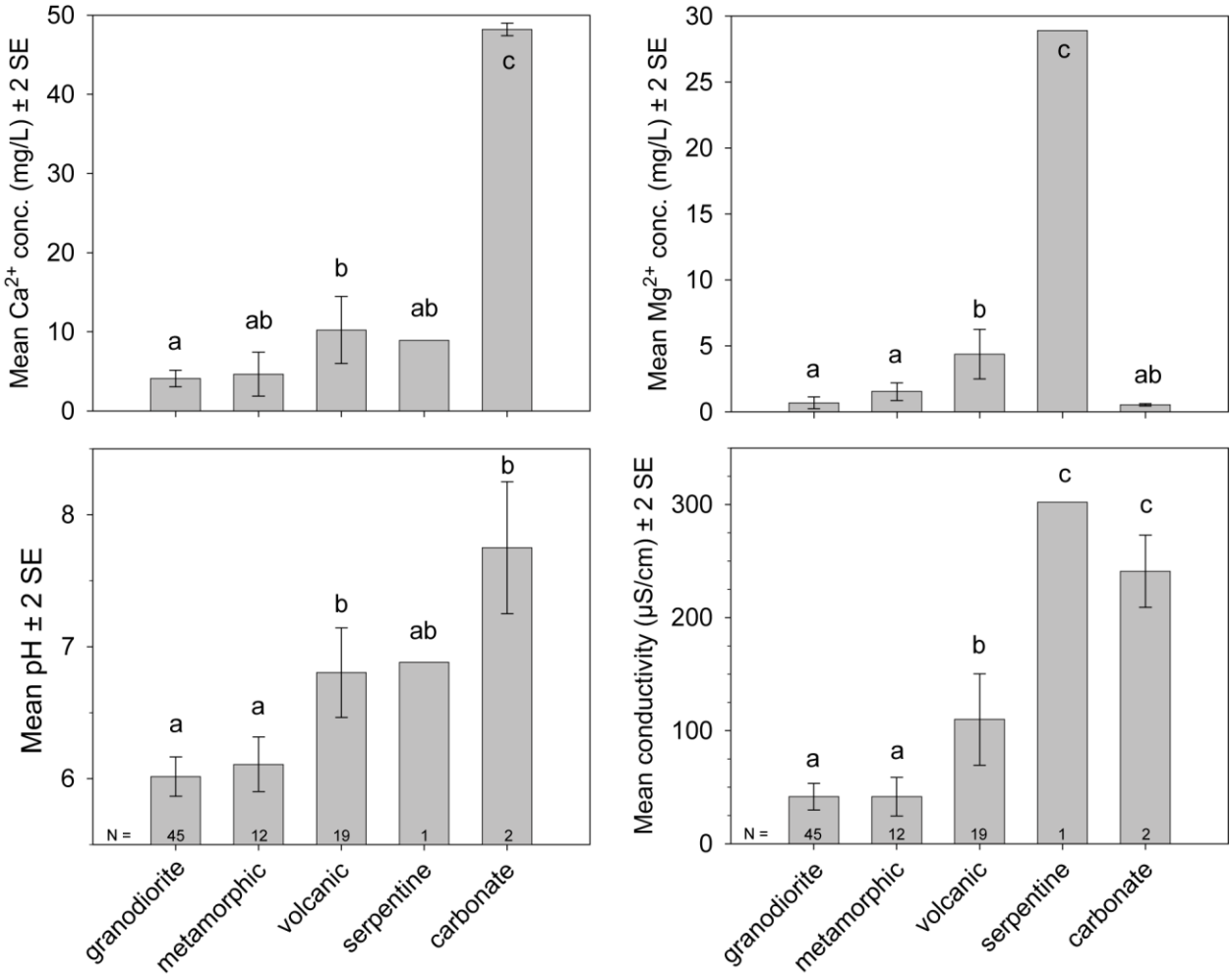

Figure 5. The pH, electrical conductivity, calcium and magnesium concentrations of groundwater in fen catchments dominated by granodiorite, metamorphic, volcanic, serpentine and carbonate rocks. N = number of fens in each category. Letters indicate significant differences determined by ANOVA with Tukey's HSD multiple comparison test.

Peat

The peat layer in sampled fens averaged 83 cm thick, ranging from as thin as 15 cm to a maximum of 253 cm. The fens with the largest catchment areas typically contained the thickest peat, but this relationship included considerable scatter in larger catchments, where peat ranged from thick

to thin (Figure 6A). The positive linear correlation between peat thickness and catchment area was statistically significant (p = 0.0163) but explained only 7 % of the variation in the data (R^2_{adj} = 0.06652). The regression was less significant (p = 0.0818) when catchment area was log transformed and compared to peat thickness, but the log-transformation allows for better visual assessment of the pattern of increasing maximum peat thickness in larger catchments (see dashed line in Figure 6A).

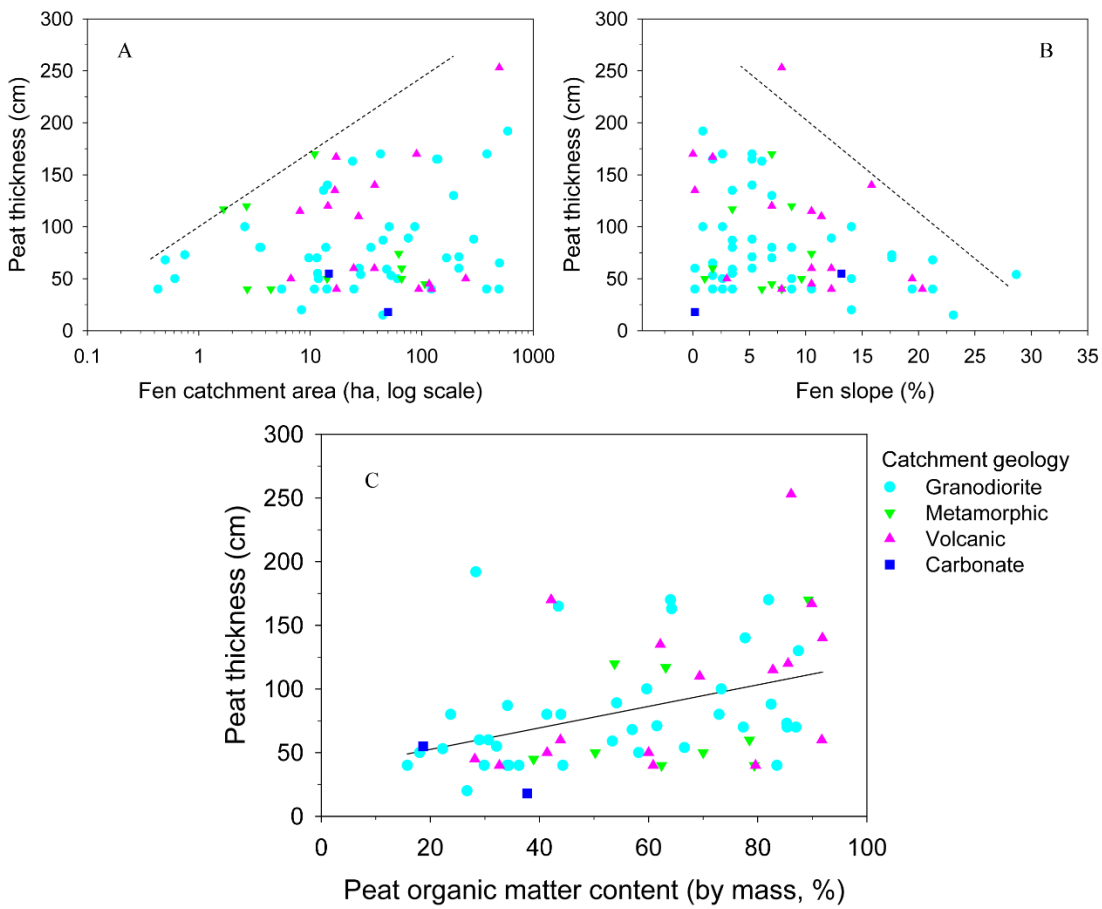

Figure 6. The relationships of peat thickness with catchment area, fen slope and soil organic content. Panel A shows peat thickness as a function of fen catchment area (note log scale). Catchment area has been log transformed to highlight (with a visually fitted dashed line) the increase in maximum peat thickness as catchment area increases. Panel B shows peat thickness versus slope. The thickest peat bodies occur on the gentlest slopes, and few peat bodies exceed 1 m thickness on slopes steeper than 15 %. A visually-fit line (dashed) shows maximum peat thickness decreasing as slope increases. Panel C illustrates that thicker peat bodies have higher organic matter content. The linear regression line is shown (P = 0.0015) and explains 14 % of the variation in the data (y = 0.8461x + 36.1937, R^2_{adj} = 0.1381). The bedrock geology of each fen's catchment is indicated by symbol shape and color. The single serpentine site is not shown because it is missing peat thickness data.

Peat thickness was negatively correlated with fen slope; fens on steeper slopes generally had thinner peat layers (Figure 6B). Although this was a statistically significant regression (P = 0.0134), fen slope only explained about 7 % of the variation in peat thickness (R^2_{adj} = 0.0711). Peat thickness varied widely in gently sloping fens, whereas its range was restricted to relatively low values in more steeply sloping fens. As with the relationship between peat thickness and catchment area, an increase in slope reduced the maximum peat thickness attained (see dashed line in Figure 6B).

The organic matter content of the sampled peat averaged 57 % and was above the 28 % organic matter threshold for organic soils (see Methods) in 91 % of the samples. Twenty-two percent of the samples contained more than 80 % organic matter. The fens with the thickest peat tended to have the highest organic matter content (P = 0.0015), and this correlation accounted for 14 % (R^2_{adj} = 0.1381) of the variation in peat organic matter content (Figure 6C).

The evaluation of 13 environmental variables in models of peat thickness produced a minimum AICc model involving six environmental variables, namely percent soil organic matter (OM), catchment area, fen area, aspect (sine transformed), pH and EC. Cross validation of the six-parameter minimum AICc model indicated a prediction error of ± 49.8 cm of peat. By evaluating nearly-equivalent models and testing variable-removal effects on prediction error, we arrived at a three-parameter model using OM (%), catchment area (ha) and fen area (ha) with a peat-thickness prediction error of ± 44.9 cm. The peat-thickness prediction interval for this three-parameter model was 90 cm, and slightly more than one-third of the total observed peat thickness range of 238 cm. The three-parameter model, with R^2_{adj} = 0.2991, is:

(peat thickness, cm) = 0.8523*(OM) + 0.1190*(catchment area) + 5.3076*(fen area) + 21.6950

Vegetation

In total, 170 vascular plant and bryophyte species were identified in the 290 relevés recorded at the 79 study fens. The relevé-level Shannon diversity index ranged from zero (one species) to 2.443 (20 species) across 290 relevés. Relevé-level richness ranged from one to 23 species. Scaled up to the fen level, species richness ranged from two to 42 species. The relationship between log10 (fen area) and species richness had a p-value of 0.0542 and fen area explained about 4 % (R^2_{adj} = 0.0384) of the variation in species richness. Altitude alone explained approximately 29 % (R^2_{adj} = 0.2894) of the variation in species richness between fens (Figure 7).

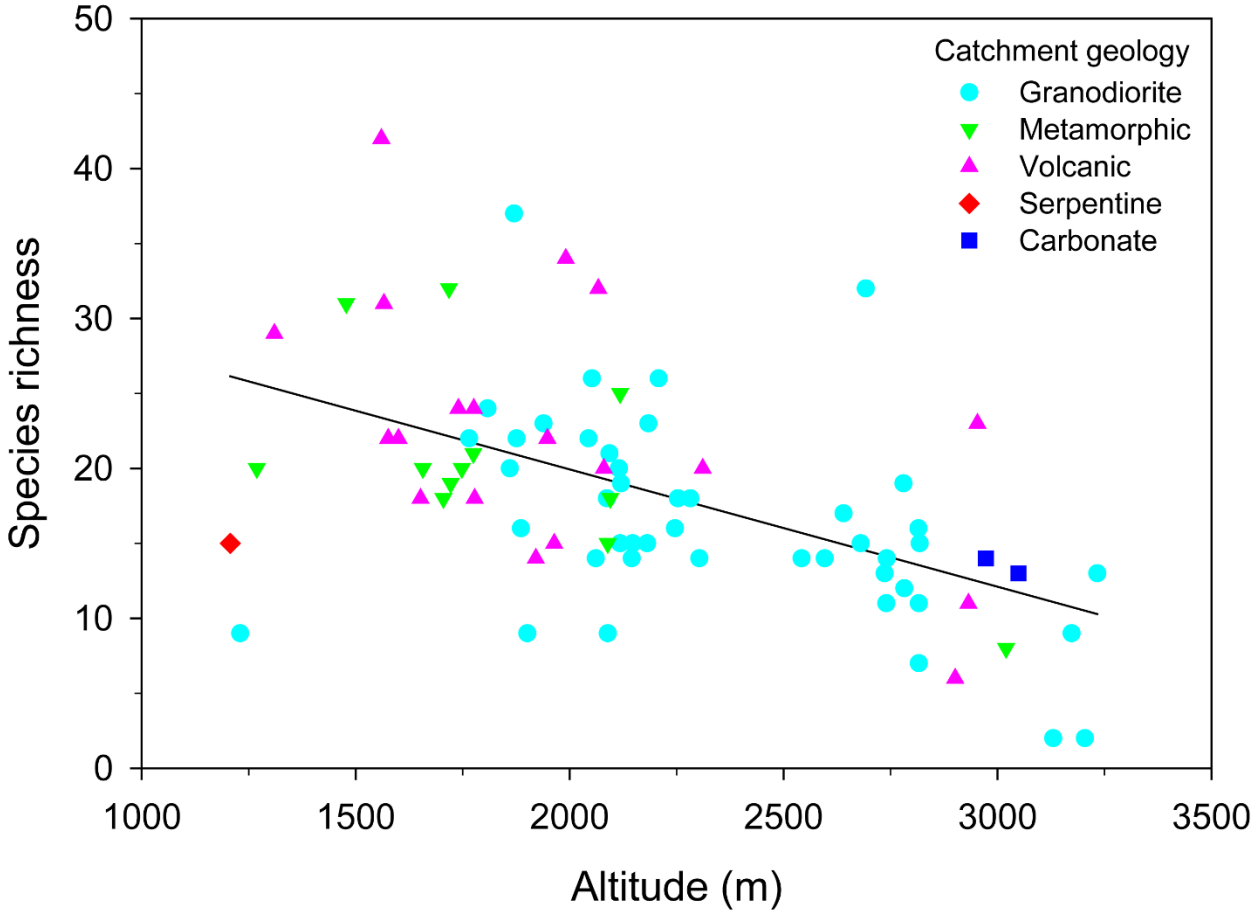

Figure 7. The relationship between species richness and altitude. Each fen's catchment bedrock geology is indicated by symbol shape and colour. Fen plant species richness decreases with altitude (p << 0.0001). The equation of the plotted regression line is y = -0.0078x + 35.5917, R^2_{adj} = 0.2894

The single-parameter altitude model had an AICc of 501 and a cross-validated prediction error of ± 6.47 species. Therefore, using altitude alone, the prediction window for fen species richness is 12.94 species wide, which is 32 % of the entire 40-species range in richness. This model has an R^2_{adj} = 0.2894 and can predict which one-third of the species richness (SR) range a given fen will fall into, based on altitude only. Multi-parameter model selection using the full set of 13 environmental variables arrived at an optimal four-parameter model with an AICc of 407. The four variables selected were altitude (m), fen slope (%), peat thickness (cm) and OM (%). This four-parameter model has a cross-validated prediction error of ± 5.78 species, yielding a prediction window 11.56 species wide. The window spans 29 % of the entire 40-species range in richness, a 3 % improvement over the altitude-only model. The four-parameter model has R^2_{adj} = 0.5121, and is as follows:

SR = -0.0072*(altitude) + 0.3488*(fen slope) + 0.1041*(OM) + 0.0399*(peat thickness) + 22.7314

Indirect ordination using DCA (Figure 8) illustrates the complex floristic gradients in the vegetation dataset. The two primary ordination axes shown are scaled in standard deviation (SD) units. A 4-SD distance between relevés along either axis represents almost no overlap in species composition (McCune & Mefford 1999). The DCA of all 290 relevés (inset, Figure 8) is roughly separated into three distinct vegetation groups. Relevés from two volcanic bedrock fens in the Lassen National Forest (Willow Lake and Domingo Lake) occur on the right side of Axis 1, about 3–4 SD units from a vertically-oriented mass containing most of the relevés. These are basin fens with floating mats dominated by *Carex lasiocarpa*, *Carex vesicaria*, *Dulichium arundinaceum*, *Menyanthes trifoliata* and *Utricularia macrorhiza*. The vegetation from the relevés in two extremely rich carbonate bedrock fens in the Inyo National Forest (Hanging Fen and Mildred Lake) is made up of *Trichophorum pumilum*, *Kobresia myosuroides*, *Thalictrum alpinum* and others. These species occur about 0.5 SD units left-of-center of the central mass of relevés. In other words, the primary (Axis 1, Figure 8 inset) pattern in the vegetation data is driven by

the distinct flora of the outlier fens, with the two volcanic sites to the right and the two carbonate sites to the left.

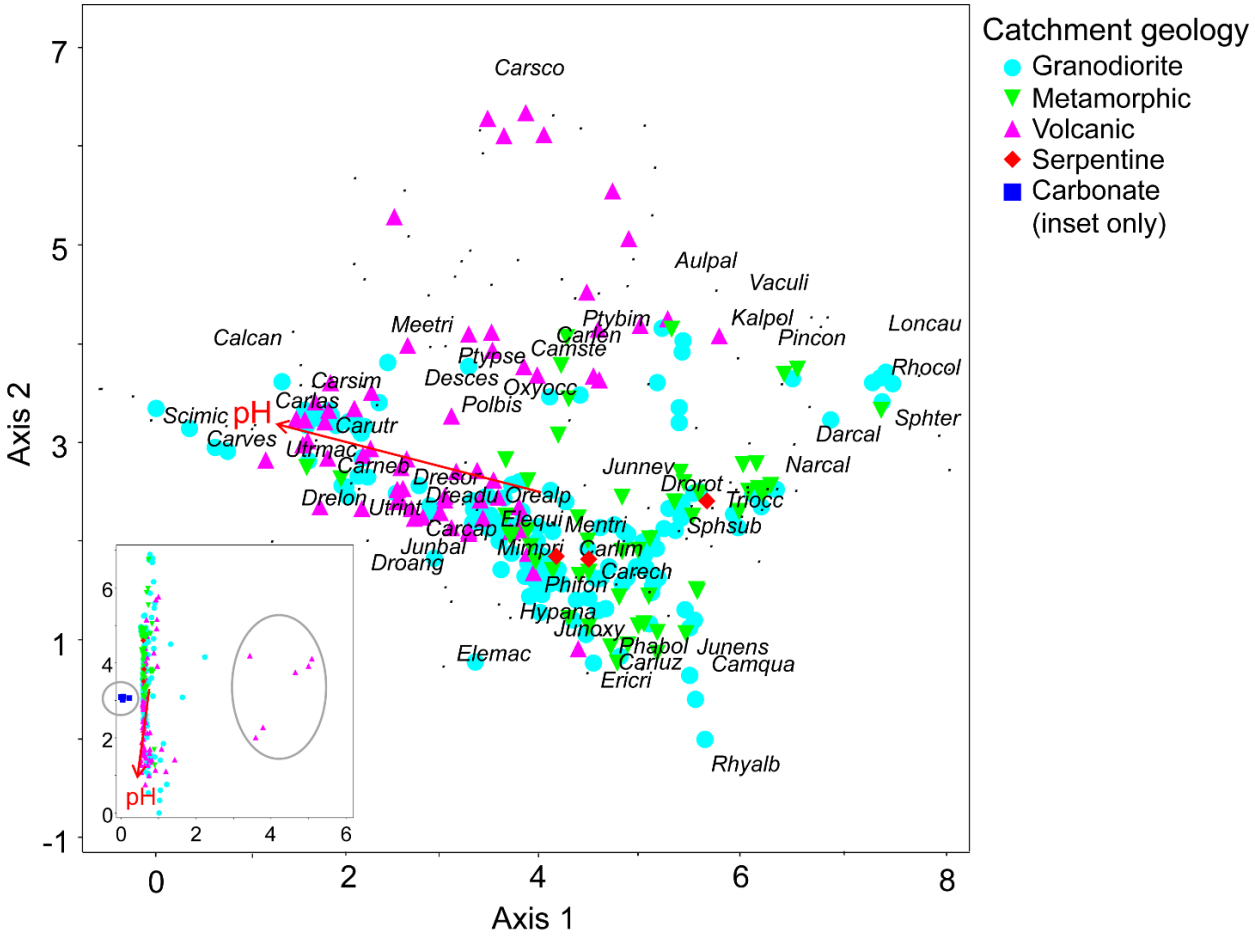

Figure 8. Detrended correspondence analysis (DCA) of the vegetation at 273 fen relevés. The DCA of all 290 relevés is shown inset, and indicates that the relevés from the two carbonate fens (black diamonds, circled on left) and two volcanic fens (grey triangles, circled on right) are outliers that dominate the structure of the full dataset. Species names show relative species positions (unlabelled species appear as small black dots); greyscale shapes show relative relevé positions, coded by catchment geology. Axes are scaled in standard deviation (SD) units. Complete species turnover occurs at a distance of ~4 SD. Axis 1 is a vegetation gradient that correlates with pH (overlaid black arrow indicates direction of increasing pH, R^2 = 0.21). Selected species abbreviations are: Aulpal=Aulacomnium palustre; Calcan=Calamagrostis canadensis; Camqua=Camassia quamash; Camste=Campylium stellatum; Carcap=Carex capitata; Carech=Carex echinata; Carlas=Carex lasiocarpa; Carlen=Carex lenticularis; Carlim=Carex limosa; Carluz=Carex luzulina; Carneb=Carex nebrascensis; Carpel=Carex pellita; Carsco=Carex scopulorum; Carsim=Carex simulata; Carutr=Carex utriculata; Carves=Carex vesicaria; Darcal=Darlingtonia californica; Desces=Deschampsia cespitosa; Dreadu=Drepanocladus aduncus; Drelon=Drepanocladus longifolius; Dresor=Drepanocladus sordidus; Droang=Drosera anglica; Drorot=Drosera rotundifolia; Elemac=Eleocharis macrostachya; Elequi=Eleocharis quinqueflora; Ericri=Eriophorum criniger;

Hypana=Hypericum anagalloides; Junbal=Juncus balticus; Junens=Juncus ensifolius; Junnev=Juncus nevadensis; Junoxy=Juncus oxymeris; Kalpol=Kalmia polifolia; Loncau=Lonicera cauriana; Meetri=Meesia triquetra; Mentri=Menyanthes trifoliata; Mimpri=Mimulus primuloides; Narcal=Narthecium californicum; Orealp=Oreostemma alpigenum; Oxyocc=Oxypolis occidentalis; Phabol=Phalacroseris bolanderi; Phifon=Philonotis fontana; Pincon=Pinus contorta; Polbis=Polygonum bistortoides; Ptybim=Ptychostomum bimum; Ptypse=Ptychostomum pseudotriquetra; Rhocol=Rhododendron columbianum; Rhyalb=Rhynchospora alba; Scimic=Scirpus microcarpus; Sphsub=Sphagnum subsecundum; Sphter=Sphagnum teres; Triocc=Triantha occidentalis subsp. occidentalis; Utrint=Utricularia intermedia; Utrmac=Utricularia macrorhiza; Vaculi=Vaccinium uliginosum.

Removing the 17 outlier relevés that represent the two carbonate and two volcanic fens allowed an analysis of the vegetation patterns in the absence of the sites with unique vegetation that dominate the DCA. The 273-relevé DCA with outliers removed (Figure 8, main panel) shows a continuous vegetation gradient within the main group of relevés. The environmental variable that correlated most strongly with the purely vegetation-derived patterns in the DCA was pH, with an R^2 of 0.2079 with respect to Axis 1. All other environmental variables had $R^2 < 0.1110$. At the extreme right of Axis 1 are fens dominated by trees, shrubs and *Sphagnum* (*Pinus contorta*, *Rhododendron columbianum*, *Lonicera cauriana*, *Kalmia polifolia*, *Vaccinium uliginosum*, *Rhynchospora alba*, *Sphagnum teres* and *Sphagnum subsecundum*) (Figure 3). At the opposite (left) end of Axis 1, correlated with basic pH conditions, are relevés dominated by several species of *Carex*, *Scirpus microcarpus* and *Calamagrostis canadensis* with the brown mosses *Drepanocladus sordidus*, *Drepanocladus longifolius* and *Meesia triquetra*.

The explicit inclusion of the environmental data into the ordination of vegetation data at the fen level, in a CCA, highlights the unique flora at the carbonate sites. In the CCA of all 79 fens, by far the strongest gradient along Axis 1 is membership of the carbonate bedrock class, followed by calcium concentration. The segregation of the carbonate fens from the rest of the sites by 8 SD units (Figure 9, inset) is the main pattern in the combined vegetation-environment CCA ordination. To further explore the environmental gradients within the main group of data, the two carbonate fens were removed because their distinct flora, structured by a unique rock type and water with very high calcium content, overshadowed the influence of other variables on the rest of the data.

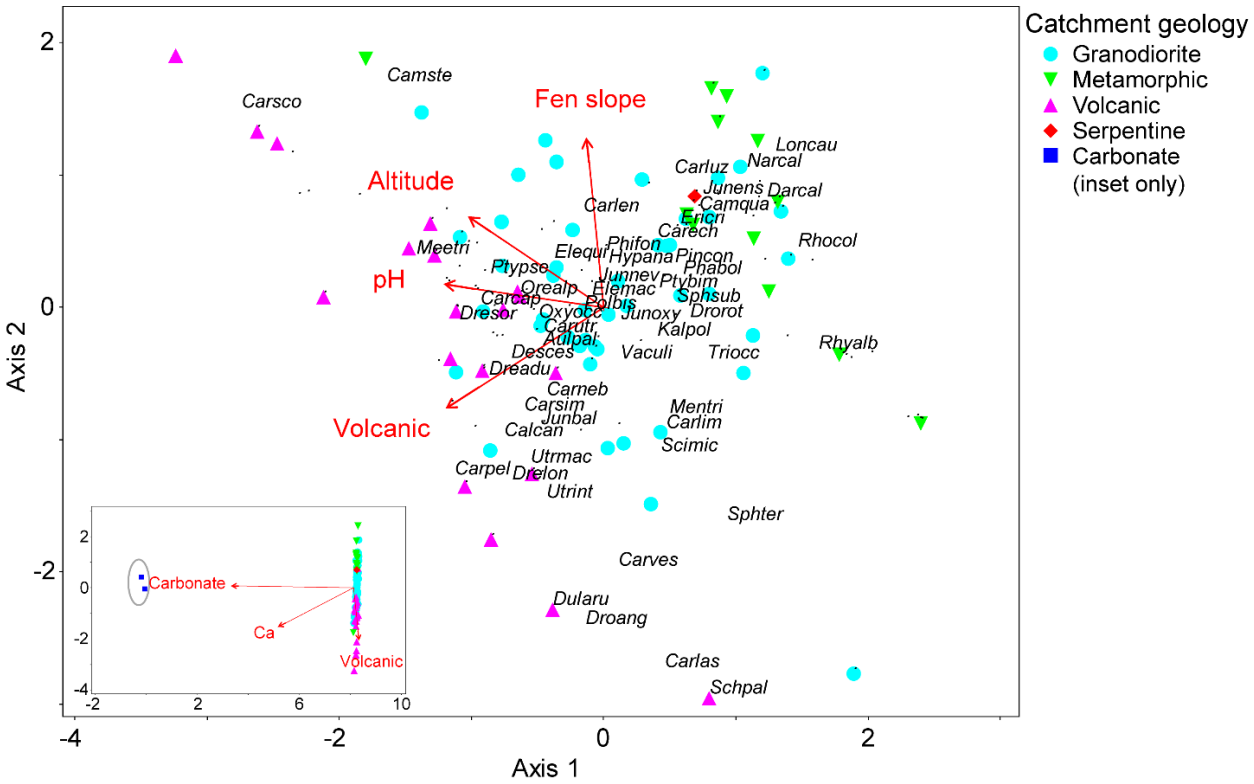

Figure 9. Canonical correspondence analysis (CCA) of the vegetation and environmental variables at 77 study fens, excluding the two carbonate fens. The CCA of all 79 fens is shown inset, indicating that the carbonate fens (black diamonds, circled on left) are extreme outliers. Catchment geology is denoted by point shape and shading. Significant environmental factors ($R^2 > 0.24$) are shown as black vectors, the value of the factor increasing in the direction indicated by the arrow. Unlabelled species appear as small black dots in the ordination, and selected species abbreviations are: Aulpal=Aulacomnium palustre; Calcan=Calamagrostis canadensis; Camqua=Camassia quamash; Camste=Campylium stellatum; Carcap=Carex capitata; Carech=Carex echinata; Carlas=Carex lasiocarpa; Carlen=Carex lenticularis; Carlim=Carex limosa; Carluz=Carex luzulina; Carneb=Carex nebrascensis; Carpel=Carex pellita; Carsco=Carex scopulorum; Carsim=Carex simulata; Carutr=Carex utriculata; Carves=Carex vesicaria; Darcal=Darlingtonia californica; Desces=Deschampsia cespitosa; Dreadu=Drepanocladus aduncus; Drelon=Drepanocladus longifolius; Dresor=Drepanocladus sordidus; Droang=Drosera anglica; Drorot=Drosera rotundifolia; Dularu=Dulichium arundinaceum; Elemac=Eleocharis macrostachya; Elequi=Eleocharis quinqueflora; Ericri=Eriophorum criniger; Hypana=Hypericum anagalloides; Junbal=Juncus balticus; Junens=Juncus ensifolius; Junnev=Juncus nevadensis; Junoxy=Juncus oxymeris; Kalpol=Kalmia polifolia; Kobmyo=Kobresia myosuroides; Loncau=Lonicera cauriana; Meetri=Meesia triquetra; Mentri=Menyanthes trifoliata; Mimpri=Mimulus primuloides; Narcal=Narthecium californicum; Orealp=Oreostemma alpigenum; Oxyocc=Oxypolis occidentalis; Phabol=Phalacroseris bolanderi; Phifon=Philonotis fontana; Pincon=Pinus contorta; Polbis=Polygonum bistortoides; Ptybim=Ptychostomum bimum; Ptypse=Ptychostomum pseudotriquetra; Rhocol=Rhododendron columbianum; Rhyalb=Rhynchospora alba; Schpal=Scheuchzeria palustris; Scimic=Scirpus microcarpus; Sphsub=Sphagnum subsecundum; Sphter=Sphagnum teres; Triocc=Triantha occidentalis subsp. occidentalis; Utrint=Utricularia intermedia; Utrmac=Utricularia macrorhiza; Vaculi=Vaccinium uliginosum.

Leaving out the two carbonate fens and running a CCA ordination on the remaining 77 sites produced a much more even spread of data in the ordination space (Figure 9, main panel). The sites that had been the farthest outliers in the DCA (vegetation data only), Willow Lake and Domingo Lake with unique occurrences of *Dulichium arundinaceum* and *Scheuchzeria palustris*, plot in the lower middle of the ordination space but are contiguous with the rest of the data. Four environmental variables were correlated ($R^2 > 0.24$) with the structure in the 77-fen ordination, namely pH, altitude, fen slope and membership of the volcanic bedrock class. The orientations of these correlations are indicated by the red arrows on the CCA (Figure 9).

The main pattern in the vegetation data, along Axis 1, is a separation of species by the dominant rock type in the catchment and the pH of the fen water. Species and fens associated with volcanic bedrock and higher pH are to the left of the ordination, granodiorite and mid-pH species and fens are central, and metamorphic and acidic plants and sites lie to the right. Although the lone serpentine fen is classified as extremely rich due to its high pH and cation concentration (Figure 4), its vegetation is most similar to that of acidic metamorphic sites with species like *Rhododendron columbianum*, *Narthecium californicum*, *Darlingtonia californica* and *Carex echinata*. The *Sphagnum* moss species plot in the middle-right, in the moderately acidic region dominated by granodiorite sites.

A secondary pattern in the CCA, along Axis 2, is the separation of species on steeply sloping sites from those in flat valleys and basins. The major outlier species in the vegetation-only DCA (Figure 8, inset), which are unique to the Willow Lake and Domingo Lake fens, occur in basin fens with no slope and plot at the bottom of the ordination. None of the measured environmental variables show a major difference between the Willow and Domingo fens and the rest of the dataset; they fit in with the broader trends of the CCA gradients, albeit at the edge. This is in sharp contrast to the carbonate sites, whose distinct vegetation is correlated with unique bedrock geology and extreme water chemistry values. A significant altitude gradient is correlated with both axes, with high-altitude sites plotting in the

upper left and low-altitude sites in the lower right. The total inertia (variance) in the CCA is 10.25, and the Axis 1 eigenvalue (the amount of variance explained) is 0.542, or 5.3 % of the total variance. The Axis 2 eigenvalue is 0.454, explaining a further 3.8 % of the variance, making a combined two-axis total of 9.7 %. The Monte Carlo test showed that the correlation between the environmental matrix and the vegetation data is significant (P = 0.03).

DISCUSSION

The broad patterns of physical and biological processes that control fen distribution and diversity in the Sierra Nevada are relevant to the study of mountain peatlands throughout the world. The higher annual precipitation in the northern portion of the study area allows the development of groundwater flow systems that are sufficient to support fens at lower altitudes. By contrast, in the drier southern part of the Sierra Nevada, fens can form only under the cooler conditions at high altitudes. Because the northern Sierra Nevada contains little high-altitude landscape, there are few opportunities for fens to occupy this zone. In the southern Sierra Nevada the most likely reason for the lack of low-altitude fens is a combination of low precipitation and warm temperatures creating high evapotranspiration demand. However, fens occur in the semi-arid mountains of northern Chile, where annual precipitation rarely exceeds 25 cm (Squeo *et al.* 2006), further illustrating the overwhelming importance of groundwater flow paths for the maintenance of saturated soil conditions and peat formation.

In addition to providing insights about the locations and landscapes where mountains fens form, the relationships between peat thickness and catchment area, fen slope and organic matter content have implications for the vulnerability of mountain fens to future climate changes, including severe droughts. Most fens in small catchments have thin peat, perhaps due to a lower volume of local groundwater aquifers that may become depleted during periodic droughts, limiting peat accumulation.

The variable that is most strongly correlated with peat thickness is organic matter content. While it is not suggested that the relationship is causative in either direction, it stands to reason that both thickness and organic content of peat would be similarly influenced by other processes such as mineral sediment input, decomposition rates and primary production rates. Wildfires, road construction and maintenance, and logging all occur frequently in National Forest mountain landscapes and have the potential to increase sedimentation to fens and impact peatland ecological processes.

Because peatlands are formed and maintained through primary production of organic matter by wetland plants, understanding the environmental drivers of plant diversity and distribution is critical to the study of peatland function. Altitude exerts strong control over fen-level species richness and distribution. The most species-rich fens occur at lower altitudes. This altitude effect is probably due to a longer snow-free growing season and warmer temperatures at the lower sites. However, the lower-altitude sites also tend to occur in the northern Sierras where more precipitation falls, so it is also possible that the trend in species richness could be related to a hydrological gradient that we did not measure directly within the fens, or a regional species pool effect.

The reduction of species richness with increasing altitude is a well-known ecological relationship that applies to many taxa and mountain ranges throughout the world (Rahbek 1995, Grytnes 2003, Bruun *et al.* 2006). Mountain peatlands provide an interesting venue for exploring this relationship because many of the key ecosystem processes (e.g. hydrology, peat formation and water chemistry) that are thought to limit plant growth and survival in fens are not necessarily affected by changes in altitude. This study was not designed to address this question explicitly, but the pattern of decreasing richness with increasing altitude is significant nonetheless. Furthermore, the pattern of richness is not a function of larger fens having more species due to a species-area effect. Targeted investigations into the specific drivers of the richness-altitude pattern within mountain peatlands would help tease apart the various contributing environmental factors.

Water chemistry, particularly calcium concentration and pH, created the largest distinctions in fen species composition. The two carbonate fens, which had many unique species, high calcium concentrations and high pH, were the main drivers of this primary structure in our dataset. After removing the outlier fens on carbonate bedrock, water pH was one of the strongest drivers of plant distribution in our CCA analyses. This is well known from previous studies that have shown pH and the poor-rich gradient to be primary factors in determining fen vegetation (Sjörs 1950, Vitt *et al.* 1995, Chapin *et al.* 2004).

The fens of the marble regions of the Inyo National Forest are unique on the west coast of the USA from a floristic, ecological and biogeographical perspective (Major & Bamberg 1963). The dominance of calciphiles including *Kobresia myosuroides*, *Trichophorum pumilum* and *Carex scirpoidea* is striking, and other extremely rich fens in the region should be more carefully investigated, as they have been in the Rocky Mountains and Canada (Vitt & Chee 1990, Cooper 1996). An example of this fen type is shown in Figure 3 (bottom right). In addition, the presence of communities similar to those in maritime coastal areas and dominated by *Narthecium californicum* should also be more thoroughly investigated. There are relatively few reports of fens in North America dominated by species other than mosses or *Cyperaceae*, and peat formed by a species belonging to the *Liliaceae* is unusual. A community dominated by *Narthecium ossifragum* and *Sphagnum tenellum* occurs in Britain, in what are characterized as oligotrophic flushes, or springs, in highly acidic rocks (McVean & Ratcliffe 1962). However, the lily-dominated California fens are not highly acidic.

The highly distinct vegetation and acidic conditions approaching poor-fen status at the Willow and Domingo Lake sites is unique in the study region and deserves further investigation. In addition, more fens on serpentine bedrock should be examined. It is well known that the high levels of magnesium and other toxic elements in serpentine soils and bedrock have profound effects on associated ecosystems (Harrison & Rajakaruna 2011). It is interesting that the environmental variables

measured in this study highlighted the distinct vegetation of the carbonate sites, while the unique flora of the highly acidic sites was not strongly differentiated in the CCA analysis. This is almost certainly due to the fact that the two carbonate sites were the only examples of sites associated with that bedrock type that we studied, whereas we sampled at a number of other volcanic-bedrock sites in addition to the uniquely-vegetated Willow and Domingo Lake sites.

The past and present influence of pack stock (horses) and livestock (primarily cattle and sheep) on fens is a critical scientific and resource management question. Many fens that are not presently used for pasture were heavily grazed in the 19th century and may not have recovered (Dull 1999), due to threshold-crossing impacts such as erosion gully formation and loss of soil organic matter. While there is considerable interest in current pack stock and livestock use, the effects of current use may be additive to historical grazing impacts. Continued research on past and present impacts to fens is clearly needed to inform restoration efforts, which should be a top priority for land managers and include the removal of hydrological modifications, road and stock impacts, and the re-introduction of local genotypes of fen-dominant species to sites from which they have now disappeared.

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APPENDIX

Table 1. Some key characteristics of the 79 study fens. Forest or Park: NP=National Park, all others are National Forests. Bedrock: c=carbonate, g=granodiorite, m=metamorphic, s=serpentine, v=volcanic. Landform: c=bedrock contact, m=spring mound, b=basin, s=slope. OM(%)=Percent soil organic matter. EC=Electrical conductivity. Sites are ordered by decreasing latitude to highlight the regional pattern of increasing altitude and decreasing precipitation from north to south.

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip. (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
South Fork Mt. Fen	Shasta-Trinity	40.6044	-123.5490	2095	140	m	s	4.90	0.63	14	75	---	---	---	5.4	19	1.7	0.3	1.4	18
Cooper Swamp	Lassen	40.4925	-121.1533	1948	140	v	b	90.15	20.00	0	180	19.0	170	42	6.3	65	7.4	2.0	2.0	22
Drakesbad Meadow	Lassen NP	40.4441	-121.4062	1740	198	v	c	248.81	1.40	3	135	---	50	60	7.6	87	4.5	2.4	4.7	24
Juniper	Lassen	40.4195	-121.2711	1921	165	v	s	116.78	0.04	11	200	14.0	45	28	7.2	50	4.3	1.9	2.2	14
Lee Camp Fen (private)	Lassen NP	40.4152	-121.3243	1576	140	v	s	119.51	2.97	5	157	---	---	---	6.6	66	2.9	1.3	2.1	22
Willow Lake	Lassen	40.4022	-121.3568	1652	165	v	b	597.00	1.00	0	305	---	---	---	4.3	63	1.4	0.9	5.3	18
Domingo Lake	Lassen	40.3972	-121.3634	1778	163	v	b	16.65	0.28	0	113	20.0	135	62	6.3	19	1.7	0.4	1.1	18
Saddle Gulch Fen	Shasta-Trinity	40.3871	-123.0839	1207	114	s	s	20.74	0.06	19	110	---	---	---	6.9	302	8.9	28.9	3.0	15
Humbug	Lassen	40.1336	-121.2641	1310	152	v	m	17.07	2.00	2	90	---	167	90	7.1	182	20.8	8.2	5.3	29
Grizzly Creek 1	Lassen	40.1312	-121.3332	1776	165	v	s	94.18	0.36	12	150	---	40	61	7.2	73	7.8	3.3	2.2	24
Willow Creek 1	Lassen	40.1257	-121.4668	1566	191	v	s	37.73	0.12	11	260	---	60	92	7.4	108	10.2	5.5	3.2	31
Willow Creek 2	Lassen	40.1237	-121.4707	1560	191	v	s	14.42	0.60	7	164	17.0	120	86	7.4	151	17.7	5.0	3.7	42
Oxypolis	Lassen	---	---	---	---	v	s	---	---	---	---	---	---	---	---	---	---	---	---	22
Butterfly Valley	Plumas	40.0123	-120.9919	1478	104	m	s	62.33	0.16	11	150	---	74	---	5.7	22	1.0	1.8	0.7	31
Smith Lake	Plumas	39.9915	-121.0252	1269	114	m	s	107.03	0.12	7	200	---	45	39	6.0	97	13.6	3.5	1.9	20
Silver Lake	Plumas	39.9579	-121.1311	1765	185	g	b	293.75	0.35	5	80	---	88	82	---	36	7.0	0.3	2.8	22
Waters Bog	Plumas	39.8690	-121.0371	1722	165	m	s	9.45	0.81	16	20	---	---	---	---	58	6.1	0.7	3.6	19

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip. (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Arkansas	Plumas	39.8263	-121.1765	1775	218	m	s	2.72	0.10	6	260	15.0	40	62	6.4	35	3.3	2.0	0.4	21
First Fen	Plumas	39.8221	-121.1740	1748	221	m	s	2.68	0.08	9	185	13.0	120	54	6.4	43	3.3	2.4	0.7	20
Terraced Fen	Plumas	39.8149	-121.1677	1705	216	m	b	14.21	0.40	10	210	17.0	50	50	6.4	35	3.1	2.4	0.4	18
China Gulch	Plumas	39.8083	-121.1709	1657	216	m	s	4.43	0.14	8	332	16.0	40	79	6.4	47	3.7	2.8	1.1	20
Greens Flat	Plumas	39.8033	-121.1908	1718	216	m	s	10.93	0.50	7	110	14.0	170	89	6.4	32	2.1	2.1	0.6	32
Severed Limb	Tahoe	39.4375	-120.2804	2080	140	v	s	6.71	0.09	19	112	14.0	50	41	7.0	171	16.1	7.7	5.5	20
Bottomless Fen	Tahoe	39.4327	-120.2802	2067	147	v	s	498.19	0.12	8	20	10.0	253	86	7.0	20	1.5	0.2	2.0	32
Kiln Fen	Tahoe	39.4311	-120.2587	1991	114	v	c	8.09	7.50	11	20	12.0	115	83	7.0	381	35.4	16.7	9.9	34
Mason Fen	Tahoe	39.4291	-120.2427	1964	114	v	c	122.69	0.24	8	48	14.0	40	80	7.0	141	15.4	5.6	4.3	15
Murphy Flat	Tahoe	39.4264	-120.7054	1876	191	g	s	11.50	0.14	7	196	12.0	70	85	5.0	26	2.3	0.3	2.7	22
Bowman View Fen	Tahoe	39.4203	-120.6964	1808	191	g	s	0.43	0.04	21	100	12.0	40	34	6.5	18	1.8	0.1	1.7	24
Hidden Fen	Tahoe	39.4189	-120.7074	1860	191	g	s	0.50	0.02	21	285	10.5	68	57	5.0	158	14.4	7.2	4.7	20
Pat Yore Flat	Tahoe	39.4137	-120.7052	1870	191	g	s	2.59	0.09	14	180	13.5	100	60	5.2	12	1.1	0.1	1.2	37
McKinstry 3	Eldorado	39.0451	-120.3342	2118	165	g	c	27.51	0.03	5	170	16.0	60	29	5.9	28	3.6	0.3	1.4	15
McKinstry 4	Eldorado	39.0400	-120.3500	2089	165	m	c	66.13	0.18	1	170	8.0	50	70	5.9	8	1.2	0.1	0.3	15
McKinstry 2	Eldorado	39.0396	-120.3462	2118	165	m	c	66.13	0.18	2	188	8.0	60	78	5.9	8	1.2	0.1	0.3	25
McKinstry Meadow	Eldorado	39.0341	-120.3407	2089	165	g	c	215.83	0.16	0	220	13.0	60	31	5.9	28	2.1	0.3	1.8	9
Sun Rock	Eldorado	38.9199	-120.3344	1886	165	g	s	24.70	0.25	3	204	16.0	40	34	5.6	22	1.7	0.4	2.0	16
Buckbean Bog	Eldorado	38.9036	-120.2613	2282	165	g	b	51.18	0.40	1	340	16.0	100	73	5.6	39	2.2	0.9	2.6	18
Lost	Eldorado	38.9013	-120.2558	2303	165	g	s	3.61	0.01	9	28	---	80	44	5.6	43	4.7	0.5	2.9	14
Morattini Meadow	Eldorado	38.8983	-120.2831	2115	165	g	s	14.29	0.32	5	210	---	140	78	5.7	23	2.7	0.2	1.5	20

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip. (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Wrights Lake 3	Eldorado	38.8357	-120.2268	2147	165	g	s	0.61	0.01	9	230	12.0	50	---	5.5	42	5.0	0.4	3.0	15
Wrights Lake 2	Eldorado	38.8330	-120.2193	2184	165	g	s	14.11	0.11	11	340	---	40	36	5.5	11	1.0	0.1	0.7	23
Wrights Lake 1	Eldorado	38.8323	-120.2204	2208	165	g	s	9.72	0.06	18	350	13.0	70	87	5.5	---	---	---	---	26
Wilson Ranch	Eldorado	38.8250	-120.2734	2087	165	g	s	11.66	0.14	3	323	15.0	55	32	5.5	23	1.6	0.3	2.1	18
Montgomery Meadow	Stanislaus	38.3614	-119.9223	1901	140	g	s	122.33	0.45	3	220	14.0	40	44	7.0	151	9.5	1.4	20.2	9
St. Mary's Pass	Stanislaus	38.3436	-119.6452	2953	140	v	c	37.93	0.60	16	180	9.0	140	92	6.6	65	6.3	3.1	1.4	23
Smokey Fen	Stanislaus	38.3429	-119.6477	2932	140	v	c	17.20	0.38	20	216	7.5	40	33	6.8	65	5.9	2.3	2.4	11
Mound Fen	Stanislaus	38.3327	-119.6426	2901	140	v	m	27.17	1.02	11	28	9.5	110	69	6.9	195	19.9	7.3	7.6	6
Eagle Meadow	Stanislaus	38.2790	-119.8357	2311	165	v	s	24.56	0.18	12	44	10.0	60	44	6.8	75	4.9	4.9	1.9	20
Happy Isles Fen	Yosemite NP	37.7307	-119.5603	1230	95	g	s	45.12	0.18	3	55	12.0	87	34	6.1	30	2.9	0.4	1.6	9
Mildred Lake	Inyo	37.5433	-118.8717	2973	89	c	b	50.06	3.20	0	350	9.0	18	38	7.5	225	47.8	0.5	0.8	14
Hornfels Fen	Inyo	37.5344	-118.8701	3020	89	m	c	1.67	0.07	3	56	12.0	117	63	6.2	95	15.4	0.4	2.0	8
Hanging Fen	Inyo	37.5336	-118.8661	3049	89	c	c	14.70	0.14	13	270	10.0	55	19	8.0	257	48.6	0.6	0.8	13
Long Meadow	Sierra	37.4897	-119.5764	1939	140	g	s	3.53	0.60	7	230	---	80	73	6.7	142	15.0	1.8	8.5	23
Mack Lake	Inyo	37.4269	-118.7506	3130	89	g	b	53.11	0.09	2	83	9.0	53	22	6.1	49	4.7	0.6	1.8	2
Crispy Fen	Inyo	37.4266	-118.7512	3173	89	g	s	48.62	0.05	3	83	10.0	59	53	6.5	96	8.6	5.0	3.1	9
2m Fen	Inyo	37.4104	-118.7564	3204	97	g	b	593.09	0.05	1	8	12.0	192	28	5.2	15	2.1	0.1	0.5	2
Steep Meadow	Sierra	37.4040	-119.5156	2061	165	g	s	8.36	0.24	14	40	16.0	20	27	6.2	---	---	---	---	14
Trapezoid Meadow	Sierra	37.4033	-119.5277	2052	165	g	s	24.07	0.63	6	260	17.0	163	64	6.2	20	2.2	0.1	1.5	26
Roadside Meadow	Sierra	37.4004	-119.5132	2093	165	g	m	13.18	0.21	3	130	---	135	---	6.3	---	---	---	---	21

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip. (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Abbot View Fen	Inyo	37.3989	-118.7595	3233	99	g	b	383.14	1.20	2	355	11.0	40	16	6.3	13	1.9	0.1	0.6	13
Poison Meadow	Sierra	37.3975	-119.5197	2044	160	g	s	42.79	0.77	5	190	16.5	170	82	6.3	13	1.1	0.1	1.4	22
North Dinky Lake	Sierra	37.1660	-119.0662	2818	114	g	s	5.54	0.05	19	210	---	40	---	6.0	36	4.0	0.2	1.5	15
Pond Below Dinky	Sierra	37.1657	-119.0693	2816	114	g	b	499.89	0.00	2	180	14.0	65	---	5.6	---	---	---	---	7
East Dinky Lake	Sierra	37.1646	-119.0650	2816	114	g	b	493.90	0.49	0	260	12.0	40	84	5.9	13	0.3	0.1	1.4	11
Swede Lake	Sierra	37.1579	-119.0745	2815	114	g	s	0.75	0.02	18	195	13.0	73	85	5.8	23	2.7	0.1	1.5	16
Upper Snow Corral	Sierra	37.0388	-119.0756	2246	140	g	s	11.85	0.20	3	210	---	50	58	6.2	60	6.2	0.5	4.1	16
Snow Corral	Sierra	37.0295	-119.0730	2145	140	g	s	86.84	4.50	3	180	---	100	---	6.2	---	---	---	---	14
Lower Ahart House	Sierra	37.0117	-119.0444	2181	114	g	s	13.82	0.08	3	270	---	80	41	6.2	76	6.1	0.8	4.1	15
Creek Meadow	Sierra	36.9996	-119.0410	2120	130	g	s	35.05	0.03	7	314	16.0	80	24	6.2	46	6.2	0.4	1.9	19
Rowell Meadow	Sequoia	36.7175	-118.7382	2692	89	g	m	385.53	0.60	3	210	13.5	170	64	6.1	42	5.2	0.4	2.4	32
Moraine Fen	Sequoia	36.7150	-118.7498	2640	89	g	s	10.91	0.10	9	226	14.0	40	30	6.1	25	2.2	0.2	1.2	17
Sphagnum Fen	Sequoia	36.7111	-118.7281	2736	89	g	s	167.46	0.04	7	226	15.0	70	77	6.0	19	2.8	0.1	0.6	13
Fire Fen	Sequoia	36.7090	-118.7235	2740	89	g	m	139.93	4.00	2	338	14.0	165	43	6.1	23	2.9	0.2	1.2	11
Junction Meadow	Sequoia	36.1759	-118.5641	2253	79	g	s	216.22	0.32	5	63	16.0	71	62	6.4	37	3.6	0.5	2.8	18
Piped Meadow	Sequoia	35.9941	-118.3522	2596	89	g	s	75.93	0.14	12	70	11.0	89	54	6.5	---	---	---	---	14
Jupiter Mushroom Meadow	Sequoia	35.9865	-118.3389	2542	89	g	b	193.43	0.15	7	72	13.0	130	87	7.0	61	7.1	0.7	4.2	14

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip. (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Middle Round	Sequoia	35.9667	-118.3551	2782	89	g	s	44.80	0.09	23	230	---	15	---	6.0	31	2.5	0.4	2.4	12
North Round	Sequoia	35.9656	-118.3586	2741	89	g	s	136.33	1.70	5	206	14.0	165	---	6.7	23	2.2	0.2	2.2	14
Split Meadow	Sequoia	35.9607	-118.3515	2780	89	g	s	28.39	0.06	29	236	12.0	54	67	6.9	35	3.1	0.7	3.3	19
Mosquito Meadow	Sequoia	35.9515	-118.3540	2680	89	g	s	60.54	0.30	14	338	14.0	50	18	6.0	34	3.5	0.6	3.1	15

Chapter 2 – Vegetation response to mammal herbivory in Tuolumne Meadows, Yosemite National Park

INTRODUCTION

Meadows cover less than 3% of the land area in the Sierra Nevada (Fryjoff-Hung & Viers 2012), but they are disproportionately important habitats 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 (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.* 2009).

The interaction of plant, soil, and hydrologic processes formed and maintains meadows in the Sierra Nevada. Plants roots stabilize soil and contribute soil organic matter, while plant growth and hydrologic processes are affected by soil organic matter content, which affects soil water holding and nutrient exchange capacity (Hudson 1994; van Erp, Houba & van Beusichem 2001; Saxton & Rawls 2006; Ankenbauer & Loheide II 2017). Meadow ecosystems appear to have been resilient to perturbation within the range of natural variations in the Sierra Nevada over the past 2,000 – 3,000 years (Wood 1975; Benedict 1982). These several millennia of meadow stability spanned a period that included major shifts in climate and runoff. For example, ~1000 years ago lodgepole pine (*Pinus contorta* subsp. *murrayana* (Grev. & Balf.) Critchf.) and other conifers formed forests in Sierra Nevada basins that are now lakes, and drowned trees are still visible standing in the lake bottoms (Stine 1994).

Many plants are adapted to, and essential components of, meadow ecosystems. Densely rooted perennial and clonal monocots typically dominate subalpine Sierra Nevada meadows (Manning &

Padgett 1995; Potter 2005; Fites-Kaufman *et al.* 2007; Keeler-Wolf *et al.* 2007) and their high belowground to aboveground (B:A) biomass ratio drives the formation of large organic carbon pools in meadow soil (Rasse, Rumpel & Dignac 2005; De Deyn, Cornelissen & Bardgett 2008). Belowground structural plant material is the primary contributor to organic soil carbon, and relatively little aboveground biomass gets incorporated into the soil (Chimner, Cooper & Parton 2002). In meadows with flowing surface water, vegetation provides channel bank stability (Hagberg 1995; Micheli & Kirchner 2002a; b). Willow roots are effective at holding soil in place during erosive flow events (Simon, Pollen & Langendoen 2006), and their flexible woody stems provide roughness that slows water flow, enhancing sediment deposition and accretion (Järvelä 2002, 2004).

One of the most extensively researched vegetation changes in western mountain meadows has been the process of conifer establishment. Conifer encroachment into meadows has been shown to be correlated with climate factors (Millar *et al.* 2004; Cooper *et al.* 2006; Lubetkin, Westerling & Kueppers 2017), coincident with the cessation of sheep grazing (Vale 1987), related to local human disturbance (Cunha 1985), and influenced by meadow vegetation and small mammal herbivory (Johnson 1986; Helms & Ratliff 1987). A hypothesized complex interaction of processes leading to forest expansion into meadows involves grazing disturbance removing a limiting factor (dense meadow vegetation), allowing initial conifer establishment, which then facilitates continued colonization (Miller & Halpern 1998; Lang & Halpern 2007; Haugo & Halpern 2010; Halpern *et al.* 2010; Haugo *et al.* 2011; Rice *et al.* 2012).

Livestock grazing was a widespread and novel impact to Sierra Nevada meadows that began around 1860 (Kinney 1996). Tuolumne Meadows, in Yosemite National Park, was grazed by domestic sheep from ~1860 to ~1900 (LeConte 1870; Townsend 1899). Although the pre-grazing condition of Tuolumne Meadows is not known, the thickness, age, and high soil organic matter content in wetland areas (Wood 1975; Cooper *et al.* 2006; Ankenbauer & Loheide II 2017) offer strong evidence that a perennially high water table and plants with high belowground production were critical to soil

formation. The stable and unimpacted groundwater hydrologic regime (Cooper *et al.* 2006; Loheide *et al.* 2009) and organic wetland soils indicate the historical presence of a densely rooted perennial monocot plant community, as occurs in similar settings throughout the region.

However, Tuolumne Meadows is currently being colonized by *Pinus contorta*, the meadow area is ~20% bare ground, and the wetland vegetation is dominated by *Oreostemma* (formerly *Aster*) *alpigenum* (Ballenger & Acree 2009). *Oreostemma alpigenum* is a tap-rooted perennial dicot with a B:A biomass ratio of ~1.4 whereas clonal perennial sedges, such as *Carex scopulorum*, that typically dominate groundwater-supported wetlands have B:A ratios between 4 and 5 (Bowman & Bilbrough 2001). The production of the current sparse vegetation is insufficient to offset soil decomposition rates, resulting in a net loss of carbon from the ecosystem (see Chapter 3).

Domesticated animal herbivory impacts to vegetation can affect ecosystem processes and result in altered ecosystem states. Livestock eat the most palatable plants, decreasing or destroying populations of sedges (*Carex*), rushes (*Juncus*), and other long-lived clonal plants with high B:A biomass ratios (DeBenedetti 1980). A 5-year study (from 1994 to 1998) in Tuolumne Meadows and two nearby meadows showed that as little as a few hours of horse or mule grazing per season produced significant decreases in peak standing biomass, basal vegetation cover, litter cover, and relative graminoid cover while increasing bare soil and altering species composition (Cole *et al.* 2004). Simulated intense grazing (by manually clipping plants) caused a decrease in the production of Sierra Nevada wet meadow vegetation, while triggering increased production in dry meadow vegetation (Stohlgren, DeBenedetti & Parsons 1989). Grazing in similar types of mountain meadows in Oregon caused a persistent shift in meadow vegetation composition, with a decline in *Carex scopulorum* and other palatable graminoids (Cole 1981). In wet and mesic mountain meadows of Argentina (dominated by *Poaceae* and *Juncus*, with *Carex*), 20+ years of grazing reduced both above- and belowground biomass and soil organic matter, resulting in a 35% loss of plant and soil carbon (Enriquez *et al.* 2014). Grazing for two years in a Rocky

Mountain montane riparian zone decreased graminoid, shrub, and litter cover and increased bare ground (Tucker & Leininger 1990). Extensive research has documented the negative impacts of grazing on vegetation and stream characteristics in riparian ecosystems (Belsky, Matzke & Uselman 1999).

Herbivory by native mammals can also significantly affect meadow and riparian vegetation. Belding's ground squirrels (*Urocitellus beldingi* Merriam, 1888) are common generalized herbivores in Sierra Nevada subalpine meadows (Sherman & Morton 1984), consuming graminoid leaves, stems, and seeds (Morton 1975; Peacock & Jenkins 1988). They can remove 35-61% of annual aboveground biomass (Jenkins & Eshelman 1984). Mountain voles (*Microtus montanus* subsp. *montanus* Peale, 1848) preferentially inhabit subalpine sedge meadows (Clark 1973), and their selective herbivory can reduce aboveground biomass by 30-72% and drive vegetation composition changes (Howe *et al.* 2006). In riparian areas of the Sierra Nevada mule deer (*Odocoileus hemionus* Rafinesque, 1817) preferentially browse willow (*Salix* spp.) (Loft 1988). Deer browsing effects may be similar to those of elk (*Cervus canadensis* Erxleben, 1777), which have caused well-documented impacts to willow stature (Singer, Mark & Cates 1994; Marshall, Hobbs & Cooper 2013), seed production (Gage & Cooper 2005), and riparian ecosystem function (Wolf, Cooper & Hobbs 2007).

We investigated how herbivory is affecting the sparse low-production vegetation occupying Tuolumne Meadows' groundwater wetland, and riparian willow stature and reproduction. Native herbivory over the past 100+ years may have prevented recovery of the depleted vegetation and maintained the vegetation in an alternate stable state. This study focuses on: (1) the effects of herbivory on the survival of transplants of perennial clonal sedges *Carex scopulorum* and *Carex subnigricans,* and emergence from seed of *Pinus contorta* in a factorial experimental framework, (2) the effect of herbivory on areal plant cover, bare ground, and aboveground biomass, and (3) the effect of deer herbivory on streamside willow height growth, stem frequency, and catkin production to determine if willow structure or reproduction is limited by browsing.

METHODS

To determine the effect of water table depth and 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, each paired with a control plot where natural herbivory was allowed. A total of 20 fenced treatment plots and 20 unfenced control plots (40 total plots) were installed in Tuolumne Meadows in 2011. Ten plots of each treatment type (fenced or control) were located in each of the two primary hydrologic settings within the meadow (dry and wet blocks) to account for distinct differences in water table, soil characteristics, and vegetation composition. In the wet block, the water table was less than 30 cm below the ground surface for an average of 45 days during the snow-free growing seasons of 2012-2014. In the dry block, the water table was within 30 cm of the surface for an average of only 9 days each growing season. Within each wet or dry block, plot pairs (2 plots, 5 m apart) were regularly spaced throughout the representative homogenous vegetation, after which treatment or control status was randomly assigned within each plot pair.

Herbivory exclosures were constructed from galvanized wire mesh with 0.64 cm square holes. Exclosures were 30 cm tall, included roofs, and extended 30 cm below ground into hand dug trenches. Each plot was a 2 m by 2 m square. Because birds were observed perching on the rebar corner posts of the fences, identical corner posts were installed at the control plots to equalize any unintended fertilization effects. All measurements within plots were made at least 20 cm inside the plot edge to reduce edge effects associated with the fence or researcher trampling of the perimeter, for a measurement plot size of 1.6 m by 1.6 m. Vegetation cover was recorded in 2011 and 2015 using a point frame with a 10 cm grid. A total of 256 point readings per 1.6 m by 1.6 m area were taken and averaged within each plot. Aboveground biomass was measured by clipping, drying, and weighing all peak-growing-season non-planted vegetation in a 20 cm x 20 cm square area within each plot each year.

To test whether herbivory is affecting perennial sedge survival, we transplanted field-excavated rhizomes of *Carex scopulorum* and seedlings of *C. 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 *C. subnigricans* germinated and produced seedlings in the greenhouse. Due to the lack of viable *C. scopulorum* seeds, cuttings of rhizomes with attached shoots were taken from existing populations in Tuolumne Meadows and transplanted in early summer 2012. The two *Carex* species are present, but minor components of Tuolumne Meadows' vegetation (Table 2). Twelve live plants of each sedge species were transplanted into each plot. Because *C. scopulorum* is a wetland-obligate plant, this species was planted only in the 10 fenced and 10 control plots of the wet block. *C. subnigricans*, a facultative species, was planted into all plots in both the wet and dry blocks (USDA & NRCS 2017). Transplants were planted and marked in summer 2012 and their survival was measured for the next 3 summers: 2013-2015.

In addition, we investigated the influence 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 removed and stored in a refrigerator until the 2014 field season. In May each plot received a 100-seed batch, sown in a 10 cm radius circle directly onto the surface of bare moist soil and left uncovered, marked at the center for relocation. In summer 2015, all *P. contorta* seedlings within 10 cm of each center marker were counted. It is unlikely that a significant number of the *P. contorta* seedlings were natural recruits. Casual observation of the density of natural background *P. contorta* seed rain in the plots indicates that it is much lower than the sowing density of 1 seed per 3.14 cm^2. The number of pine seedlings that emerged from sown seeds was a combination of the germination rate and seed/seedling mortality from herbivory and other factors. To test for the maximum expected germination and

emergence of seedlings, a well-mixed random sample of 216 lodgepole seeds was sown indoors in late May 2014, in 72 cells filled with a moist peat and sand soil mix. Each cell received 3 seeds and seedling emergence was recorded at least weekly for 140 days. All figures and text that use the term 'seedling' are referring to the planted rhizome and shoot cuttings of *C. scopulorum*, the transplanted seedlings of *C. subnigricans*, and/or sprouted *P. contorta* from seeds sown directly on site.

To determine the effect of deer herbivory on riparian willows, we identified three stream reaches along the Tuolumne River within Tuolumne Meadows where abundant willows (*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 species. At one gravel bar and one bank within each reach we selected a continuous 7 m x 14 m rectangular area, long axis parallel to river flow, of homogenous topography and willow cover. The area was divided into two adjacent 7 m x 7 m plots, and deer fencing treatment or control status was assigned randomly at each of the six reach/landform combinations. In each plot, six parallel 5m-long transects were established, 1 m apart, leaving a 1 m buffer from the plot edge. The end points of each transect were marked with rebar for relocation. 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 every 20 cm along each of the six 5m-long transects per plot. Shoot frequency was calculated as the proportion of measurement locations with a willow stem present. As with herbivory plots in the meadow, the riparian plots were blocked according to hydrologic variability. The two blocks for this study were plots on gravel bars and on the vegetated tops of banks. Gravel bar plots were lower in elevation, closer to the water table, and inundated more frequently.

Survival data for sedge and pine seedlings, and the proportion of flowering willows, related to fencing treatment and hydrologic blocks were evaluated using beta-binomial distributed generalized

linear models (library 'aod' in R, Lesnoff & Lancelot 2012). The beta-binomial distribution is an appropriate model for overdispersed non-negative binary count data. The maximum likelihood probability of success (survival or flowering) was modeled as a function of the independent variables of treatment and block, an intercept, plus a beta-distributed overdispersion parameter modifying either of the independent variables or the intercept.

The change in aboveground biomass and bare ground at the meadow plots and the change in willow height and willow shoot frequency at the riparian plots were modeled using normally distributed linear models. Although change in percent bare ground and change in willow frequency cannot exceed positive or negative 100, the data were nowhere near these limits, so were effectively unbounded. Because these response variables are unbounded continuous values, a normal distribution was appropriate.

We exhaustively evaluated all possible permutations of models containing terms for fencing treatment, hydrologic block, block and fence interaction, and intercept. For the beta-binomial models, an overdispersion parameter, associated with either the fence, hydrology, or intercept variable, was also modeled. Explanatory variables were uncorrelated, and plots of each parameter were visually examined for outliers (none found). Models were ranked by AICc (library 'AICcmodavg in R, Mazerolle 2017) and single model terms were deleted to find the simplest AICc-equivalent (within 2 AICc of the minimum) best model. Partial residual plots were constructed for models with multiple explanatory variables to isolate and visualize the treatment effects of the best model. Maximum likelihood estimates and 95% asymmetric confidence intervals (CI) were calculated for the best beta-binomial models (library 'stats4' in R, R Core Team 2017), while means and standard errors (SE) were reported for normal models.

RESULTS

In the meadow herbivory experiment, no significant changes were found in areal cover of any species from 2011 to 2015. The wet block plots were dominated by *Oreostemma alpigenum* with 38.5% cover, 22.2% bare ground, and aboveground biomass of 124 g m^{-2}. The dry block plots were dominated by *Stipa kingii* with 20.8% cover, 17.3% bare ground, and aboveground biomass of 198 g m^{-2} (Table 2). Over the study period, bare ground in control plots remained statistically unchanged (mean change +2.2% areal cover, ± 2 SE of 2.7% areal cover), while in the treatment bare ground declined significantly (mean change -3.5% areal cover, ± 2 SE of 3.1% areal cover). Aboveground biomass did not significantly change in the control plots (mean change +11 g m^{-2}, ± 2 SE of 38 g m^{-2}) but significantly increased in the treatment plots (mean change +106 g m^{-2}, ± 2 SE of 66 g m^{-2}). The AICc-best models for change in aboveground biomass and bare ground both included only an intercept and treatment term; including terms for hydrologic block or hydrology/fencing interaction did not improve either model.

The survival of both *Carex* species transplants was significantly affected by the fencing treatment. The AICc-best beta-binomial models for survival of *Carex subnigricans* and *Pinus contorta* included terms for the fencing treatment and hydrologic block, but not a fence:hydrology interaction. The best *C. subnigricans* model contained one fitted overdispersion term, modifying the model intercept. In the best *P. contorta* model, two overdispersion parameters were fitted to the fence treatment parameter, one each modifying the control and fenced levels (Table 3). Both *C. subnigricans* and *P. contorta* had significantly higher survival in the wet block. The block and overdispersion effects were removed through partial-residual analysis to illustrate the fencing effects (Figure 11). The largest fencing effect in the meadow plots was the increased survival of *C. scopulorum* seedlings from 21.5% (95% CI 9.9 – 42.1) in the control plots to 68.7% (95% CI 58.1 – 77.2) in the fenced plots. In the riparian experiment the fencing treatment increased the percentage of willows flowering from 24.4% (95% CI 11.3 – 47.6) in control plots to 73.6% (95% CI 68.1 – 78.2) in fenced plots.

In the greenhouse 67% of *P. contorta* seeds germinated and developed into seedlings, with the rate of emergence slowing significantly by the end of the designated 140-day growing season. Although *P. contorta* seedling survival was lower than either of the two sedges, at least 33% of the loss was due to failure of seeds to germinate, even under greenhouse conditions.

Willow height change after 4 years was best modeled with only a fencing treatment term. Control plots lost an average of 7.6 cm (±2SE of 4.3) of height from 2011 to 2015, while fenced plots gained an average of 9.1 cm (±2SE of 5.5), for a net average 4-year treatment effect of +16.7 cm (±2SE of 7.0). The geomorphic/hydrologic position of the willows on bars or banks did not significantly affect height. However, control plots on bars lost less height each year than control plots on banks (Figure 12). Willows on gravel bars were already very short (mean of bar plots in 2011 was 12.6 cm ±2SE of 3.5) and limited in the height they could lose. By comparison, the bank plots at the beginning of the experiment in 2011 had an average height of 31.8 cm ±2SE of 9.9 (Figure 12).

Similarly, change in willow shoot frequency was best modeled with only a fencing treatment term. Control plots lost an average of 8.6% (±2SE of 8.0) shoot frequency, while fenced plots gained an average 5.3% (±2SE of 8.4) frequency for a net average treatment effect of +13.8% (±2SE of 11.4) shoot frequency over the 4-year experiment. Shoot frequency at the start of the experiment, in 2011, was similar between control and fenced plots, with an overall average of 46.6% (±2SE of 16.4).

Table 2. Average cover of naturally occurring (not planted) meadow plant species and bare ground, and total aboveground biomass in the wet- and dry-block control plots. Areal cover sums to more than 100% due to averaging across multiple plots and measurement periods. Species names follow the Jepson eFlora (Jepson Flora Project 2017).

Wet-block species or cover type	Mean areal cover
Oreostemma alpigenum var. *andersonii*	38.5%
Bare ground, no vegetation	22.2%
Eleocharis quinqueflora	12.7%
Muhlenbergia filiformis	8.2%
Antennaria corymbosa	5.6%
Deschampsia cespitosa subsp. *cespitosa*	5.5%
Carex subnigricans	5.4%
Danthonia intermedia subsp. *intermedia*	2.6%
Juncus mexicanus	1.9%
Trichophorum clementis	1.7%
Primula tetrandra	1.1%
Carex scopulorum var. *bracteosa*	0.8%
Mean ± 2SE total aboveground biomass:	124 ± 11 g m^{-2}

Dry-block species or cover type	Mean areal cover
Stipa kingii	20.8%
Bare ground, no vegetation	17.3%
Antennaria corymbosa	13.2%
Danthonia intermedia subsp. *intermedia*	12.5%
Calamagrostis breweri	11.1%
Muhlenbergia filiformis	8.5%
Vaccinium cespitosum	6.6%
Bistorta bistortoides	5.4%
Carex subnigricans	3.7%
Oreostemma alpigenum var. *andersonii*	3.6%
Deschampsia cespitosa subsp. *cespitosa*	1.8%
Trichophorum clementis	1.1%
Pinus contorta subsp. *murrayana*	0.6%
Mean ± 2SE total aboveground biomass:	198 ± 31 g m^{-2}

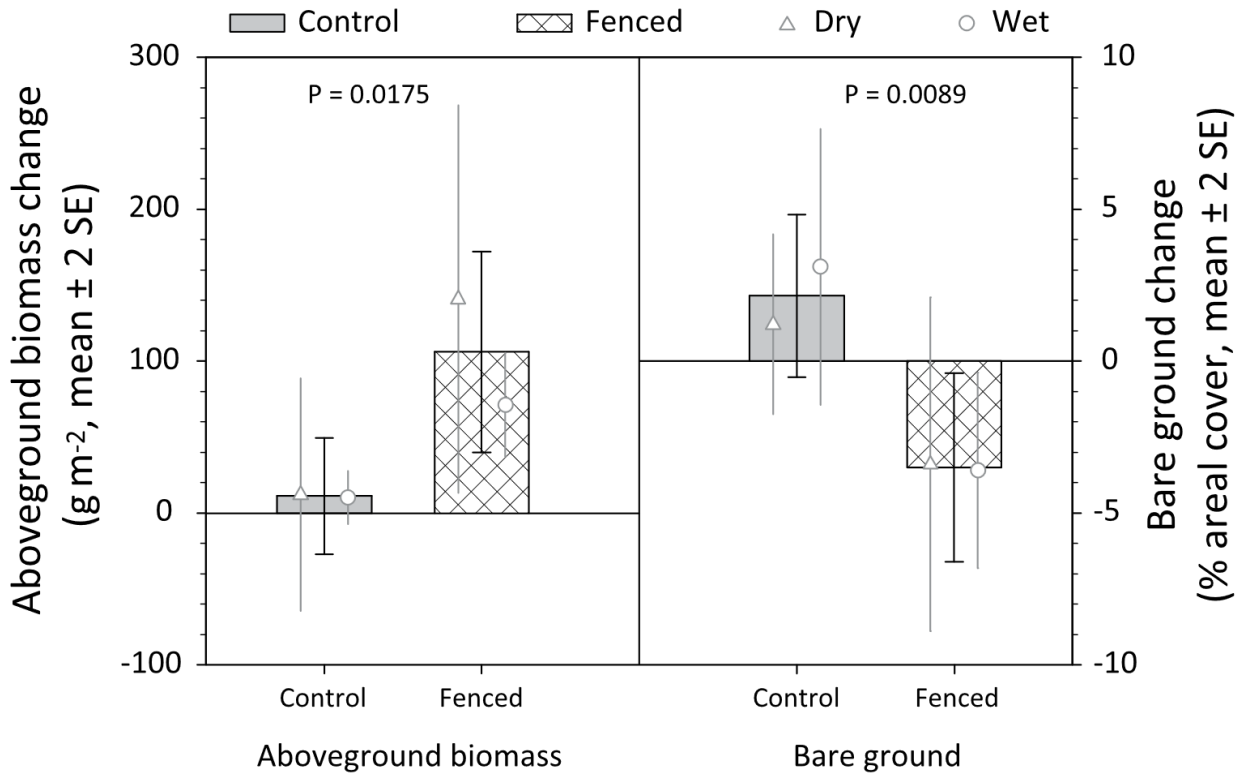

Figure 10. The best-model treatment effect on the 4-year change in aboveground biomass (left) and cover of bare ground (right) in control (gray bars) and fenced (hashed bars) meadow plots. Points display the data divided into the wet and dry hydrologic blocks (hydrologic block was evaluated and rejected for inclusion in the best models for both bare ground and biomass).

Table 3. Summary of the parameter estimates for the AICc-best models. The parameters prefaced with OD indicate over-dispersion factors applied to either the model intercept or the indicated level of the treatment (control or fenced).

AICc-best model	Parameter estimate	Standard error	P-value
Normal distribution models. Parameter and SE estimates are in measured units.			
Bare ground areal cover, change over 4 years			
Intercept	2.1500	1.4480	0.1459
Fence	-5.6500	2.0480	0.0089
Above-ground biomass, change over 4 years			
Intercept	10.9900	27.0300	0.6866
Fence	94.9700	38.2200	0.0175
Willow height, change over 4 years			
Intercept	-7.5670	2.4640	0.0118
Fence	16.6670	3.4850	0.0007
Willow shoot frequency, change over 4 years			
Intercept	-0.0855	0.0402	0.0592
Fence	0.1380	0.0568	0.0355
Beta-binomial distribution models. Parameter and SE estimates are log odds.			
Proportion of willows flowering , in year 4			
Intercept	-1.1710	0.4796	0.0147
Fence	2.1620	0.4929	0.0000
OD.control	0.2347	0.1122	0.0182
OD.fence	0.0032	0.0085	0.3505
Carex subnigricans survival, in year 4			
Intercept	0.0808	0.2352	0.7314
Hydrology	0.9350	0.3088	0.0019
Fence	0.9970	0.3030	0.0010
OD.intercept	0.0882	0.0362	0.0075
Carex scopulorum survival, in year 4			
Intercept	-1.0200	0.3097	0.0010
Fence	1.7670	0.4214	0.0000
OD.intercept	0.1074	0.0540	0.0233
Pinus contorta survival, in year 4			
Intercept	-3.2590	0.2940	0.0000
Hydrology	0.7892	0.3189	0.0133
Fence	1.0490	0.3361	0.0018
OD.control	0.0362	0.0180	0.0225
OD.fence	0.1636	0.0491	0.0004

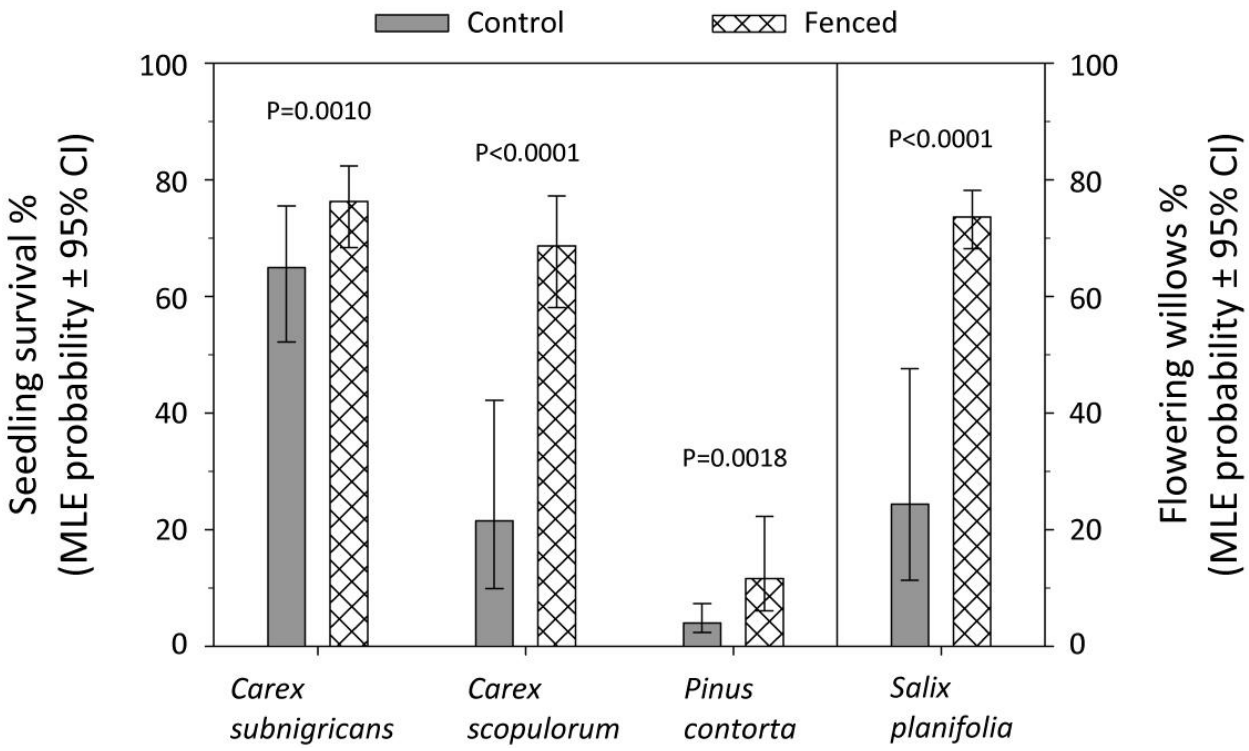

Figure 11. Partial residual plot showing the beta-binomial-modeled maximum likelihood estimate of probability and 95% confidence intervals for fencing treatment effect on planted meadow seedling survival (left) and riparian willow flowering (right). The hydrologic block effect has been removed from the C. subnigricans and P. contorta data displayed here. There was no hydrologic effect in the best model for willow (Salix planifolia.) flowering, and C. scopulorum was only planted in the wet block.

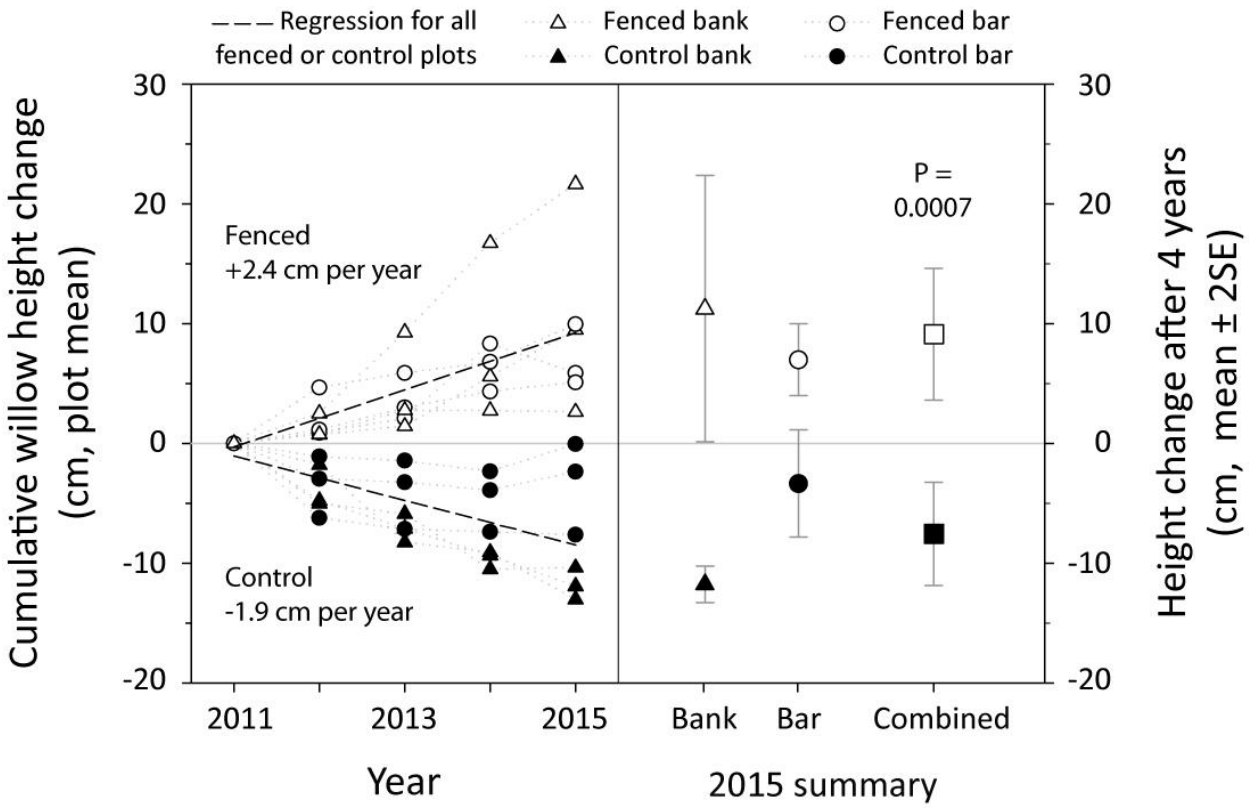

Figure 12. The change in willow height compared to the start of the fencing treatment in 2011. Annual measurements are shown at left, with a significant linear regression fit to each of the fenced or control datasets. A summary of the final year of the experiment (2015) is shown on the right. Bank and bar plot summaries are shown for illustration, although block was not a term included in the AICc-best model for willow height. The fencing-treatment only effect is shown by the bank and bar plots "Combined".

DISCUSSION

Native rodent and deer herbivory is significantly impacting the meadow vegetation community and riparian willows in Tuolumne Meadows. On gravel bars and streambanks, deer herbivory is reducing willow height, shoot frequency, and sexual reproductive capacity. These impacts to willows may be contributing to bank instability, erosion, channel widening, and reduction of bird habitat. A wider channel produces lower stage flows and a lower water table in the meadow riparian zone (Loheide II & Lundquist 2009; Loheide & Booth 2011).

In fenced meadow plots protected from herbivory, bare ground decreased, aboveground biomass increased, and the survival of planted sedges and lodgepole pine was significantly higher.

Survival of *Carex subnigricans* and *Pinus contorta* was also higher in the wet block, but known differences between blocks included water table depth, vegetation composition, and soil characteristics, any or all of which could have produced the observed block effect.

Herbivory effects can help explain why the *Oreostemma alpigenum* dominated meadow vegetation in Tuolumne Meadows appears anomalous when compared with smaller and generally more remote, but otherwise similar, subalpine meadows in the region. A broad survey of Sierra Nevada meadows and riparian areas found at least 10% average cover of *O. alpigenum* in 14 different plant community types, but no community was classified as predominantly *O. apligenum*. The two communities with the greatest *O. alpigenum* cover were dominated by *Carex subnigricans* (mean 60% cover) and *Carex scopulorum* (mean 53% cover), with an average of 33% and 26% *O. alpigenum* cover, respectively, each with an average of 1% bare ground. The community with the highest average bare ground (12%) was dominated by *Carex filifolia* and *Calamagrostis brewerii*, and had 14% *O. alpigenum* cover (Potter 2005). A study of pack stock use in 26 subalpine meadows (not including Tuolumne Meadows) in Yosemite found that *O. alpigenum* plant communities had a mean of 11.2% bare ground in high-use meadows, and a significantly lower mean of 4.1% in low-to-no-use meadows (Ballenger, Baccei & Acree 2010). The same study found 19.0% bare ground in high-use *Carex scopulorum* stands, compared to 5.3% in low-to-no-use stands.

Herbivory is the most likely cause of *Oreostemma alpigenum* dominance, the paucity of *Carex*, and the prevalence of bare ground in the groundwater-supported high-organic-soil wetland in Tuolumne Meadows. There are no major anthropogenic impacts to the groundwater hydrology of the meadow from the most plausible source, the Tioga Pass Road (Cooper *et al.* 2006), and climatic impacts to water table depth would be expected to affect not just Tuolumne Meadows, but all the groundwater-supported subalpine meadows of the Sierra Nevada synchronously. Tuolumne Meadows' large size and relatively early and easy access to shepherds following the Gold Rush may have led to greater historic

grazing impacts compared with smaller, more remote sites. Tuolumne Meadows may have lost most of its perennial clonal sedges, such as *Carex scopulorum* and *Carex subnigricans* which typically dominate wetlands with *O. alpigenum*. This study has shown that current native herbivory significantly reduces the survival of these species, especially *C. scopulorum*. The current dominance of *O. alpigenum* along with a high proportion of bare ground may have been initiated by late 1800s sheep grazing and maintained by relatively lower-intensity native herbivory preventing the recovery of sedges.

Lodgepole pine establishment in meadows is an area of ongoing research and management concern. Establishment frequency in meadows has been correlated with variation in climate (Jakubos & Romme 1993; Millar *et al.* 2004; Lubetkin *et al.* 2017), fire (Norman & Taylor 2005; Frenzel 2012), and livestock grazing (Vankat & Major 1978; Miller & Halpern 1998). In addition, the biotic processes of competition and facilitation can influence establishment patterns, and all of these factors can interact in complex ways (Lang & Halpern 2007; Haugo & Halpern 2010; Halpern *et al.* 2010; Haugo *et al.* 2011; Rice *et al.* 2012). The results of this experiment concur with previous findings that protection from herbivory significantly increases the emergence and survival of lodgepole pine from seed (Johnson 1986; Helms & Ratliff 1987). Ground squirrel populations are strongly affected by climate, particularly winter conditions, so in meadows with small mammals, some of the lodgepole-climate correlation is likely indirect, mediated through fluctuations in herbivore populations (Morton & Sherman 1978; Sherman & Morton 1984).

In the stable groundwater-supported wetland, with thick, 1000+ year-old high-organic soils, the sparse *Oreostemma alpigenum* plant community is not productive enough to offset soil respiration, and so the ecosystem is experiencing a net loss of carbon (see Chapter 3). The organic carbon material in Tuolumne Meadows soils retains the equivalent of 8.8 cm of precipitation as plant-available water, increasing the water-stress-free growing season by 35 days (Ankenbauer & Loheide II 2017). With a low-production plant community, soil is decomposing faster that it is being formed, and the loss of soil

carbon is resulting in a concomitant loss of water holding capacity, which will result in drier site hydrology. If hydrology changes enough, the site will no longer support wetland obligate species such as *Carex scopulorum*. A pilot restoration project is being implemented in the *O. alpigenum* wetland of Tuolumne Meadows, with the goal of establishing large populations of *C. scopulorum* that can persist and spread in the presence of native herbivory. The carbon flux of the restored community is being monitored to determine if the high belowground production of the sedge can offset decomposition, and prevent further loss of soil carbon.

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Chapter 3 – The effect of native herbivory on the net ecosystem exchange of carbon dioxide in Tuolumne Meadows

INTRODUCTION

Organic matter in soil is the largest terrestrial carbon pool, and understanding fluxes to and from that pool is essential for modeling the global carbon cycle (Scharlemann *et al.* 2014). Soil carbon is also essential to ecosystem function, retaining soil water (Hudson 1994; Saxton & Rawls 2006), increasing soil cation exchange capacity (van Erp, Houba & van Beusichem 2001), and supporting the soil microbial community (Drenovsky *et al.* 2004). The net amount of carbon added to or lost from a soil-plant ecosystem (net ecosystem exchange, NEE) is primarily the balance between the carbon extracted from the air by autotrophs via photosynthesis (gross primary production, GPP) and the carbon released back to the air by both autotropic and heterotrophic respiration (ecosystem respiration, ER). In wetlands, flooding can create anoxic soil conditions leading to slower microbial respiration and accumulation of soil organic carbon (Moore & Bellamy 1974). The main source of soil carbon in wetland ecosystems is plant roots (Chimner, Cooper & Parton 2002), which reside in the soil longer than shoot-derived carbon (Rasse, Rumpel & Dignac 2005). Higher plant belowground-to-aboveground ratios (B:A) promote greater relative belowground production which is more likely to contribute to soil carbon storage than aboveground production (De Deyn, Cornelissen & Bardgett 2008). Impacts to a plant community that alter total production or B:A allocation of carbon are likely to affect NEE.

Herbivory occurs in all nearly all ecosystems, but the effects of herbivore-plant interactions on ecosystem carbon balance are not well-understood (Tanentzap & Coomes 2012). Historic herbivory effects can complicate the assessment of present-day vegetation and carbon interactions (Han *et al.* 2014). The mountain wetlands of the Sierra Nevada in California (colloquially termed meadows) experienced intense, widespread, and novel herbivory by sheep and cattle grazing beginning around

1860 in response to the Gold Rush (Kinney 1996). Tuolumne Meadows in Yosemite National Park, one of the largest and most-visited subalpine meadows in the Sierra Nevada, was grazed by domestic sheep from approximately 1860 to 1900 (LeConte 1870; Townsend 1899). The sparse existing vegetation in Tuolumne Meadows is being significantly impacted by native deer and rodent herbivory, and it is difficult to determine how much of the current vegetation and ecosystem state is related to modern versus legacy herbivory impacts (see Chapter 2).

The goal of this study was to determine how small mammal and deer herbivory currently affects the carbon pools and fluxes in Tuolumne Meadows. We expected that (1) control plot vegetation experiencing herbivory would have insufficient GPP to offset carbon lost by ER, resulting in NEE values indicating net carbon lost from the ecosystem, and (2) in fenced herbivore exclosures greater GPP would result in NEE values indicating significantly more carbon retained in fenced compared to control plots.

METHODS

Tuolumne Meadows is a 1.5 km^2 riparian and groundwater wetland complex located at 2,620 m elevation in Yosemite National Park, CA. The Tuolumne River and four small tributaries flow through the meadow and interact with the meadow water table (Lowry *et al.* 2010). A mosaic of plant communities occupies a variety of meadow and alluvial landforms with different soil and water table characteristics (Cooper *et al.* 2006; Ballenger & Acree 2009). On the western end of the meadow, a lateral moraine stores and discharges groundwater to a wetland dominated by *Oreostemma alpigenum*, with higher and drier zones dominated by *Stipa kingii*.

We implemented an experiment that excluded small mammals and deer from treatment plots in Tuolumne Meadows, from fall 2011 to fall 2014. Ten sites were chosen for the study, five each representative of the wet and dry hydrologic settings and separated by at least 40 m. Each site consisted of four plots, two fenced herbivory exclosure treatment plots and two control plots, randomly assigned.

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 30 cm below ground in hand-dug, backfilled trenches. Each plot was 2m by 2m. Because birds were observed perching on the corner posts of the fences, identical corner posts were installed at the unfenced control plots to equalize any unintended effects of birds. In addition, all measurements within plots were made >20 cm from the plot edge to reduce edge effects associated with the fence or researcher trampling of the perimeter immediately around the outside the plots.

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 regularly during the snow-free growing seasons (as early as 5 May to as late as 31 Oct) of 2012-2014. 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 quantify gross primary production (GPP). We measured soil temperature, air temperature, PAR, and soil moisture concurrently with each CO_2 flux reading, and continuously (hourly) at several fixed locations using sensor/data-logger installations. The satellite-sensed Enhanced Vegetation Index (EVI, a measure of greenness) was used to quantify meadow-wide plant phenology.

Aboveground biomass (AGB) was measured by clipping, drying, and weighing all seasonal peak-biomass vegetation in a 20 cm x 20 cm square area within each plot each year. Belowground biomass (BGB) was measured using in-growth root bags (Neill 1992; Chimner & Cooper 2003), which were exhumed, live roots removed, and soil replaced at the same time that AGB clipping occurred.

We modeled carbon dioxide fluxes (GPP and ER) for a 180-day snow-free period from 5 May to 31 Oct to fill in the gaps between our direct gas flux measurements and produce a seasonal carbon budget. GPP was modeled as the product of 5 nonlinear terms associated with measured environmental variables, and 1 linear seasonal-hysteresis term to account for different rates during plant growth or senescence (Figure 13). This model structure was chosen to allow a zero value of any of the terms to result in zero GPP. Graduated shade-cloth measurements were used to model GPP response to changes in PAR parameters for each of the wet and dry vegetation types. An initial rate of increase (Q) and an asymptotic maximum (Gpmax) parameter value within a rectangular parabola PAR term (Riutta *et al.* 2007; Strack, Keith & Xu 2014; Millar *et al.* 2016) were estimated for each of the two vegetation types, wet and dry. The same fitted Q and Gpmax parameters were applied to all five sites with in the same wet or dry block. The other nonlinear term parameters were estimated for each site individually (Table 4).

Table 4. Fitted parameters for the GPP and ER gap-filling models. The Q and Gpmax parameters were fitted for the entire dry or wet hydrologic block vegetation types, using a shade-cloth dataset. See methods for details.

		GPP parameters						ER parameters			
Site	Hydrologic block	Q (PAR)	Gpmax (PAR)	a (VWC)	b (AGB)	c (EVI)	d (Ts)	f (Ts)	g (VWC)	Rs	Rp
1	Dry	0.0013	3.0176	0.1742	0.3853	2.2623	1.1255	2.1514	0.4549	0.6624	0.0211
2	Dry	0.0013	3.0176	0.2913	0.2411	1.4690	1.4632	3.3978	0.5527	0.6041	0.0549
10	Dry	0.0013	3.0176	0.2443	0.2139	1.5434	1.5770	0.7052	0.7306	0.2006	0.4342
27	Dry	0.0013	3.0176	0.3104	0.4623	2.2141	1.2991	2.7406	1.0000	1.0247	0.1704
28	Dry	0.0013	3.0176	0.3530	0.4043	1.5304	1.5816	3.6396	1.0000	0.7678	0.1252
3	Wet	0.0013	3.3552	0.1570	0.6214	2.4579	1.0822	3.2589	1.0000	0.7077	0.0079
4.5	Wet	0.0013	3.3552	0.1921	0.5100	2.3945	1.1558	2.4329	1.0000	0.9303	0.0046
6	Wet	0.0013	3.3552	0.1429	0.5403	1.8921	1.3075	1.8900	1.0000	0.9520	0.0329
8	Wet	0.0013	3.3552	0.3807	0.2386	1.8428	1.5686	2.3909	0.8396	0.9405	0.1025
9.5	Wet	0.0013	3.3552	0.3682	0.1252	1.3982	1.4880	1.2978	0.6636	0.4820	0.4732

Photosynthesis (GPP) model:

(VWC / 0.3) ^***a***	← Volumetric Water Content
*	
(AGB / 100) ^***b***	← Above-ground peak biomass
*	
(EVI / 0.3) ^***c***	← Enhanced Vegetation Index
*	
d ^((Ts-10) / 10))	← Soil temperature
*	
((PAR * ***Q*** * ***GPmax***)/(PAR * ***Q*** + ***GPmax***))	← Saturating PAR function
*	
(1+scaled EVI slope)	← Growth/senescence hysteresis
*	
-1	← GPP negative by convention

Respiration (ER) model:

-- Temp and seasonality are factors to both soil and plant respiration —

f ^((Ts-10) / 10))	← Soil temperature
*	
(1+scaled EVI slope)	← Growth/senescence hysteresis
* {	
--Soil components—	
[	
1 - ((VWC – ***g***) ^2) / (VWC + (***g*** ^2))	← Inverted parabola, soil water
*	
Rs	← Soil respiration at ref. values
] +	
--Plant components—	
[	
Rp	← Plant respiration at ref. values
*	
(AGB / 100)	← Above-ground peak biomass
*	
(EVI / 0.3)	← Enhanced Vegetation Index
]}	

Figure 13. The equations used to model GPP and ER. Estimated parameters are shown in red type. See Table 4 for fitted values.

GPP response to soil temperature (Ts) was modeled as an exponential Q_{10} (the factor by which a 10°C increase in temperature will increase the rate of decomposition) function (Kirschbaum 1995; Fierer *et al.* 2005, 2006). GPP response parameters for volumetric soil water (VWC as proportion), summer peak aboveground biomass (AGB, g m^{-2}), and vegetation phenology as measured by the remotely sensed

Enhanced Vegetation Index (EVI) were all modeled as exponents (Figure 13). By modeling these three parameters as exponents, a zero value for any of the measurements (VWC, AGB, or EVI) would result in a response value of zero, which is desirable. It is expected that no GPP would occur 1) in completely dry, VWC = 0, conditions, 2) with no peak-growing-season plant material (AGB = 0), or 3) when there is no "greenness" visible (EVI = 0). The fitted parameter exponent values express the response relationship: an exponent of 0 indicates the variable has no effect on GPP, ~0.5 is a rapid rise leveling off, ~1 is a linear increase, ~2 is an initially slow response followed by ever-increasing rise. In addition, the exponentially modeled variables are scaled by dividing the measured values by a mid-range reference value. Each variable is equal to 1 at its corresponding reference value: 0.3 for VWC, 0.3 for EVI, 100 for AGB, and 10 for Ts. Therefore, the fitted values for the parameters Q and Gpmax represent the light response at the reference values for the other four GPP-modeled parameters. Note that, by convention, GPP increases from zero in the negative direction, so that higher rates of GPP are more negative.

Ecosystem respiration (ER) was modeled as the sum of two sets of terms; one representing soil respiration and one plant respiration. Thus, plant and soil respiration terms are additive, so if one is zero, the other can still contribute to the modeled ER response, even when plants are absent. Soil temperature and seasonality were modeled as factors common to both soil and plant respiration terms. The soil respiration set of terms consists of an inverted parabolic function of VWC, matching observations of a unimodal peak for respiration response to soil moisture, and a fitted parameter representing the soil respiration rate (Rs) when all parameters are at their reference values (Linn & Doran 1984; Ilstedt, Nordgren & Malmer 2000). Unlike the scaled GPP parameters that have fixed reference values, the VWC function returns a value of 1 at the peak of the unimodal function. The plant respiration set of terms is a linear combination of scaled AGB, scaled EVI, and a fitted parameter representing the plant respiration rate (Rp) when all parameters are at their reference values.

The nonlinear models were optimized by minimizing the root mean squared deviation (RMSD) of predicted vs. observed values separately for each site while iteratively estimating parameter values using the generalized reduced gradient algorithm implemented in a spreadsheet (Frank & Wolfe 1956; Lasdon & Waren 1977, 1981). Numerous model configurations were systematically evaluated for minimum RMSD, mean absolute error (MAE), residual distribution, parsimony, and ecological interpretability. The current model was selected as the best because it contains terms based on empirical research (PAR, VWC, and temperature) with simple and intuitive construction for other terms that lack an empirical basis, and it achieves good prediction of measured values.

Using the GPP and ER models (Figure 13) with fitted parameters (Table 4) and hourly measurements of the environmental variables, we filled in the gaps between measured GPP and ER to estimate the carbon flux at the experimental plots every hour during each 180-day summer growing season for 2012-2014. Using the annualized carbon fluxes and physical parameters determined in other studies (soil bulk density, biomass carbon content, etc.), we estimated the size of the soil carbon pool in Tuolumne Meadows and the change to that pool that the measured seasonal fluxes represent.

RESULTS

The GPP and ER models (Figure 13 and Table 4) explained 68% and 62% of observed variability, with mean absolute error (MAE) of 0.3678 and 0.2032, respectively, and normally distributed residuals (Figure 14, GPP and Figure 15, ER). The modeled seasonal carbon flux, using the hourly measured environmental parameters, indicated that ER flux is approximately double that of GPP, resulting in summer NEE ranging from 469 to 666 g CO_2-C m^{-2} across all block-treatment groups for all 3 years (Figure 16). NEE was significantly higher in the wet block ($p = 0.0004$) and the block and fencing treatment interacted weakly ($p = 0.0484$). Therefore, we examined the treatment effect separately within each block (Figure 17). In the dry sites, differences between control and fence plots in both GPP

and ER were significantly greater than zero in all 3 years. However, NEE was not significantly different than zero in any year although it was positive and increasing each year, and nearly significant in 2014 (p = 0.0671). At the wet sites, the fencing treatment effect on GPP was significantly non-zero in all years, while the fencing effect on ER was not significantly different from zero. The fencing treatment effect on NEE was significant each of the 3 years, indicating that exclusion of herbivory resulted in significantly lower positive NEE values at the wet sites. Total NEE in wet fenced sites was positive in all years, indicating net efflux of CO_2 to the atmosphere (Figure 16). However, the wet fenced sites lost significantly less CO_2 to the atmosphere than did the wet control plots (Figure 17).

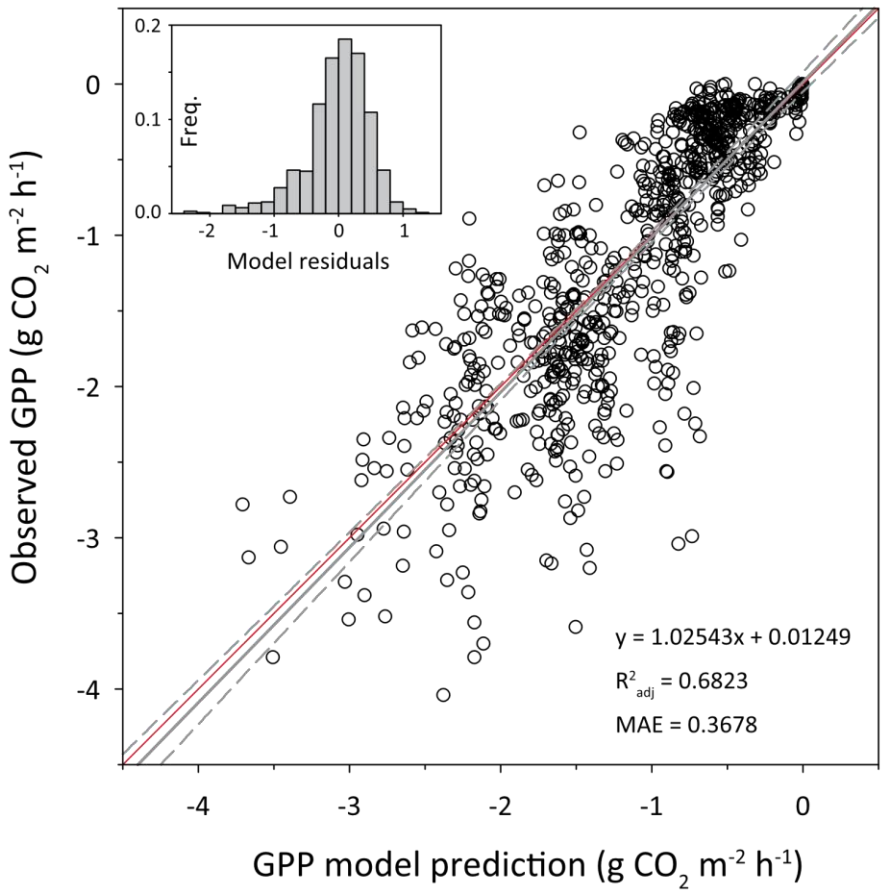

Figure 14. Gross primary production (GPP) model predictions compared to observed values. The 1:1 line is shown in red, and linear fit to the data is shown as a gray line with grey-dashed 95% CI. A histogram of model residuals is shown inset in the upper left. MAE = mean absolute error of the model. Note that the units are expressed as the values measured in the field, mass of carbon dioxide, rather than mass of carbon alone.

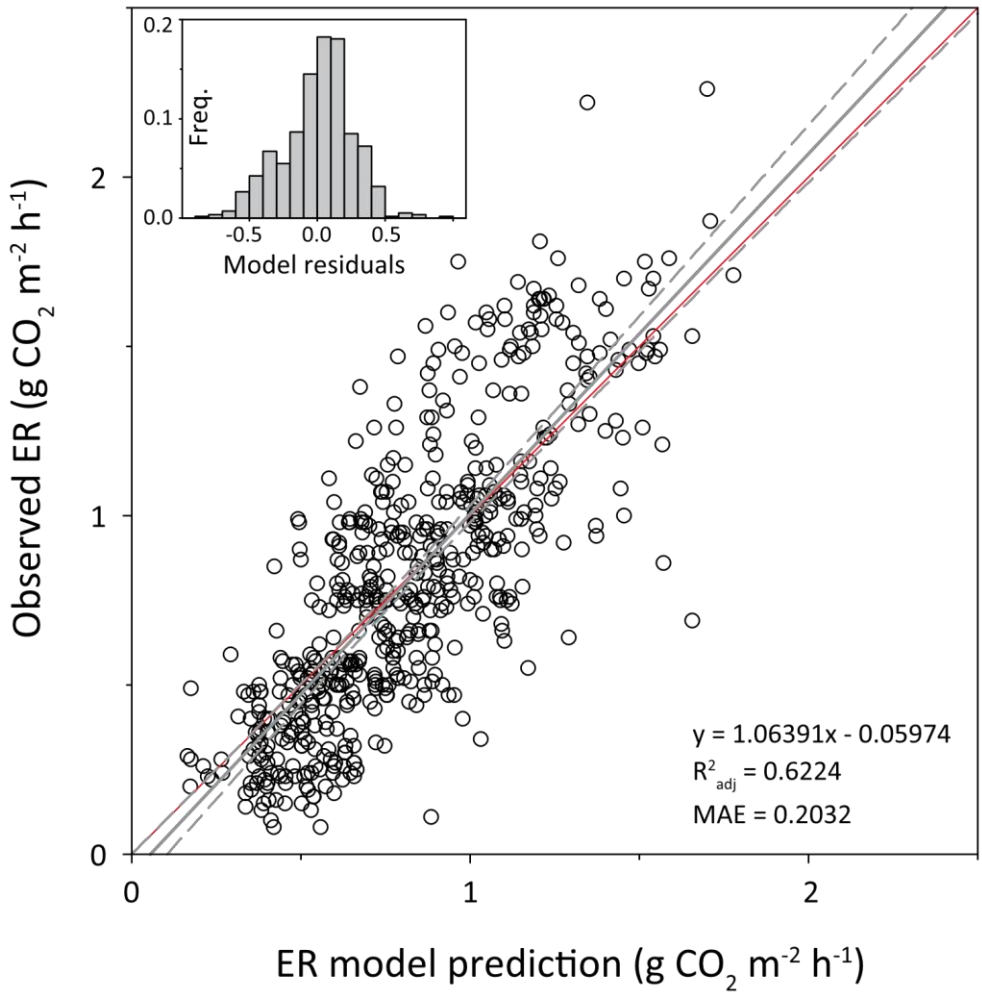

Figure 15. Ecosystem respiration (ER) model predictions compared to observed values. The 1:1 line is shown in red, and linear fit to the data is shown as a gray line with grey-dashed 95% CI. A histogram of model residuals is shown inset in the upper left. MAE = mean absolute error of the model. Note that the units are expressed as the values measured in the field, mass of carbon dioxide, rather than mass of carbon alone.

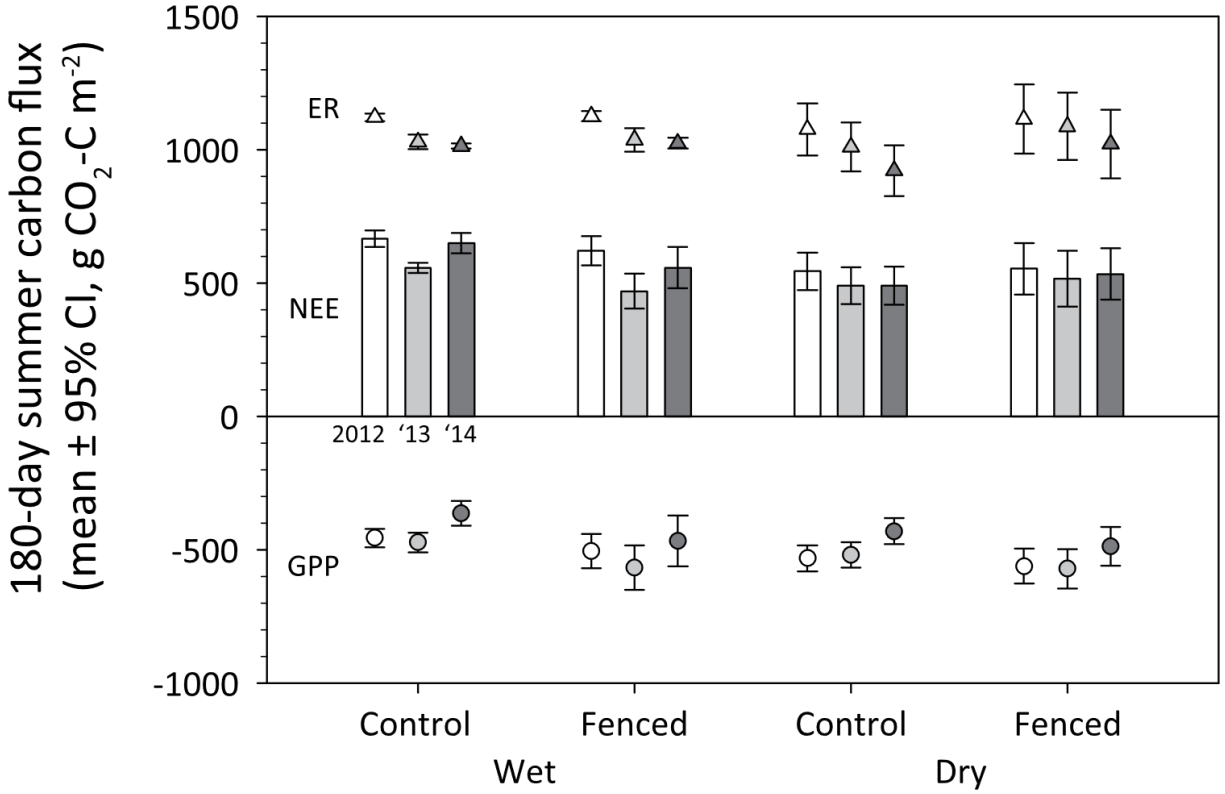

Figure 16. The full gap-filled model of carbon in each block-treatment group, for the 3 study years, 2012 (white bars), 2013 (light grey), and 2014 (dark grey). Note: units are carbon mass.

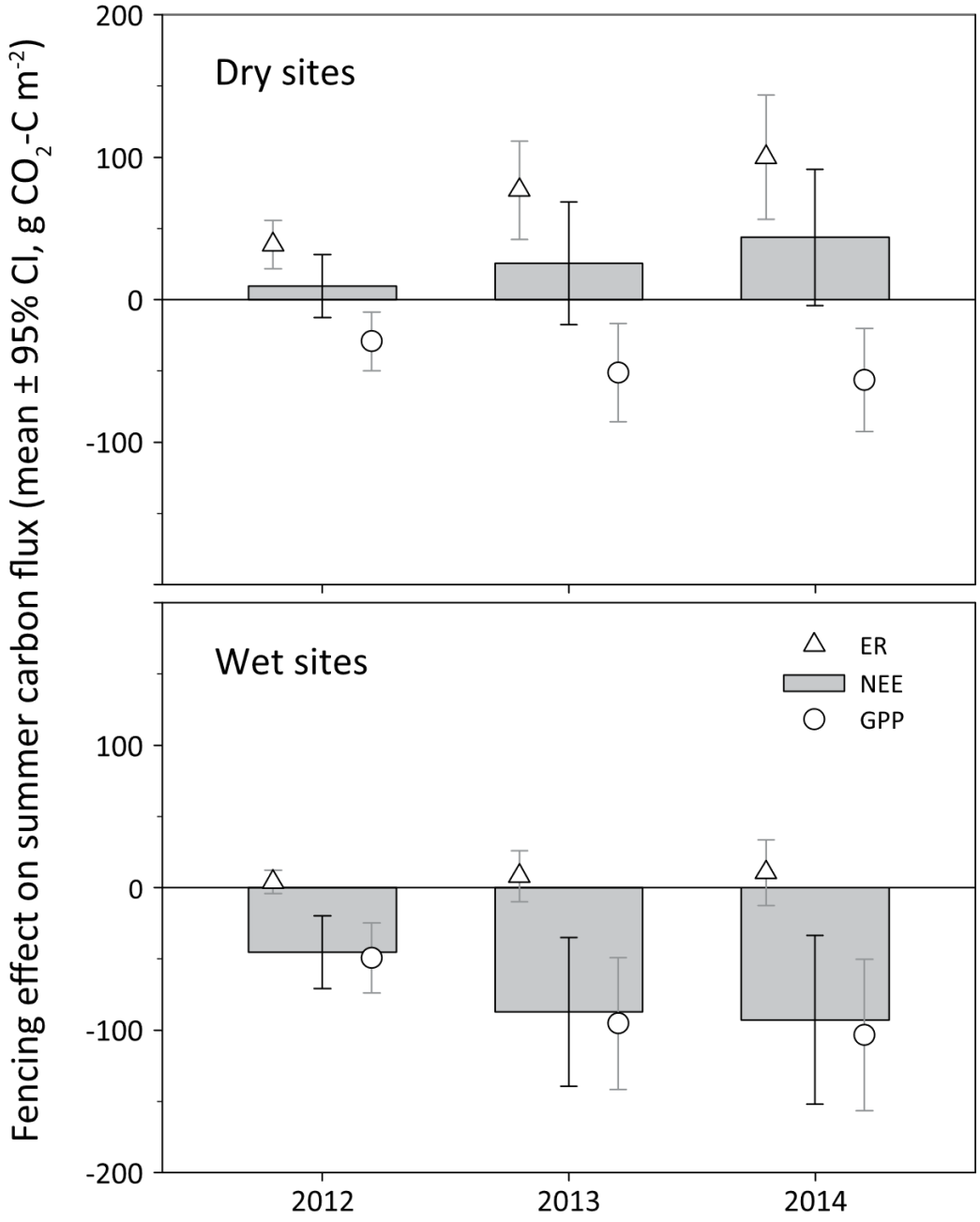

Figure 17. The difference between fenced and control plot seasonal carbon flux in dry (upper panel) and wet (lower panel) for 2012-2014. Note: units are carbon mass.

Aboveground, belowground, and full plant (above + below) biomass changes in wet fenced plots were significantly greater than zero, and significantly different than the changes in wet control plots (Figure 18). The average total belowground biomass was 177 g m^{-2} in the wet control plots and 207 g m^{-2} in the dry plots. Average total aboveground biomass was 128 g m^{-2} in the wet control plots and 200 g m^{-2} in the dry control plots (Table 5).

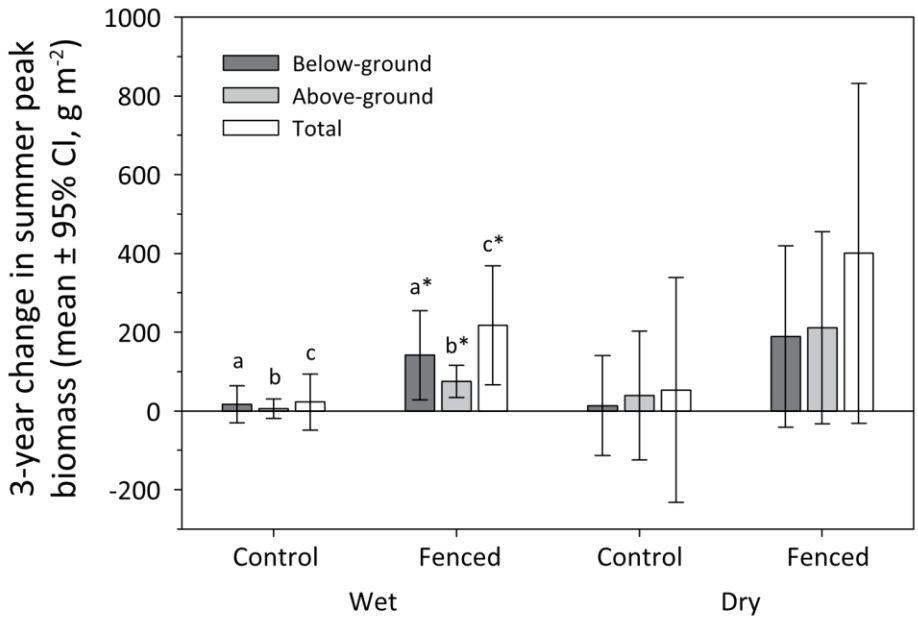

Figure 18. The change in belowground, aboveground and total biomass from 2011 to 2014. Note that these mass measurements are for dry biomass, not converted to carbon-only weight. See Table 5 for control plot absolute biomass totals (as opposed to between-year change) and biomass to carbon conversion. P-values for significant differences: a-a = 0.0219; b-b* = 0.0037; c-c* = 0.0120. Additionally, a*, b*, and c* are the only datasets significantly different than zero, as can be seen by the lack of overlap of the 95% CI with zero.*

The soil carbon pool was quantified using data on soil organic matter, carbon content, and bulk density, from other studies (Table 5). These data indicate that, in the top 80 cm of soil, there are 38 kg C m^{-2} in the wet block and 31 kg C m^{-2} in the dry block. The modeled NEE values from this study indicate that 1.64 % of this soil C is lost per summer in the wet control plots, and 1.66 % is lost in the dry control plots. The fencing treatment reduces this loss to 1.44 % per summer in the wet fenced plots, but

increases the estimated loss to 1.75 % in the dry fenced plots (Table 5). However, the fencing treatment NEE effect was not shown to be significant (in 2014, p = 0.0671) in the dry block (Figure 17).

Table 5. Summary of the carbon budget in the wet and dry hydrologic blocks of Tuolumne Meadows.

Carbon budget component	Wet	Dry	
Below-ground live plant biomass, control plot mean	177.47	206.68	g m^{-2}
Below-ground live biomass C content [a]	33.79	33.79	%
Below-ground live plant C, control plot mean	59.97	69.84	g C m^{-2}
Above-ground live plant biomass, control plot mean	128.11	200.09	g m^{-2}
Above-ground live biomass C content [b]	43.70	43.70	%
Above-ground live plant C, control plot mean	55.98	87.44	g C m^{-2}
Below-ground biomass : Above-ground biomass	1.39	1.03	ratio
Below-ground C : Above-ground C	1.07	0.80	ratio
Soil organic matter, by mass (in top 80 cm) [c]	17.13	10.96	%
Soil organic matter C content [d]	55.61	55.35	%
Soil bulk density [d]	0.50	0.63	g cm^{-3}
Soil C content (in top 80 cm)	38.10	30.57	kg C m^{-2}
Mean summer C loss (2012-14 control plot NEE)	0.62	0.51	kg C m^{-2}
Soil C pool lost per summer, control	1.64	1.66	%
Mean summer C loss in fenced plots	0.55	0.53	kg C m^{-2}
Soil C pool lost per summer, fenced	1.44	1.75	%

a (Wang *et al.* 2005, 2010; Kumar, Udawatta & Anderson 2010)
b (Poorter & Pothmann 1992; Jo & McPherson 1995; Jones & Muthuri 1997; Chimner & Cooper 2003; Giese *et al.* 2003; Hughes *et al.* 2006; Wang *et al.* 2010; McFarland *et al.* 2016)
c (Baldwin, unpublished data; Ankenbauer & Loheide II 2017)
d (Baccei 2014).

DISCUSSION

Vegetation production (GPP) was insufficient to offset respiration losses (ER), leading to a net loss of carbon from Tuolumne Meadows. In the control plots exposed to herbivory, the wet sites lost an average of 0.62 kg C m^{-2} each summer, and the dry sites lost 0.51 kg C m^{-2}. At the wet sites, the plots that were fenced and protected from herbivory had higher GPP and unchanged ER, and so lost less carbon, 0.55 kg C m^{-2}, per summer. At the dry sites increased production in the fenced plots was offset by increased ER, and net carbon losses were similar to the control plots. The period of this study, from

installation of the experiment in fall 2011 through the three summer growing season measurements in 2012-2014, coincided with a millennial-scale drought in California (Griffin & Anchukaitis 2014). Our findings that all plots had seasonal net losses of carbon must be considered in the context of this drought. Because soil moisture, temperature, and growing season length are influenced by climate conditions, it is likely that net ecosystem exchange would be different in wetter years. Measurements from a range of climatic conditions will be needed to validate against our model for non-drought conditions.

Our measured and modeled carbon flux rates are similar to those found in many other studies. For example, Delaney Meadow located approximately 5 km north of Tuolumne Meadows, had an average July ER flux of 0.59 g CO_2 m^{-2} h^{-1} (Blankinship & Hart 2014), and a Canadian peatland had ER fluxes ranging from 0.5 – 1.0 g CO_2 m^{-2} h^{-1} (Strack *et al.* 2014). Fens in the Colorado Rockies had hourly rates of GPP of 0 – 5 g CO_2 m^{-2} h^{-1} and ER of 0 – 2 g CO_2 m^{-2} h^{-1}(Millar *et al.* 2016), which are very similar to our observed range of hourly rates (Figure 14 and Figure 15). Millar *et al.* used a similar gap-filling method to produce seasonalized carbon flux estimates for GPP of 400 – 800 g CO_2-C m^{-2} and ER of 400 – 1000 g CO_2-C m^{-2}. The Colorado fen sites ranged from net loss to net storage of C, with a range of seasonal NEE from -250 to 300 g CO_2-C m^{-2}.

A study measuring carbon flux during the summers of 2011-2013 in Dana Meadows, 12 km east of Tuolumne and 360 m higher in elevation (Arnold, Ghezzehei & Berhe 2014) had similar results. Their measurements in the drought years of 2012-2013 overlap with ours. Peak summer aboveground biomass (AGB) was similar to our control plots (~200 g m^{-2}) and their 165-day seasonalized ER measurements of 700 – 1500 g C m^{-2} were similar to our 180-day ER values of ~1000 g C m^{-2}. Their measurements during 2011, a short growing season of 106 days following a snowy winter, show higher peak ABG of 200 – 520 g m^{-2} and lower seasonalized ER of 400 – 650 g C m^{-2}. They attribute the higher 2012-13 ER to drier soil conditions that rapidly decomposed soil carbon. However, the different lengths

of growing season over which they summed seasonal ER (106 days in 2011, 163 in 2012, and 167 in 2013) explain most of the between-year carbon flux differences. This indicates that the daily ER rate is similar in summers following wet or dry winters. So, rather than soil dryness causing greater daily rates of ER in 2012 and 2013, it is likely that the greater seasonal ER is simply a result of having more days in the season, each with about the same daily ER rate as in the wet season of 2011.

Furthermore, Arnold *et al.* attribute the lower 2012-13 AGB to plant-damaging frost events during the abnormally early snow-free seasons, while plants remained protected under snow in 2011. This is certainly a possibility; however, it is not the only explanation for why the 2011 summer following a snowy winter would have had higher peak AGB. The 50-200 g m^{-2} higher AGB that they observed in the short, wet season of 2011 compared to the succeeding drought years of 2012-13 is similar to the AGB response to herbivory that we observed in our fencing treatment (75-200 g m^{-2}). This is important because the Dana Meadows Belding's ground squirrel (*Urocitellus beldingi* Merriam, 1888) population is strongly affected by climate, with severe mortality and major population reductions occurring during severe winters (Morton & Sherman 1978; Sherman & Morton 1984). Belding's ground squirrels are common in Sierra Nevada subalpine meadows including Tuolumne Meadows. They are generalized herbivores of graminoid leaves, stems, and seeds (Morton 1975; Peacock & Jenkins 1988) and can remove 35-61% of annual aboveground biomass (Jenkins & Eshelman 1984). This level of herbivory corresponds with our fencing treatment effect.

Casual observation of the Belding's ground squirrels in Tuolumne Meadows during 2012-2016 indicated a large population actively grazing our control plots in both the wet and dry hydrologic blocks all summer. By contrast, the Tuolumne Meadows Belding's population in the summer of 2017, following a winter with one of the highest snowpack accumulations on record, appeared much smaller and less actively grazing the meadow study area. A study of the Belding's ground squirrel population in Tuolumne Meadows, and its response to annual climate fluctuations, is needed to determine whether

squirrel populations respond predictably to winter conditions. Because climate and herbivory co-vary and both influence carbon flux, it is important to implement another herbivory exclosure study that spans both wet and dry years and explicitly monitors herbivore activity.

We have demonstrated that mammal herbivory has significant effects on plant production and carbon flux in Tuolumne Meadows. Because at least one significant meadow herbivore's population dynamics are linked to climate conditions, correlative studies of meadow processes that consider climate factors alone may be confounded by herbivory effects, leading to potentially erroneous conclusions.

Our gap-filling model provides a physically-based method for determining growing season carbon dioxide fluxes from periodic direct flux measurements and hourly-logged environmental parameters. Although the carbon dioxide fluxes are well modeled they provide an incomplete accounting of all C fluxes. Allochthonous inputs of forest litter and dissolved organic carbon (DOC) may occur during spring floods. External inputs were not captured by our measures of GPP, but their decomposition would have added to ER. Other potential sources of non-GPP carbon that were not quantified include insect movement and the transfer and defecation of grazed material. Although these sources and transfers of C were not accounted for, they are likely to be minor in comparison to GPP and ER and would not influence our conclusion of net C loss in Tuolumne meadows during the study years. Our calculated seasonal respiration fluxes exceeded GPP by approximately 0.5 kg m-2, and we noted no significant outside inputs, so this net loss is most likely decomposition of the soil carbon pool.

Despite a significant fencing treatment effect, elimination of native mammal herbivory did not restore enough plant production to offset ecosystem respiration. It is possible that GPP and ER would be much closer to balance in non-drought years with shorter growing seasons, and potentially reduced herbivore populations. Ongoing studies at Tuolumne Meadows are assessing carbon flux in wetter years.

However, there are indications that the vegetation community at Tuolumne Meadows contains more bare ground and fewer belowground-productive species than in a similar nearby meadows.

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Chapter 4 – Effects of Groundwater Pumping on the Sustainability of a Mountain Wetland Complex, Yosemite National Park, California

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SUMMARY

Groundwater pumping from mountain meadows is common practice in many regions of the world. However, there is little quantitative analysis of the hydrologic or ecological effects of pumping. We analyzed the effects of groundwater pumping in Crane Flat, a fen and wet meadow complex in Yosemite National Park, California from 2004-2010 using nested monitoring wells and piezometers, groundwater modeling, and vegetation plots. Fens in the Sierra Nevada, such as Crane Flat, have formed over thousands of years where inflowing groundwater maintains the water table near the soil surface even on average to dry water years, and fen formation and persistence relies on perennial flow of groundwater into meadows.

Daily head pressure and water table declines observed at sampling locations within 100 m of the pumping well were strongly correlated with the timing and duration of pumping. The effect of pumping varied by distance from the pumping well, depth of the water table when the pumping started, and that water year's snow water equivalent (SWE). Pumping in 2004, 2007, 2008, and 2009 all years with below average SWE and/or early melting snowpacks, resulted in the water table and piezometric head pressure declining to just above, or below (respectively), the base of the fen peat body by mid-summer. Pumping in 2005, 2006, 2009 and 2010, years with higher SWE and later melting snowpack, resulted in much less water level drawdown from the same pumping schedule. The numerical model confirmed the

water table is a consequence of convergent groundwater flow paths from two inflow sources, and also the strong dependence of summer water table position on the amount of precipitation during the preceding winter and spring. The short system memory of the system reflects the relatively small volume of permeable aquifer sediments, as well as the direct hydraulic connection between the recharge areas and the fen. Predictive scenarios developed using the model showed that even in a dry water year like 2004, distinct increases in fen water table elevation can be achieved with reductions in pumping. Site vegetation composition analyzed using canonical correspondence analysis indicated that maintenance of a high water table during summers following low snowpack water years had a more significant influence on vegetation composition than depth of water table in wet years or peat thickness. This highlights the significant impact that water level drawdown due to pumping has on wetland vegetation. Plots closest to the pumping well have the deepest summer water tables, and plots further from the well generally had higher water tables in 2004 and 2005.

Key Words: Fen, groundwater pumping, modeling, mountain, meadow, water table.

INTRODUCTION

Mountain meadows are groundwater dependent ecosystems with seasonally or perennially high water tables and highly productive herbaceous vegetation that limits tree invasion (Lowry *et al.* 2011, Loheide *et al.* 2009). Meadows provide vital ecosystem services by maintaining the biotic and geochemical integrity of mountain watersheds. They are critical habitat for many plant (Hajkova *et al.* 2006, Jimenez-Alfaro *et al.* 2012) and animal (Semlitsch 2000) species, support regional biodiversity (Stohlgren *et al.* 1998, Hatfield and LeBuhn 2007, Flinn *et al.* 2008, Holmquist *et al.* 2011), form carbon-rich soils (Chimner and Cooper 2003), and filter water by storing or transforming mineral sediment and nutrients (Hill 1996, Knox *et al.* 2008, Norton *et al.* 2011). In most mountain regions in the temperate zone meadows cover less than 2% of the landscape, and their persistence is threatened by human

activities such as road building and logging that can increase sediment fluxes, overgrazing by domestic livestock that can alter meadow vegetation and cause soil erosion, and dams, diversions, channel incision, ditching and groundwater pumping that alters meadow hydrologic regimes (Patterson and Cooper 2007, Loheide and Gorelick 2007, Chimner *et al.* 2010). The effect of hydrologic alteration on meadows is poorly understood, however hydrologic changes are often identified as the main cause of conifer tree invasion into meadows (Jakubos and Romme 1993, Vale 1981).

Several ecological processes maintain mountain meadows in their treeless state, including seasonally or perennially high water tables and highly productive vegetation (Lowry *et al.* 2011), climate and landform (Jakubos and Romme 1993, Zald *et al.* 2012), fire regime (Norman and Taylor 2005), and herbivory (Manson *et al.* 2001). In the Sierra Nevada of California many mountain meadows receive sufficient groundwater discharge to maintain areas of surface soil saturation throughout the nearly precipitation-free growing season (Cooper and Wolf 2006).

Two main types of mountain meadows occur in western North America: wet meadows that have seasonal saturation in the root zone, and fens that are perennially saturated (Cooper *et al.* 2012). Organic matter production and decomposition are nearly equal in wet meadows, which limit organic matter accumulation in soils. Fens form where the rate of organic matter production exceeds the rate of decomposition due to suppressed microbial activity in saturated, anoxic soils, allowing partially decomposed plant matter to accumulate over millennia, forming organic, or peat soils (Moore and Bellamy 1975). Fens support a large number of plant, amphibian and aquatic invertebrate species that rely on permanent water availability. They are uncommon in steep mountain landscapes because slopes are excessively well drained (Patterson and Cooper 2007). However, where hillslope aquifers recharged by snowmelt water support sites of perennial groundwater discharge, fens have formed (Benedict 1982). Radiometric dating indicates steady peat accumulation in mountain fens in western North America through the Holocene, suggesting long-term hydrologic stability in groundwater-fed fens (Wood 1975,

Bartolome *et al.* 1990, Chimner and Cooper 2003).

Seasonal and inter-annual variation of groundwater level and water chemistry influences the floristic composition and production of fen vegetation as well as the rate of peat accumulation (Allan-Diaz 1991, Cooper and Andrus 1994, Chimner and Cooper 2003). Even short periods of water table decline allow oxygen to enter soils, increasing organic matter decomposition rates and initiating soil and vegetation changes (Cooper *et al.* 1998, Chimner and Cooper 2003). Ditches and water diversions are commonly constructed to lower the water table of fens (Glaser 1983, Glaser *et al.* 1990, Wheeler 1995, Fisher *et al.* 1996, Chimner and Cooper 2003), however, groundwater pumping may also influence water levels in fens and other wetlands (Johansen *et al.* 2011).

Previous studies have addressed the effects of groundwater pumping on riparian ecosystems, coastal wetlands, prairie potholes, and intermittent ponds (Winter 1988, Bernaldez *et al.* 1993, van der Kamp and Hayashi 1998, Alley *et al.* 1999). Groundwater pumping in riparian areas can result in the death of leaves, twigs and whole trees, such as cottonwoods (Cooper *et al.* 2003). However, little is known about the long-term effects of groundwater pumping on mountain meadows. Quantitative models developed to analyze pumping in mountain valleys and basins must consider the characteristic steep terrain and bedrock outcrops in these watersheds, as well as the limited volume of aquifer sediments and strong seasonality of precipitation inputs.

More than 3 million people visit Yosemite National Park each year, most during the dry summer months. Providing a reliable public water supply for staff and visitors is a critical issue. The California climate produces abundant winter precipitation and nearly rain-less summers in the Sierra Nevada. Most mountain soils dry excessively (Lowry *et al.* 2011) and most small streams are intermittent during the summer (Lundquist *et al.* 2005). Thus, surface water supplies are limited and most water for human use in Yosemite National Park is derived from groundwater sources. Some deep groundwater sources are

available, such as along the Merced River in Yosemite Valley, while others are from shallow aquifers. One such shallow aquifer is located at Crane Flat, an important visitor services area that supports a large wet meadow and fen complex important for foraging bears, deer, great gray owls and other wildlife. A single production well was installed in Crane Flat meadow in 1984 and provides water for a campground, gas station, residences, and an environmental campus. The well was drilled 122 m deep, with the intention of drawing water from a deep bedrock aquifer, and the influence of pumping on the meadow ecosystem was assumed to be minimal.

This study was designed to analyze the influence of groundwater pumping on the Crane Flat mountain meadow complex in Yosemite National Park, California. Specifically, we address the following questions: (1) How does groundwater pumping influence the water table in a meadow supported by a shallow aquifer? (2) Can a physically based numerical model be used to predict the effects of pumping on meadow water levels for small and large snow years? (3) What are the long-term effects of pumping on the meadow vegetation composition, (4) Are there pumping regimes that might sustain the hydrologic processes that support the Crane Flat wetland complex?

STUDY AREA

Crane Flat is a 20-hectare meadow complex, located at 37°45’16”N and 119°48’9”W, in the west-central portion of Yosemite National Park, California, USA (Figure 19). Land surface elevations at Crane Flat range from 1870 to 1890 meters above mean sea level (m amsl). The underlying watershed bedrock is igneous intrusive Arch Rock Granodiorite and El Capitan Granite, with the metamorphic Pilot Ridge Quartzite outcropping on the northwest side of the study area. A surface layer of peat 10 to 140 cm thick covers 0.5 ha of the meadow. Most of this area is a fen (Figure 19) that we define as a groundwater-supported wetland with 20-40 or more cm of organic soil. The peat is underlain by mineral sediments comprised of sand- and gravel-sized particles. This material is a mixture of weathered

bedrock, glacial till, and colluvium derived from adjacent slopes. The sand and gravel sediments are over 10 m thick in this area. Other portions of Crane Flat are wet meadows with mineral soil. During mid- to late-summer the organic soils are cracked and uneven with patchy vegetation suggesting oxidation and subsidence (Leifeld *et al.*, 2011). Upland areas support conifer forest dominated by white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and lodgepole pine (*Pinus contorta*).

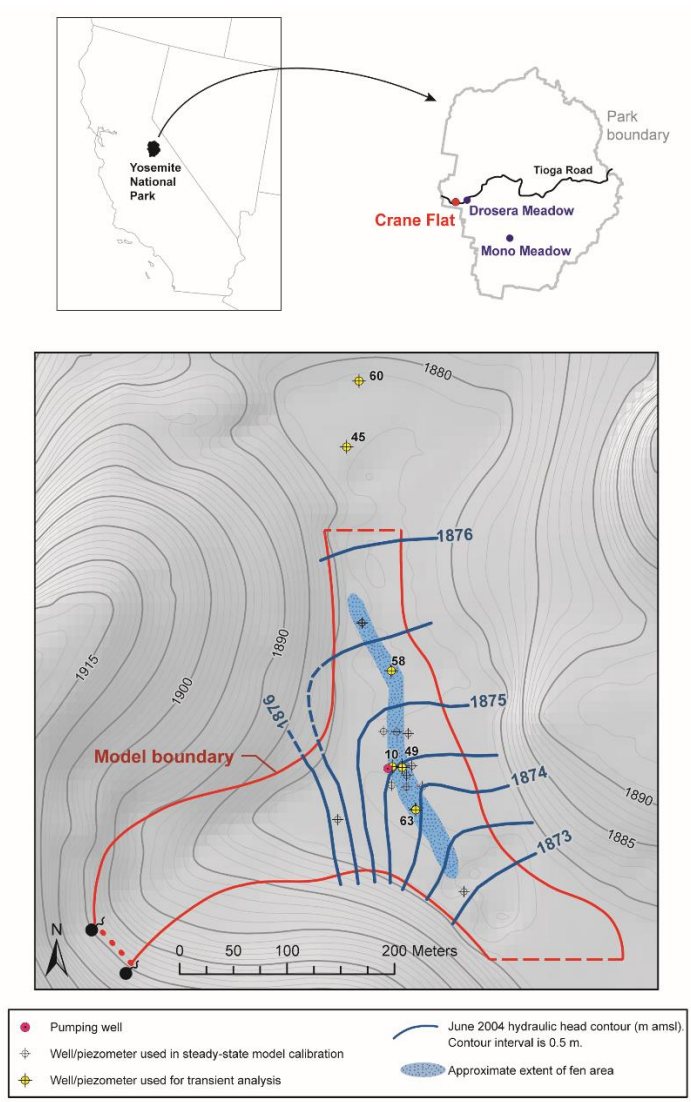

Figure 19. Overview of the Crane Flat area showing land-surface elevation contours (1-m interval) from a 10-m digital elevation model (USGS National Elevation Dataset). Hydraulic head interpretation is based on piezometers that are open to the sand and gravel. Model boundary segments: dashed line indicates a head-dependent flux boundary; dotted line indicates a constant-head boundary; solid line indicates a no-flow boundary.

The sand and gravel sediments comprise the primary near-surface aquifer unit at Crane Flat. High water levels around the fen are produced by convergent groundwater flow paths originating from two areas. Springs that emerge from faults in the metamorphic bedrock (west arm springs, Fig.1) provide a source of water that locally recharges the aquifer in the western portion of the study area. Inflow from valley sediments to the north represents the other major source of groundwater inflow to the fen. In addition to these two main inflow areas, the aquifer is recharged directly by precipitation (primarily snowmelt) throughout the meadow. Intermittent surface water flow does occur during snowmelt. These surface flows are characterized by low velocity, occurring over a rough vegetated surface, and are generally not contained within well-defined channels. During wet years, intermittent surface water is observed between April and July. However, saturated conditions at the fen are not dependent on surface water inflow.

We considered two reference sites, Drosera Meadow (37°46’0”N, 119°45’44”W) and Mono Meadow (37°40’31”N, 119°34’58”W), to analyze the hydrologic regime and vegetation of undisturbed fens. Drosera Meadow is 7.03 ha in area located 3.79 km northeast of Crane Flat at 2070 m elevation, and Mono Meadow is 5.69 ha at 2080 m elevation, 21.6 km southeast of Crane Flat (Figure 19).

The Crane Flat pumping well is located at the edge of the fen as shown in Figure 19. The well is 122 m deep, with the upper 15 m of borehole sealed with a solid steel casing, while the bottom 107 m is uncased. The casing was built to be a sanitary seal preventing surface water and near surface groundwater from leaking into the well casing. The pump intake is at 98 m depth (Crews and Abbott, 2005) and has a maximum production of 127 to 137 L/min. Packer testing conducted by Crews and Abbott (2005) indicated that the vast majority of pumped water comes from the upper portion of the well, above a depth of 27.7 m. Below this depth, the fractured granite has very low permeability and does not contribute significant water volumes during pumping. Therefore, the productive interval of the well is between 15 and 27.7 m below ground surface (bgs). During the summer period of high water

demand, pumping occurs for 8 to 12 hours each night, to produce 60,000 to 100,000 L for storage. On an annual basis the largest volumes of water are needed in July and August, particularly weekends when visitation is highest.

Precipitation and snow-water-equivalent data, recorded at the Gin Flat weather station (37°46'1"N, 119°46'23"W) ~ 3 km northeast of Crane Flat at 2150 m elevation, was obtained from the California Department of Water Resources (http://cdec.water.ca.gov). During the study period of water years 2004-2010 peak snow water equivalent (SWE) ranged from 39.7 to 107.5 cm, and the timing of peak was as early as 9 March and as late as 19 April (Table 6). A water year as defined by the U.S. Geological Survey is the 12-month period between 1 October and 30 September designated by the calendar year in which it ends.

Table 6. Date and peak snow water equivalent (SWE) for the water years 2004–2010 for the Gin Flat climate station, located 3.7 km NE of Crane Flat, and 260 m higher in elevation. Also shown are total water year (October 1–September 30) precipitation (Total precip.), and the date that snow melted from the station (<1 cm).

Year	Peak date	Peak SWE (cm)	Total precip. (cm)	Melt date
2004	Mar 09	71.9	88.7	May 03
2005	Apr 13	107.5	205.8	Jun 11
2006	Apr 19	75.0	161.9	May 28
2007	Mar 15	39.7	73.6	May 03
2008	Mar 12	79.0	NA	May 16
2009	Mar 27	57.2	88.7	May 12
2010	Apr 16	86.8	96.1	Jun 14

METHODS

Field measurements and hydrologic analysis

We collected and analyzed water table levels and hydraulic heads, as well as soil and vegetation composition data in Crane Flat Meadow, and the two reference sites from 2004-2010 (Figure 19). A total of 57 monitoring wells and piezometers were installed in Crane Flat in June 2004. Nests of two or more instruments (a well and one or more piezometers) were installed in the peat body near the Crane Flat

pumping well to determine differences in pumping response at different soil depths and types. We do not present the entire 57-well dataset, but use a representative subset of the data from wells with long, high quality records.

Monitoring wells were installed by hand-augering 10 cm diameter bore holes and fitting them with 5 cm inside-diameter fully slotted Schedule 40 PVC pipe, capped on the bottom, backfilled around the pipe with native soil, and bailed to develop the water flow to the well. In fen areas where the peat layer exceeded 20-40 cm in thickness, monitoring wells were installed completely within the peat body.

Piezometers were installed in the fen around the pumping well with screened sections completely below the peat layer in the underlying coarse sand. The total depths (approximate measurement points) ranged from 116.5 cm to 315 cm bgs. Each piezometer consisted of a steel drive point with a 38 cm long screened section of 3 cm diameter schedule 80 steel pipe coupled to sections of unslotted steel pipe. The drive point and pipe were hammered to the desired depth using a post-pounder striking a drive cap.

The location and elevation of all monitoring wells and piezometers, and ground surface topography were surveyed using a TOPCON® total station. The survey data were used to calculate water level elevations and to develop a detailed representation of the land surface. The wells and piezometers were instrumented with pressure transducers (Global Water GL-15 and Onset Hobo Level Logger) that recorded water level at fixed time intervals of 5, 30, or 60 minutes, depending on the season and application. Non-vented loggers were corrected for atmospheric pressure using data from an on-site barometric pressure data logger. See Table 7 for a complete description of the physical properties of the wells and piezometers.

Table 7. Physical characteristics of the water level data collection instruments.

Well #	Pipe diameter (cm)	Instrument type	Depth of lowest opening (cm)	Depth of highest subsurface opening (cm)	Peat thickness (cm)	Depth to coarse sand/ gravel (cm)	Distance to pump (m)	Longitude (WGS84)	Lattitude (WGS84)	Elevation (m)
10	5.1	well	-127.0	0.0	-132.0	-132.0	4.53	-119.80185	37.75472	1874.660
45	1.3	piezometer	-116.5	-116.5	-27.0	-86.0	301.49	-119.80232	37.75740	1876.499
49	3.2	piezometer	-315.0	-277.0	-130.0	-155.0	13.45	-119.80174	37.75471	1874.542
58	5.1	piezometer	-129.0	-99.0	-103.0	-103.0	90.95	-119.80185	37.75552	1875.423
60	5.1	well	-122.3	0.0	0.0	-123.0	360.00	-119.80213	37.75794	1877.568
63	5.1	piezometer	-209.0	-179.0	-100.0	-155.0	46.51	-119.80160	37.75436	1874.225
Pump	15.2	pumping well	-12200.0	-1585.0	?	?	0.00	-119.80189	37.75470	1874.714

We analyzed vegetation composition in a 1 m radius circular plot around each monitoring well/piezometer nest. In each plot a complete list of vascular plants and bryophytes was made, and the canopy coverage, by species, was estimated. The percent cover of plant species occurring at 17 well locations was analyzed to determine the correlation with hydrologic parameters and peat thickness using Canonical Correspondence Analysis, CCA (PC-ORD v4.37). Two hydrologic variables were used, the highest water table elevation during the very dry 2004 growing season (July-Sept), and the lowest water table during the very wet 2005 growing season. These were selected because 1) the maintenance of a high water table in a dry year is critical for supporting peat and fen vegetation and 2) deep water table declines in a wet year would be indicative of an abnormal impact such as pumping drawdown. Distance from each plot to the Crane Flat pumping well is shown on the CCA diagram as unique symbols, but distance was not used in the CCA calculation. The CCA axes were calculated as linear combinations of the hydrologic parameters and peat thickness for each plot. Vegetation data displayed on the ordination include the plot location relative to other plots and plant species centroids, which is the average position of species along the axes based on their abundance at each well. To evaluate the statistical significance of the CCA, we ran a 9,998-iteration Monte Carlo test that randomly reassigned the environmental data to different plots. The proportion of Monte Carlo outcomes with an axis-1 eigenvalue greater than the observed eigenvalue is the p-value for the CCA.

On September 20th, 2005, Todd Engineers (Crews and Abbot 2005) conducted a packer test on the pumping well at Crane Flat to determine the relative contribution to well discharge of shallow-source

water (<28 m) and deep-source water (>28 m). An inflatable packer was installed at 28 m depth to isolate the sections of the bore hole above and below this depth. Separate pumping tests were conducted above and below this seal to determine the contribution to well production from shallow and deep aquifers.

Numerical Modeling

Groundwater flow in an unconfined aquifer can be described by the following partial differential equation:

$$\nabla \cdot (Kb\nabla h) + W = S_y \frac{\partial h}{\partial t} \quad (1)$$

where h is hydraulic head (L), K is the hydraulic conductivity (L/T), S_y is the specific yield (-), b is the aquifer thickness (L), and W is a source/sink term (L/T) that includes the effects of groundwater pumping and distributed areal recharge to the water table. We used the finite difference code MODFLOW-SURFACT (HydroGeoLogic, 2011) to obtain numerical solutions to Equation (1) for the study area.

The numerical model encompasses an area of 6.77 ha. Boundary segments are shown in Figure 19. The segments to the north (inflow) and southeast (outflow) were treated using head-dependent flux boundaries (General Head Boundary cells in MODFLOW-SURFACT). For the northern inflow boundary, external heads were specified using data from piezometer 45 (Figure 19). No wells or piezometers were available to the south of the model domain. Therefore, external heads for the outflow boundary were estimated using the interpreted hydraulic gradient in the southeastern part of the meadow (Figure 19). During transient simulations the external boundary heads were varied using available time-series data, which allowed for realistic seasonal variations in the simulated boundary flows. Constant-head cells were used along the southwestern boundary to simulate inflow from the west arm springs. The remainder of the model boundary was specified as no-flow, following the bedrock outcrop around the meadow. The total modeled aquifer thickness is 27.7 m, which is the depth of permeable material determined by packer testing at the Crane Flat pumping well (see Study Area).

The horizontal grid spacing in most of the model domain is 2 m × 2 m. Near springs in the southwestern part of the meadow we used larger grid cells. This part of the domain is more than 100 m from the main meadow area and detailed simulation of heads and flow directions was not necessary. The model column spacing was increased gradually from 2 to 10 m in this southwestern area. The aquifer thickness was discretized using seven finite-difference layers. Surveyed ground elevations were used to develop a TIN representation of the land surface. This surface provided a starting point to define the model layers. The top model layer has a uniform thickness of 1 m and is used to locally represent the peat body, which has distinct hydraulic properties, in the fen. Layer 2 is 1.5 m thick, and extends from 1.0 to 2.5 m below the ground surface. The layer spacing was systematically increased and the deepest model layer, 7, has a thickness of 8.3 m. There are 101,389 active grid cells in the model. Given the presence of relatively thin layers near the land surface, some model cells are in the unsaturated zone during flow simulations. In certain areas, the water table drops below the base of a model layer during the summer dry season and may subsequently rise into the layer during periods of higher recharge. We adopted the pseudo-constitutive relation approach in MODFLOW-SURFACT to effectively deal with the drying and rewetting of finite-difference cells (Panday and Huyakorn, 2008).

Hydraulic properties were varied using a zonation approach. The peat (Figure 19) was assigned a hydraulic conductivity of 5.8 m/d, which is the average value estimated from slug tests at three monitoring wells that were located near (< 20 m) the Crane Flat pumping well and installed within the peat. The modeled specific yield value was 0.35. These values for K and S_y are within ranges reported for sedge root peat (Boelter, 1965; Schimelpfenig *et al.*, 2013). To reproduce the observed steep head decline between the springs ($h \approx 1895$ m elevation) and the meadow, we used a low-conductivity zone throughout the west arm area. Although no wells have been drilled near the springs, the overall steep hydraulic gradient suggests less weathering of the bedrock in this area. Elsewhere throughout the model, we assumed a constant hydraulic conductivity within each layer.

Model Calibration

For the initial steady-state model development and calibration, we utilized hydraulic heads measured in early June 2004 (Figure 19). Groundwater levels in the meadow tend to be relatively stable in late spring, prior to warm and dry conditions and increased groundwater pumping in the summer. The calibration considered point locations where measured hydraulic heads can be clearly attributed to the peat or underlying sand and gravel material, based on stratigraphic logs from well/piezometer installation. In total, there were seven heads within the peat body and 14 from the sand and gravel used in the calibration. During steady-state model calibration, hydraulic conductivity values were adjusted within reasonable ranges for all zones except the layer 1 peat.

Transient simulations

A 16-month transient simulation was conducted using data collected between June 2004 and September 2005. This period includes the last four months of the 2004 water year and the entire 2005 water year (October through September). The simulation time was discretized using monthly stress periods with daily time steps. Pumping and recharge rates, as well as the external heads for the head-dependent flux boundaries, were varied on a monthly basis using averages from measured data (gauged pumping at the meadow well, measured precipitation, and measured hydraulic heads near the north and southeast boundaries). Well pumping is simulated in layers 6 and 7. This modeled vertical interval corresponds to the aquifer depth where there is significant water production, as determined from the well completion details and packer testing (Crews and Abbott 2005).

Simulated hydraulic heads from the transient model were compared to observed heads at selected well/piezometer locations where continuously recorded data are available from pressure transducers. During initial transient runs, we further calibrated the model to identify appropriate values of specific yield and groundwater recharge rate. The transient modeling allowed us to investigate the

seasonality of the system and evaluate the relative importance of precipitation and pumping in controlling fen area water levels.

Two additional predictive transient simulations were conducted to investigate how water levels within the fen would be affected by reduced groundwater pumping. These simulations focus on the high groundwater use summer months (June-Sept). The 2004 water year was treated as the base case (i.e., a representative dry year). The first predictive scenario considers a 50% reduction from the actual June-Sept 2004 pumping. The second scenario considers no groundwater pumping during this 4-month period.

RESULTS

Water Level Variations

Winter water use in the Crane Flat area is minor and pumping occurred only 1-2 times per week. During September 2005, after a full summer season of daily pumping, water extraction produced distinct daily water level changes. For example, water levels in piezometer 49 had a sharp decline of up to 40 cm beginning around midnight, followed by a rapid rise in the morning to near the previous day's high (Figure 20). Water level declines in well 10, which is completed within the peat body, were up to 10 cm per day. Monitoring well 60, included as a reference well, is 360 m from the Crane Flat pumping well. Daily water level fluctuations at this well were not substantially affected by the pumping at Crane Flat (e.g., measured water levels did not respond to increased or decreased pumping intensity on Sept 12 and Sept 14-16, respectively). Rather, the smaller variation at well 60 is associated with evapotranspiration. The magnitude of water level decline was controlled by the duration of pumping, distance to the pumping well, and whether the well/piezometer is open to the peat body or underlying gravel. Nights with longer duration pumping produced deeper and more sustained water level declines than those with shorter duration pumping. Pumping occurred for an extended period on the weekend of

Sept 11-12 in 2005 and produced a very large drawdown (Figure 20). Nights with short duration or no pumping resulted in a water level rise, for example on September 14-15, 2005 (Figure 20).

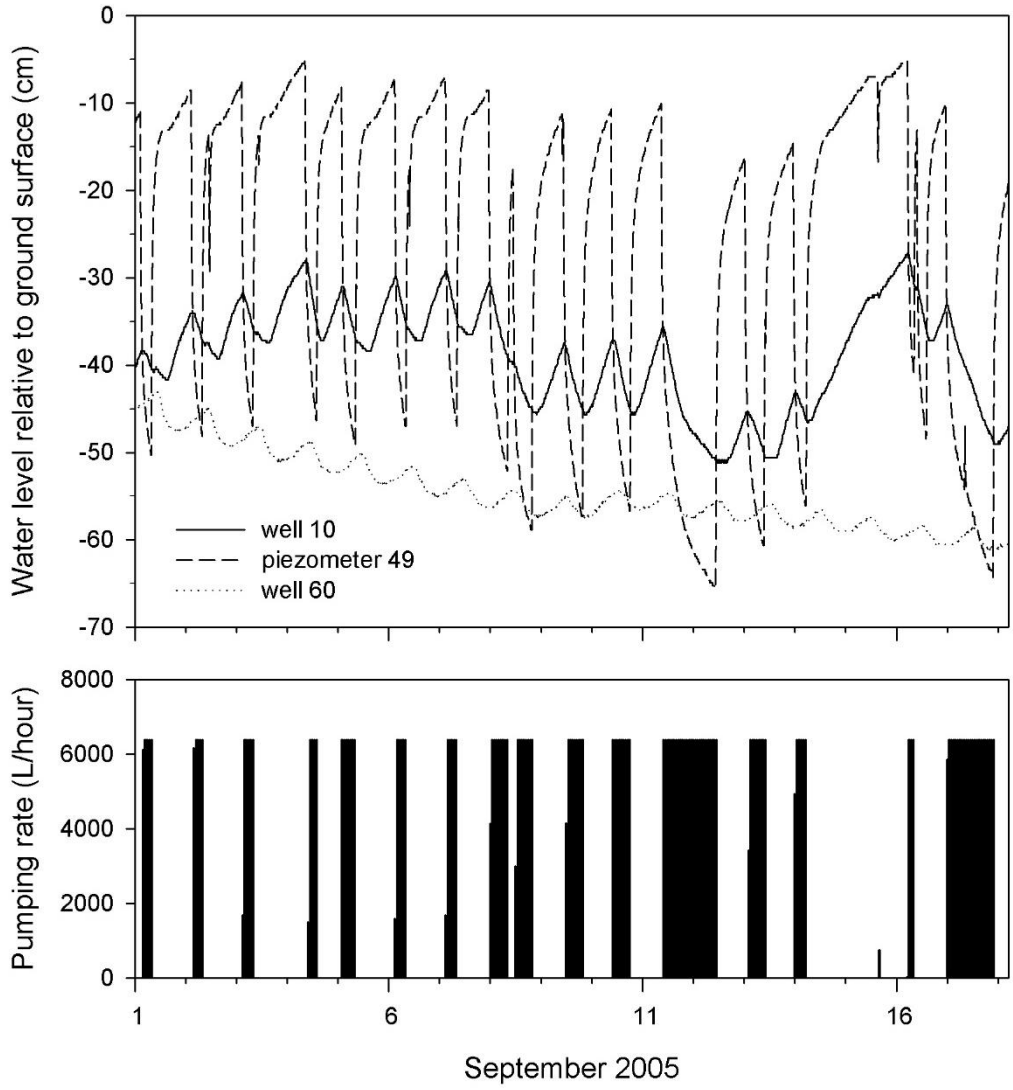

Figure 20. Hourly pumping (bottom panel) for 1–17 September 2005, and the water level response in wells 10 and 60 and piezometer 49.

During the summer of 2004, following a very early melt of the snowpack (Table 6) the water table in Crane Flat declined more than 100 cm from mid-June to late-September (Figure 21). Similar deep declines also occurred in 2007, 2008, and 2009, all years with low or early peaking, and thus early melting, winter snowpack (Figure 21, Table 6). In water years 2005, 2006 and 2010 larger winter

snowpacks persisted into April, resulting in water level declines of less than 50 cm under a similar summer pumping regime. In 2004 the water table was below the entire peat body by August, while in 2005 water levels remained within the peat body for the entire summer. Groundwater levels in the reference meadows Drosera and Mono remained within a few cm of the soils surface for the entire summers of 2004 and 2005.

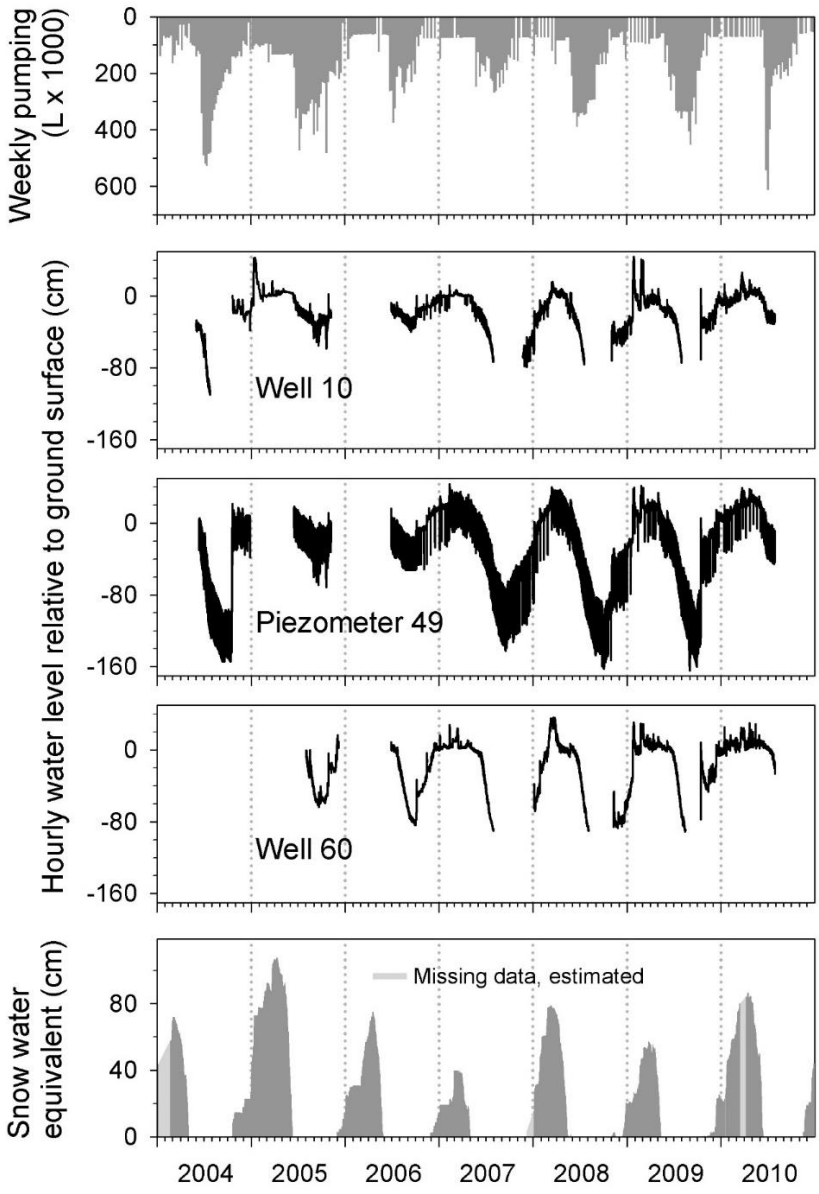

Figure 21. Weekly pumping schedule and volume, hourly water level in wells 10 and 60 and piezometer 49, and daily snow water equivalent for the years 2004–2010.

The meadow water table responded rapidly to precipitation events. A 3.0 cm precipitation event on June 30, 2004 produced a 10 to 20 cm water table rise that lasted for more than 6 days. A 10.8 cm precipitation event on October 16, 2004 led to a 100 cm water level rise.

On September 20th, 2005 a packer test was completed in the Crane Flat pumping well. With a packer inflated at 28 m depth to isolate the lower portion of the bore hole, a pump placed at 61 meters depth initially produced high pumping rates (72 L/min) that declined to a stable rate of less than 11 L/min after 10 minutes, at which point the pump discharge was observed to be sputtering, indicating that the water level in the well had dropped to the level of the pump (61 m). The measured stable discharge rate below the packer (11 L/min) divided by the estimated water level draw down in the well of 33m (61m - 28m), gives an estimate of the specific capacity for the well of 0.33 L/min/m of drawdown. This value corresponds to other values (0.33-0.66 L/min/m of drawdown) that Todd Engineers measured in near-by wells drilled into fractured granite bedrock (Crews and Abbott 2005).

When the packer was deflated to initiate the pump test in the open, unrestricted well bore hole, water was heard cascading down from the upper (<28 m deep) section into the just-pumped lower section. Pumping from the unrestricted bore hole produced a stable rate of 83 L/min, drawdown of 6.1 m giving a specific capacity of 13.6 L/min/m of drawdown, much higher than would be expected from fractured granite bedrock.

During the packer test, water levels in several monitoring wells were recorded. Only piezometer 49 showed a response, and then only to pumping from the open bore hole, not to deep pumping from below the packer. The head in piezometer 49 also dropped after the cessation of pumping and following deflation of the packer, when water was heard cascading down the borehole.

For all years, 2004 through 2010, when the head pressure in piezometer 49 remained within the thickness of the peat body (above -130 cm) the water level measurement made just before the initiation

of a pumping period explained 72% of the variation in how far the water level was drawn down after 6 hours of pumping ($P << 0.0001$, $R^2_{adj} = 0.7172$, 537 df). For head pressures that remained within the depth of the peat body, greater 6-hour drawdown was observed when initial water levels were lower (black-outlined triangles, Figure 22). However, once the drawdown caused piezometer 49 head pressures to drop below the base of the peat (when initial water level plus 6-hour drawdown was below -130 cm), the relationship reversed and lower initial water levels resulted in less 6-hour drawdown ($P<<0.0001$, $R^2_{adj} = 0.2728$, 111 df; grey-outlined triangles in Figure 22). Note that pre-pumping water levels were always above -130 cm, within the peat body. Drawdown after 6 hours of pumping caused initial water levels of about -70 cm and below to drop beneath the base of the peat body (at -130 cm), into the underlying sand and gravel.

The water level drawdown in well 10 was negatively correlated with the initial groundwater level (black-outlined circles, Figure 22). Deeper initial water levels resulted in smaller drawdowns, although this correlation only accounted for 3% of the variation in drawdown ($P = 0.0002$, $R^2_{adj} = 0.0314$, 411 df).

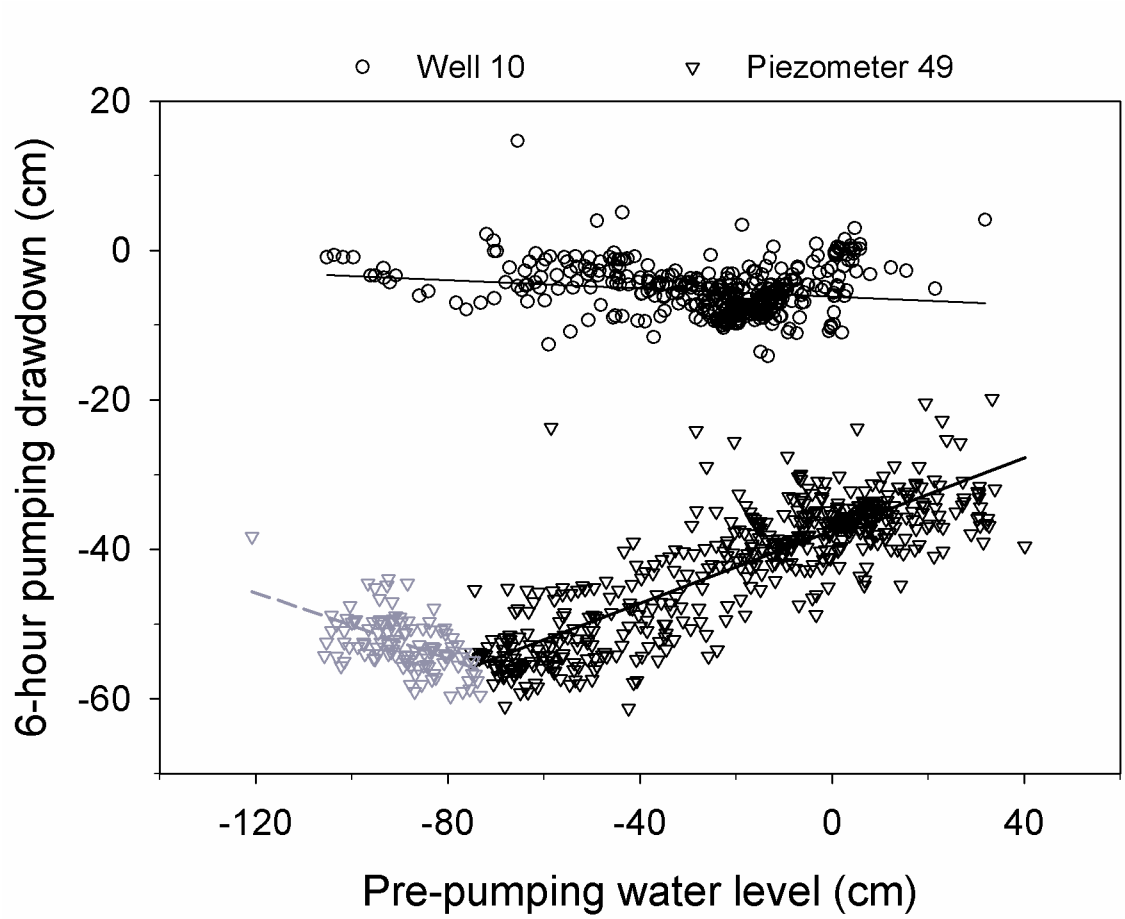

Figure 22. Water level drawdown in well 10 and piezometer 49 after 6 h of pumping, relative to pre-pumping water level, analyzed for the years 2004–2010. Black triangles show piezometer 49 for water levels (pre-pump + drawdown) above −130 cm (within the surface peat layer), Y = −37.4975 + 0.2431x, R^2_{adj} = 0.7172, p << 0.0001, 537 df. Gray triangles show piezometer 49 for water levels below −130 cm (within the sand below the peat), Y = −72.3662 − 0.2219x, R^2_{adj} = 0.2728, p << 0.0001, 111 df. Black circles show well 10, Y = −6.6967 − 0.0608x, R^2_{adj} = 0.2561, p << 0.0001, 597 df.

Numerical Modeling

Calibrated hydraulic conductivities ranged from 10 m/d in the top layer to 0.3 m/d in the bottom layer. These values bracket the hydraulic conductivity (4.4 m/d) that was estimated during an October 2005 aquifer test and are within typical ranges reported for sands and weathered granite (Freeze and Cherry 1979). The low-conductivity value used in the west arm area was 0.04 m/d. Excluding the peat, the calibrated specific yield was 0.25 in the top layer and 0.1 in all other layers. Transient modeling results were not sensitive to specific storage values.

Using observed hydraulic heads from early June 2004, the mean error and mean absolute error (MAE) for the steady-state model are 0.02 m and 0.12 m, respectively. The observed heads ranged from 1873.05 m to 1875.71 m. The model reasonably reproduces the heads over the entire data range; the MAE/range is 0.045. Simulated inflow in the steady-state model included spring flow at the southwest boundary (22.6 m^3/d), flow across the northern head-dependent boundary (27.9 m^3/d), and areal recharge derived from precipitation (25.6 m^3/d). The simulated outflow across the southeast boundary was 76.1 m^3/d.

The transient model provided a good match to observed hydraulic heads in the central and southern parts of the meadow (Figure 23). For well 10, which is screened within the peat (elevation corresponding to model layer 1), and piezometer 63, completed in the underlying coarse sand (layer 2), the model captured the marked decline in heads during summer 2004 and the rapid rise that occurred in October 2004. In the northern part of the meadow (piezometer 58), the simulated heads are lower than the observed heads by 0.1 to 0.5 m, however the model accurately reproduces the trend behavior.

The 16-month transient model considered variations in recharge and pumping between June 2004 and September 2005. For each stress period, a single recharge rate was applied over the modeled area. Given the scale of the model and the relatively coarse temporal discretization (monthly stress periods), the modeled recharge represents a net inflow (recharge – ET). Although this recharge rate was treated as a calibration parameter, its value was constrained by the measured precipitation at Gin Flat meteorological station. In mid-October 2004, a storm delivered 10.8 cm of precipitation, resulting in a rapid water level rise throughout the meadow. The model-calibrated recharge rate was 80% of the measured precipitation for this event. For the remainder of the simulation period, the calibrated recharge varied from 5 to 25% of monthly precipitation.

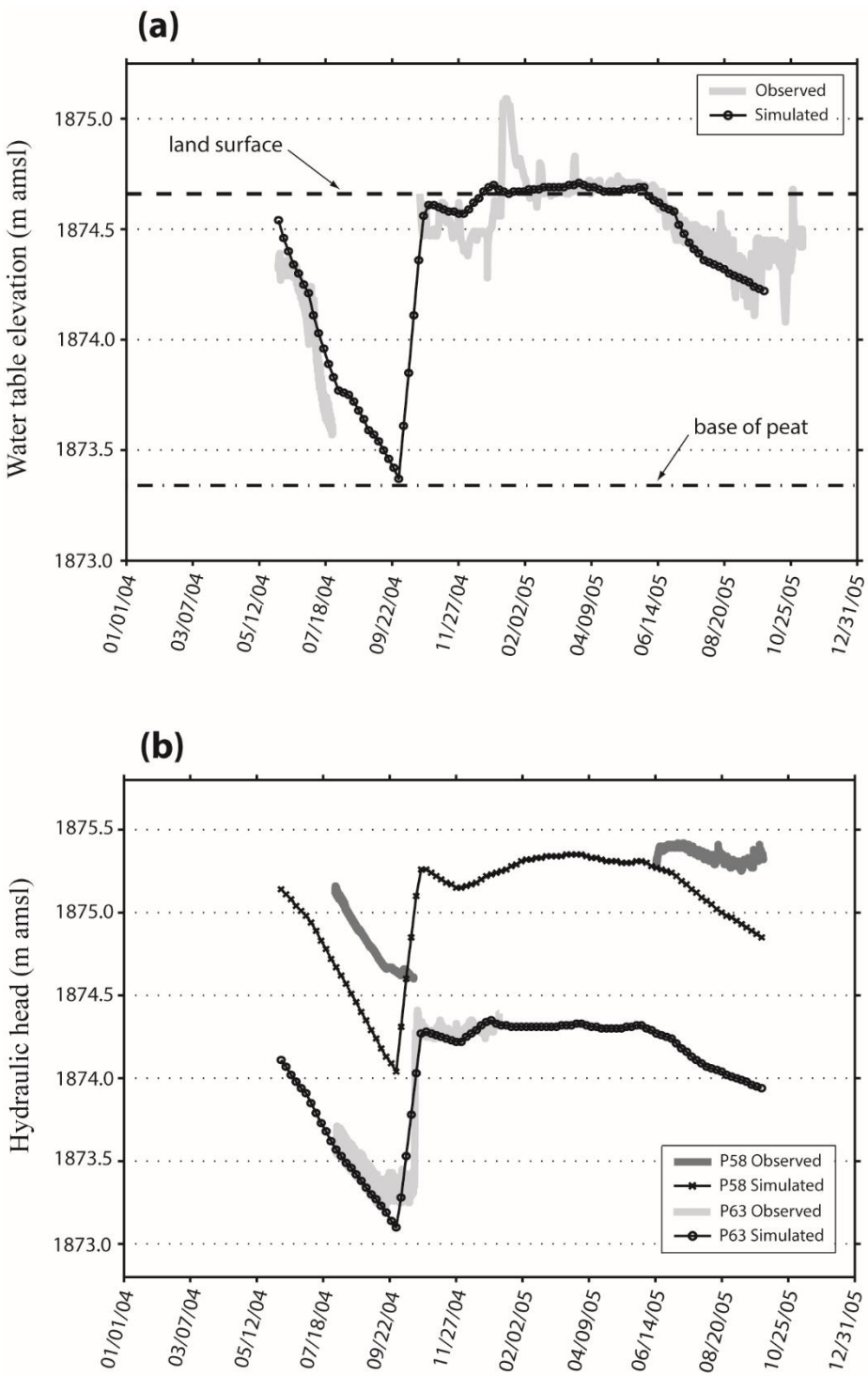

Figure 23. Transient modeling results for the period June 2004 through Sept 2005. (a) Comparison of simulated and observed water table elevation at well 10, which is screened within the peat. (b) Model comparison at piezometers 58 and 63, which are open to the sand/gravel unit.

The hydrograph for well 10 illustrates a key characteristic of the system behavior (Figure 23a). In the low snow 2004 water year, water levels declined rapidly in response to summer pumping and the lack of precipitation. In the high snow 2005 water year, the meadow water level decline was gradual and the peat remained saturated even though June through September rainfall and pumping totals were nearly identical to 2004. The summer water level response was controlled largely by the volume of shallow groundwater in storage and inflow from the meadow boundaries, which are a function of the previous winter and spring precipitation.

Results of the predictive groundwater use scenarios indicate that reduced groundwater pumping significantly affects fen water levels (Figure 24). During 2004, the model predicted that if the pumping was reduced by 50%, June-September drawdown near well 10 would be reduced from 1.20 m (Figure 24a) to 0.75 m (Figure 24b). With no pumping the predicted summer water table decline is only 0.40 m (Figure 24c).

Analysis of the fen water storage loss for each predictive scenario indicated that a significant fraction of the pumped water is offset by storage decline within the peat (Figure 24). The monthly pumping for the base case scenario for June, July, August and September was 1074, 1953, 1203, and 831 m^3. The simulated storage loss within the fen is 343, 556, 403, and 148 m^3 for these months (Figure 24a). The relatively low September storage loss is due to the already low water table elevation leading into this month during the base case scenario. In this representative dry year, the base case pumping results in almost complete dewatering of the peat body by the end of August; therefore additional storage loss is minimal. With reduced groundwater pumping (Figs. 7b and 7c), there is less storage loss during June-August and significant saturation of the peat occurs during September.

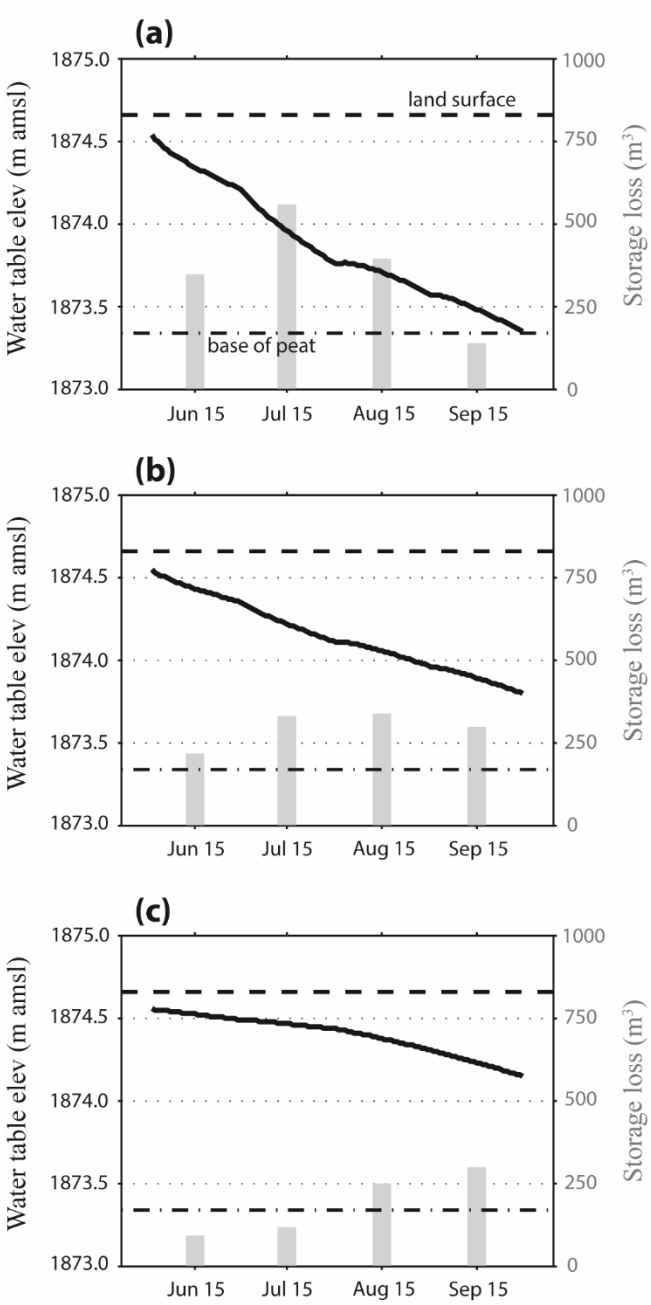

Figure 24. Predicted water table position and storage loss within the fen for three groundwater use scenarios during a dry year. The simulated water table (solid black line), land surface, and peat bottom elevations are provided for the well 10 locations. The storage loss reported for each month (bars) represents the total modeled reduction in water storage within the saturated zone for the fen area polygon shown in Fig. 1. (a) Base case transient model with actual pumping during June–September 2004. (b) and (c) are predictive model results with 50% of actual pumping (b) and no pumping (c).

Meadow Vegetation

The vegetation of undisturbed fens in the region is dominated by plants that occur primarily in sites with perennially high water tables, including *Eleocharis pauciflora, Carex scopulorum, Drosera rotundifolia, Vaccinium uliginosum* and *Sphagnum subsecundum*. These species are common in the two reference meadows, but are uncommon or absent in Crane Flat. Crane Flat vegetation in the area with peat soil is dominated by plants that occupy seasonally wet meadows including *Potentilla gracilis, Veratrum californicum, Poa pratensis,* and *Solidago canadensis.* Reference meadow sites Drosera well 4 (labeled DR) and Mono Meadow well 70 (labeled MO) are plotted on the far left side of the CCA ordination space, and are correlated with the smallest summer water table declines (Figure 25). Crane Flat Meadow plots in areas with thickest peat (plots 1, 10 and 14) appear on the far right side of the ordination space, indicating that their summer water table is deep, and their vegetation is dominated by wet meadow, not fen plant species. The centroids of fen indicator plant species are plotted on the left side of the ordination space, in sites with sustained high summer water table, while dry meadow species are on the right, in plots with deeper summer water tables (Figure 25). The fen portion of Crane Flat Meadow has peat up to 140 cm thick yet the position of plots in the ordination space opposite the reference fens indicates that the hydrologic regime and vegetation has shifted significantly from its historical natural range of variation.

The total variance (inertia) in the CCA dataset was 2.344, of which 0.420 (17.9%) was explained by axis 1. The Monte Carlo test of axis 1 produced a p-value of 0.0491 indicating a statistically significant correlation between axis 1 and the vegetation data at $\alpha = 0.05$. Axis 1 is most strongly correlated (-0.986) with the 2004 maximum growing-season water level data. Axis 2 has an eigenvalue of 0.127 (5.4% of total variance), and is correlated (-0.787) with peat thickness. Minimum growing-season water level in 2005 is the second-ranked correlate with both axis 1 (-0.707) and axis 2 (-0.408). The vectors shown in Figure 25 indicate the direction of increase in the values of the specified environmental variables. Plots

closer to the pumping well generally occur to the right side of the ordination, and those further away are towards the left, in a gradient aligned roughly parallel to axis 1.

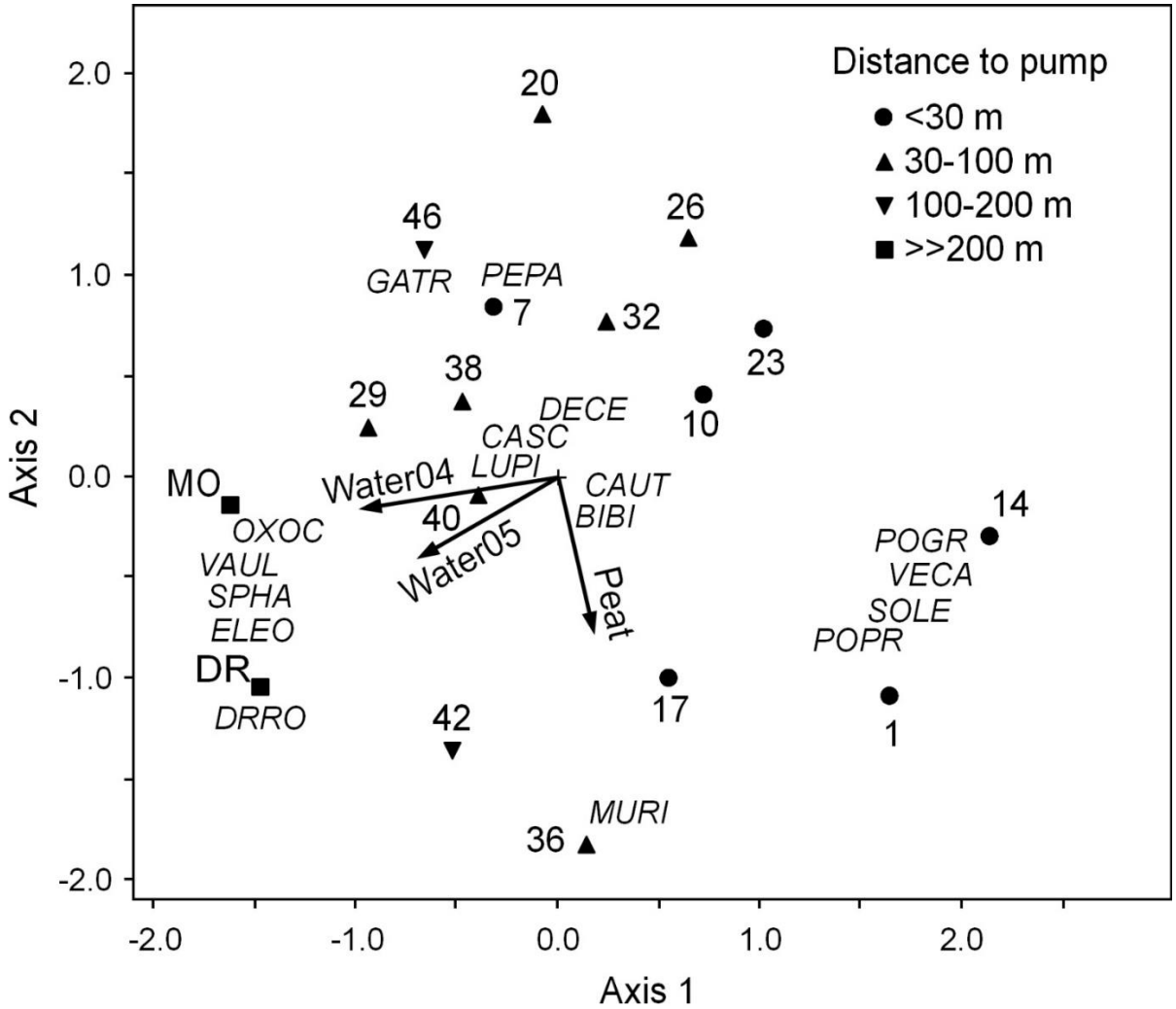

Figure 25. Canonical correspondence analysis of the vegetation, hydrology, and peat thickness at 17 plots. The reference meadows outside of Crane Flat are plot MO in Mono Meadow and DR in Gin Flat (Drosera) fen. The other 15 plots are all within the Crane Flat wetland. Hydrologic gradients and peat thickness are shown by the vectors Water04 and Water05, which indicate the highest water level in the dry summer of 2004 and lowest water level in the wet summer of 2005 respectively, and Peat. Higher water elevations and thicker peat occur in the direction of the arrow moving away from the intersection, and lower water elevations and thinner peat in the opposite direction. The distance of each plot from the groundwater pumping well is shown, but this variable was not used in the CCA. Plant species are represented by the following codes: DRRO = Drosera rotundi- folia, VAUL = Vaccinim uliginosum, OXOC = Oxypolis occidentalis, CASC = Carex scopulorum, LUPI = Lupinus sp., DECE = Deschampsia cespitosa, MURI = Muhlenbergia rigens, SPHA = Sphagnum subsecundum, ELEO = Eleocharis pauciflora, CAUT = Carex utriculata, SOLE = Solidago lepida, POPR = Poa pratensis, BIBI = Bistort bistortoides, VECA = Veratrum californicum, POGR = Potentilla gracilis, PEPA = Perideridia parishii, GATR = Galium trifidum

DISCUSSION AND CONCLUSIONS

Groundwater pumping on summer days produced distinct hydraulic head declines in Crane Flat meadow. The duration of daily pumping controlled the magnitude of decline. Daily head declines were greatest in the coarse sand aquifer beneath the peat, but water level changes also occurred in the peat body. The effect of pumping varied by distance from the pumping well, depth of the water table when the pumping started, and that water year's SWE. The effects were somewhat similar to ditches where the greatest hydrologic effects occur closest to the ditch (Price *et al.* 2003).

Pumping in 2004, 2007, 2008, and 2009 all years with below average SWE and the snowpack melting in early to middle March, resulted in the water table declining to the base of the peat body by mid-summer. The water table decline produced dry soil conditions and peat cracking, which has allowed upland plants such as *Poa pratensis* to invade the peatland. The rapid daily water table decline each day due to pumping was only partially matched by the water table rise after pumping ceased. This suggests that by mid- to late- growing season during dry years, such as 2004, insufficient groundwater inflow occurred to offset the amount of water removed by pumping and to maintain the meadow water table near the soil surface. This was in contrast to reference fens during the same time periods where the water table remained within 20-40 cm of the soil surface.

Pumping in 2005, 2006, and 2010, all years with higher SWE and later melting snowpack, resulted in little water level drawdown due to the same pumping schedule in those years. For example, in the large snowpack year 2005, the season-long effects of pumping were reduced as daily groundwater inflow matched pumping volumes and nearly maintained fen water levels.

Our data indicate that, contrary to the intended design of the well, nearly all of the volume of water pumped from the production well is drawn from shallow (<28 m depth) sediments. This extraction produces an almost immediate reduction of piezometric head in the highly conductive sands underlying

the much less conductive peat body. As pre-pumping head levels drop near the base of the peat, pumping causes increasing drawdown until head levels drop below the peat. We interpret the increased drawdown as heads approach the bottom of the peat as a signal of increasing peat density with depth, and a resultant decrease in pore size and free-draining water content.

As head levels drop below the peat layer they enter the underlying sand layer and the drawdown rate decreases with ever-lowering initial water levels, presumably due to greater porosity and hydraulic conductivity of the deep sand compared to the deep peat. Maintenance of upward piezometric head from the deep sand is critical to maintaining saturation of the surface peat body.

We attribute the trend in well 10 (within the peat body) of reduced drawdown with decreasing initial water levels to a late-summer reduction in connectivity between the head pressure in the underlying sand and the water table within the peat. The lack of drawdown response at the lowest well 10 water levels within the peat suggests that there was either not enough time, and/or insufficient upward head within the underlying sand to elevate the water level in the peat between pumping intervals, and therefore, no decline is seen when pumping occurs.

Fens in the Sierra Nevada, such as Crane Flat, have formed over thousands of years, due to the accumulation of partially decomposed plant litter (Bartolome *et al.* 1990). This has occurred where inflowing groundwater maintains the water table near the soil surface even on average to dry water years (Chimner and Cooper 2003). Water table declines produced by ditching (Cooper *et al.* 1998), or water extraction such as groundwater pumping, can lead to rapid peat oxidation, erosion and subsidence (Schumann and Joosten 208, Schimelpfenig *et al.* 2013).

Hydrologic changes have allowed the invasion of small mammals into Crane Flat, including pocket gophers and voles. These mammals are absent from intact fens because they cannot survive in perennially saturated or inundated soils, however they are naturally present in seasonally saturated wet

meadows. Mammal digging and disturbance exposes peat to rapid oxidation and erosion and creates habitat for plants exotic to the meadow, such as Kentucky bluegrass (Patterson and Cooper 2007). Small mammal activity has exacerbated the rate of peat degradation, erosion and subsidence in Crane Flat. Peat losses occur at a much faster rate than peat accumulation (Schimelpfenig *et al.* 2013), and cumulative impacts from hydrologic changes produce drying (Cooper *et al.* 1998), reduced plant production (Chimner and Cooper 2003), and physical disturbance by small mammals (Patterson and Cooper 2006) all of which can lead to rapid meadow degradation.

The numerical model developed for this study provides a quantitative description of groundwater movement and seasonal water level dynamics throughout Crane Flat meadow. The modeling confirmed that the high water table within the fen is a consequence of convergent groundwater flow paths from two distinct inflow sources. Model-simulated inflows were consistent with stable isotope data indicating that the pumped groundwater is a mixture of these water sources. Also captured by the model is the strong dependence of summer water table position on the amount of precipitation that occurs during the preceding winter and spring. The short memory of the system reflects the relatively small volume of permeable aquifer sediments, as well as the direct hydraulic connection between the recharge areas and the fen.

In addition to providing insights into the hydrologic dynamics of the meadow, the groundwater model offered an important tool for evaluating the effects of different pumping regimes. Predictive scenarios showed that, even in a dry water year like 2004, distinct increases in the fen water table elevation could be achieved with reductions in pumping. In years with above average SWE, such as 2005, groundwater inflow nearly maintains water levels in the peat even under full pumping scenarios.

Fens are relatively uncommon ecosystems in Yosemite National Park, and only 10 of 31 meadows along the Tioga Pass road had peat soil (Cooper and Wolf 2006). Fens occupy <1 % of the

Yosemite landscape, yet they are the only perennially wet terrestrial environments and provide important habitat for many species of plants, amphibians, and birds, including the Great Gray Owl, a regionally endangered species. Fen formation and persistence relies on the perennial flow of groundwater into meadows, the maintenance of saturated soils through the summer, and the support of clonal plant biomass that forms the peat body (Chimner and Cooper 2002, Cooper and Chimner 2003).

The CCA indicated that a high water table during summers following low snowpack water years has a more significant influence on vegetation composition than depth of water table in wet years or peat thickness. This highlights the significant impact that water level drawdown due to pumping has on wetland vegetation. In addition, plots closest to the Crane Flat pumping well have the deepest summer water tables, and plots further from the well generally had higher water tables in 2004 and 2005. The two reference sites have distinctly different water levels and vegetation composition distinct from that in Crane Flat.

Management Implications

Groundwater pumping has apparently shifted the Crane Flat fen from a peat accumulating to a peat-losing ecosystem. In the long-term, peat that has accumulated over thousands of years will be lost through oxidation and erosion and the system could be changed to a seasonally wet meadow, as has been documented with drained peatlands throughout the world (Waddington *et al.* 2002, Coulson *et al.* 1990, Leifeld *et al.* 2011). This change has functionally already occurred as indicated by the summer water table depth and vegetation composition. Further decomposition and loss of peat could facilitate the invasion of trees such as lodgepole pine into the meadow, and the switch from meadow to forest habitat. Maintaining a high water table will reduce the chances of invasive plants altering the meadow composition (Timermann *et al.* 2006). An additional danger is the potential of wildfire to burn the dry peat body during the summer, resulting in the loss of organic matter and alterations of the soil physical

properties (Dikicl and Yilmaz 2006). Changes in the thickness or decomposition state of the peat body could also reduce its water storage capacity and hydraulic conductivity, further altering the hydrologic function of the meadow (Loheide *et al.* 2009, Lowry *et al.* 2011). However, the decomposed peat likely has increased capillary rise producing higher volumetric water content higher above the water table than pristine peat (Macrae *et al.* 2012).

This research provides guidance for the development of water management strategies to maintain or restore the hydrologic processes that formed the Crane Flat fen, and this information is critical to fen and wet meadow management any place in the world where hydrologic alterations occur. For Crane Flat, two options that are supported by the data analysis and modeling performed in this study include: (1) reduce or eliminate pumping during July and August in water years with below average SWE, and (2) allow normal pumping in summers following winters with above average SWE. Other beneficial strategies may involve adjusting the timing and duration of pumping to maintain soil saturation in the plant root zone, which will sustain the peat body and limit the invasion of small mammals and dry land plants. The installation of larger water tanks to store winter snowmelt for summer use is another alternative. However, tanks are expensive and may hold insufficient water to meet the demands of human users. Since the initial investigation, Yosemite National Park has replaced the water distribution system at Crane Flat, which had been leaking up to 75% of pumped water. Based on the analysis presented here, this action may have resulted in a reduction in groundwater extraction impacts to the fen. Replacing the existing well remains an objective, though two new boreholes drilled since 2004 have failed to yield a viable alternative water source.

The methods and results presented here are applicable to fens in many mountain regions of the world particularly in mountain regions where the peat is underlain by coarse textured mineral sediment. Fens support high biodiversity and are a top conservation priority in many regions (Lunt *et al.* 2011, Schumann and Joosten 2008). Reinitiating peat-forming processes to disturbed fens and bogs is a goal

for many restoration programs (Rochefort *et al.* 2003). A key to such restoration efforts is avoiding large water table declines that allow aerobic conditions to develop and persist for extended periods of time during the summer (Deppe *et al.* 2010). Therefore, understanding how well connected fen peat bodies are with the underlying sediments is critical for water and ecological management, and modeling the potential effects of water extraction programs.

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Chapter 5 – Organic matter amendments reduce soil compaction and increase dissolved phenolics, affecting wetland plant growth

INTRODUCTION

Human impacts have eliminated roughly one-third of Earth's wetland area (Hu *et al.* 2017), more than half of the wetlands within the coterminous United States (US), and about 90% of wetland areas in California (Dahl 1990). Although wetland loss still occurs each year in the US, coordinated wetland programs for restoration and mitigation have resulted in significant offsetting gains (Dahl 2011). About 1/8th (12.5%) of the remaining ~621,000 ha of freshwater non-lake wetlands in California (SFEI 2016) are located in the Sierra Nevada mountains, and are called mountain meadows (Viers *et al.* 2013). A significant number of these mountain meadows are in need of restoration (Odion, Dudley & D'Antonio 1988; Kattelmann & Embury 1996). Meadows in the Sierra Nevada formed by sediment and organic matter accumulation, without major channel processes, during the past 10,000 years (Wood 1975). However, high-intensity grazing between the 1860s and 1940s has produced large erosion gullies in sloping meadows (Sumner Jr. 1941; Armstrong 1942; Wolf & Cooper 2016), lowering the water table (Hammersmark, Rains & Mount 2008), altering vegetation composition and cover (Loheide II & Gorelick 2007; Lowry *et al.* 2011), and exposing soil organic matter to rapid decomposition (Chimner & Cooper 2003; Schimelpfenig, Cooper & Chimner 2014). In most cases management intervention is required to restore gullied meadows' pre-eroded ecosystem processes and function.

A large-scale and potentially highly effective meadow restoration technique involves completely filling deep erosion gullies to recreate original topography, hydrology, and vegetation. This contrasts with more widely applied techniques for building and maintaining dams (using rock, wood, soil, etc.) periodically along a gully's length (Heede 1960, 1979; Lindquist & Wilcox 2000). A key component of the complete gully-fill technique is to reestablish vegetation on the soil surface of the newly filled channel.

Dense, well-rooted wetland vegetation forms a sod layer that is highly resistant to erosion (Micheli & Kirchner 2002), and is thought to have been essential in stabilizing meadows over their multi-millennial existence (Wood 1975; Ratliff 1985; Bartolome, Erman & Schwarz 1990). Because it takes several years for transplanted wetland areas to reach reference-plot shoot density (Cooper *et al.* 2017), the filled gully soil is vulnerable to re-erosion during the years that the plants are becoming established. Faster plant establishment reduces the length of time the soil is exposed to erosion and at risk of gully re-formation.

Heavy vehicles hauling sediment are required to fill large erosion gullies and their repeated trips across soil surfaces can cause high levels of compaction. In addition, high soil-moisture typically present in wetlands increases soil compactibility (Amir *et al.* 1976). Mechanical soil compaction is known to affect a broad range of plants (Unger & Kaspar 1994; Passioura 2002; Nawaz, Bourrié & Trolard 2013), but effects often differ between soil types (Gomez *et al.* 2002). Although elevated soil compaction in created wetlands as compared to natural sites has been observed (Nair *et al.* 2001; Campbell, Cole & Brooks 2002; Bruland & Richardson 2005), no studies have directly related in-situ wetland plant growth to field-measured soil compaction. Because compaction reduces soil pore volume and average pore size, the diffusion of gasses (Xu, Nieber & Gupta 1992) and soil hydraulic conductivity (Watabe, Leroueil & Le Bihan 2000) are reduced in compacted soils. Reduced movement of air and water through soil can lead to hypoxia, which is hypothesized to be one of the contributing factors to stunted plant growth (Tardieu 1994). However, wetland plants are adapted to hypoxic soil conditions and form aerenchyma to provide oxygen to their roots (Drew, He & Morgan 2000), which may confer some degree of resistance to the effects of soil compaction and resulting hypoxia, as compared to the most-studied upland agricultural species.

Adding organic matter to soil can decrease its compactibility by increasing aggregate strength and elasticity (Soane 1990). The most cost effective and readily available organic matter in the Sierra Nevada is chipped conifer wood and bark. However, a potential drawback of amending gully fill with

woody organic matter is that wood and bark contain phenolic compounds that can inhibit plant growth (Siqueira *et al.* 1991; Taylor, Goudey & Carmichael 1996; Garnett *et al.* 2004). Inhibition may involve direct toxicity to plants, complexing of phenols with nutrient-bearing proteins, or suppression of soil microbiota that play a key role in plant nutrient acquisition (Kuiters 1990; Hättenschwiler & Vitousek 2000). Plants, as well as other organisms, produce the enzyme polyphenol oxidase (PPO) in the presence of phenolics, and when exposed to other stresses such as herbivore damage (Appel 1993). Presumably the enzyme confers a protective effect on the plant, although the specific functions and mechanisms are not completely known (Mayer 2006; Constabel & Barbehenn 2008). However, it is clear that PPO activity is oxygen limited, and its ability to transform phenolic compounds helps facilitate the activity of many other enzymes that are important to the decomposition of soil organic matter and plant acquisition of nutrients (Freeman, Ostle & Kang 2001).

We investigated how soil compaction and leached phenolic compounds from soil amendments may slow wetland plant growth in complete gully-fill wetland restoration projects. Additionally, we tested the effect of soil amendments (chipped wood and bark) on reducing compactibility of placed gully fill. Our specific hypotheses were: (1) soil amendments (chipped wood and bark) would reduce the compactibility of soil, (2) leachates from chipped wood and bark contain phenolic compounds that inhibit plant growth and stimulate PPO production, and (3) plant growth metrics would be negatively correlated to soil compaction.

METHODS

Soil compaction and plant growth at Upper Halstead Meadow

In September 2007, 6,100 cubic meters of stockpiled local mineral soil and sediment were used to fill a 330 m-long erosion gully in Upper Halstead Meadow in Sequoia National Park. Heavy machinery placed and contoured the fill material to recreate the original level-in-cross-section meadow surface. In

June 2008, 37,300 *Scirpus microcarpus* J. Presl & C. Presl (a native wetland sedge) 3-month-old seedlings were planted 40 cm apart in parallel offset rows in the gully-fill soil. In September 2009, after two growing seasons of approximately three months each, we measured soil compaction and transplant size in a spatially stratified random sample of 110 plants. At each transplant maximum height, width, and soil compaction were measured. Plant height was measured vertically as the tallest leaf. Plant width was the maximum horizontal distance between ramets of the original seedling at ground level. Soil compaction was measured as the average resistance to penetration in the top 20 cm; it is expressed in units of pressure, megapascals (MPa). Readings were taken and averaged among three points within the growth radius of each plant using a soil penetrometer (FieldScout SC900; Spectrum Technologies; Aurora, IL). In addition, penetrometer readings and plant height measurements were made at random locations within an intact relict area of natural wetland in Upper Halstead as a comparison between the levels of compaction in the fill to reference site conditions. Individuals of *S. microcarpus* in the intact natural wetland are intergrown, indistinguishable, and of indeterminate age, so no width measurements were possible. Correlations between soil compaction and plant width and height in the fill were analyzed by linear regression.

To quantify the range of phenol concentrations in a field setting, interstitial soil water samples were collected in Upper Halstead Meadow, above, within, and below a gully-fill area that contained 30% wood chips by soil volume.

Soil compaction and organic matter amendments in a test trench

To test the effect of adding wood chips and bark (hereafter wood chips) on soil compactibility, we dug a 0.9 m deep, 4 m wide, 21 m long trench and refilled it as a grid of 24 test cells. Wood chips were mixed with mineral soil at 0%, 5%, 15%, 30%, 50% and 75% added wood chips by volume. Test cells were each 1.2 m by 1.2 m by 0.9 m deep (1.3 m^3 in volume). Each treatment level was randomly

assigned to a test cell in each of 4 replicate blocks arranged along the long axis of the trench to test for potential spatial bias. Water-impermeable pond liner was placed on the trench bottom to maintain saturated conditions within the trench.

Wood chips were obtained from stockpiles in Sequoia National Park, and were composed of wood and bark fragments derived from a mix of conifer species including *Abies concolor*, *Pinus lamberitiana*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Abies magnifica, and Pinus contorta*. Approximately half of the volume of wood chips were fragments 1 – 6 cm in length, and the other half were small particles <1 cm long. The volume of wood for each treatment was measured using graduated buckets. Cells were filled in 0.3 m deep lifts using 1.2 m x 1.2 m x 0.3 m plywood forms with mineral sediment placed in them by a backhoe and the wood chips added and mixed by a hand crew. A 0.3 m-wide buffer of pure fill sediment (0% wood chips) was placed completely around and between each cell. The buffer provided walking space to move between cells without disturbing the test soil and prevented direct hydrologic and compression interaction between treatments. Once the test cells and buffer were filled to 0.3 m depth, the forms were lifted and moved along the trench until all test cells and buffers were filled. After all cells and buffers within a lift were filled, the entire 0.3 m-thickness of soil was wetted and compacted evenly using a jumping jack plate-rammer (DS 72Y; Wacker Neuson; Munich, Germany). The boundaries between buffer and test cells were marked to ensure accurate re-location of the cells and stacking of the lifts. The entire test trench was regularly irrigated to maintain saturated soil conditions. Two months after construction, soil compaction in the top 20 cm was measured and averaged at five points within each test cell using an SC900 soil penetrometer. Correlation between volumetric wood chip addition and soil compaction was analyzed using linear regression.

Plant growth, PPO production, and phenolics in a greenhouse experiment

A 16-day greenhouse phytometer experiment (Dietrich, Nilsson & Jansson 2013) was conducted to measure the effect of phenol on wetland plant growth. Seventy-two *Scirpus microcarpus* seedlings were grown in a 1% Hoagland nutrient solution (Hoagland & Arnon 1950) for four weeks to serve as phytometers (Clements & Goldsmith 1924). All plants were weighed at the start of the experiment, and a size-stratified random sample of 12 plants was removed for measurement of initial aboveground (leaves) and belowground (roots and rhizomes) dry biomass. The remaining 60 size-stratified plants were then randomly assigned to one of six treatments, 10 plants per treatment: 1) deionized (DI) water, 2) 10% Hoagland solution, 3) wood leachate, 4) wood leachate with 10% Hoagland, 5) bark leachate, and 6) bark leachate with 10% Hoagland. The wood and bark leachates were extracted by soaking wood chips and bark mulch from Sierra Nevada mixed conifers (same species mix as the chips in the test trench) in DI water (115 g dry wood or bark per L of DI) for 6 days. Deionized water was added regularly to each phytometer flask to maintain a constant liquid level. The experiment ended after 16 days of treatment, and plants were separated into above- and below-ground parts, dried, and weighed.

The phenol concentration of the wood and bark lab leachate and Upper Halstead field samples was determined using the Folin-Ciocalteau method (Singleton & Rossi 1965; Yu & Dahlgren 2000) with (E)-3-(4-hydroxyphenyl)-2-propenoic acid (*p*-Coumaric acid) standards. Phenol concentrations are expressed as *p*-Coumaric acid equivalent mass per volume (mg/L).

The polyphenol oxidase (PPO) activity of each phytometer was determined from two ~2 cm long clippings (with intact side roots and hairs) from the middle of two separate randomly-selected roots. The root pieces were collected from the plants at the end of the 16-day treatment, rinsed with DI, and placed into 20mL of 10 mM L-3,4-dihydroxyphenylalanine (L-DOPA) substrate solution with 25 mM MES buffer and shaken for 15 mins. The liquid was spectrophotometrically analyzed for absorbance at 475

nm in a 4 cm path-length cell. Using the Beer-Lambert Law and an empirically-derived (Muñoz *et al.* 2006) value for the molar absorptivity coefficient (3600 absorbance * M^{-1} * cm^{-1}), we converted measured absorbance values to molar concentrations of 5,6-dioxo-2,3,5,6-tetrahydro-1*H*-indole-2-carboxylic acid (dopachrome), the PPO-catalyzed oxidation product of L-DOPA. After analysis of PPO activity, the root sections were scanned for root length and dried and weighed for dry mass. PPO activity is expressed as the molar concentration of dopachrome produced per minute per cm root length.

Treatment effect on plant growth and PPO activity was evaluated by multiple linear regression. Using multi-model selection (library 'glmulti', Calcagno 2013) in R 3.4.0 (R Core Team 2017) we exhaustively evaluated all possible permutations of models with the explanatory variables of phenol treatment concentration, Hoagland treatment level, initial plant mass, ratio of above- to below-ground plant biomass, and the six possible 2-way interactions, for a total of 10 model terms (and an intercept) considered. The four primary variables were evaluated for multi-collinearity by calculating their variance inflation factors (VIF, library 'usdm' in R, Naimi 2015), and all were found to have VIF < 2, so were appropriate to use together in the models. Homogeneity of variance across levels of tested variables was confirmed by examining plots of model residuals. All variances were well within a 4-factor similarity, so were considered homogenous (Zuur, Ieno & Elphick 2010). Plots of each parameter were visually examined for outliers, and no data points appeared erroneously extreme. Models were ranked by AICc and single model terms were deleted to find the simplest AICc-equivalent (within 2 AICc of the minimum) best model. Using leave-one-out cross validation (library 'boot' in R, Canty & Ripley 2017), we estimated the prediction error for the best model. Partial-residual plots (library 'visreg' in R, Breheny & Burchett 2017) were constructed to isolate and visualize important and interacting effects of the best model. Effects of explanatory variables not shown in partial residual plots were held constant, removing their influence on the patterns in the data.

RESULTS

Soil compaction and plant growth at Upper Halstead Meadow

Soil compaction within the top 20 cm of the fill at *Scirpus microcarpus* plantings ranged from 0.74 to 4.50 MPa, with a mean of 2.36 MPa (n=110). Compaction within the intact natural wetland reference areas ranged from 0.13 to 0.64 MPa, with a mean of 0.39 MPa (n=14). All compaction measurements within the fill exceeded the maximum compaction measured within the reference areas. Height and width of the transplants were each significantly ($p << 0.0001$) negatively correlated with soil compaction, with linear regression intercepts of 62.0 and 65.1, slopes of -9.77 and -11.90, and adjusted-R^2 of 0.353 and 0.366, respectively (Figure 26). After two growing seasons the tallest transplant (90 cm) was 1 cm shorter than the shortest measured reference plant (91 cm).

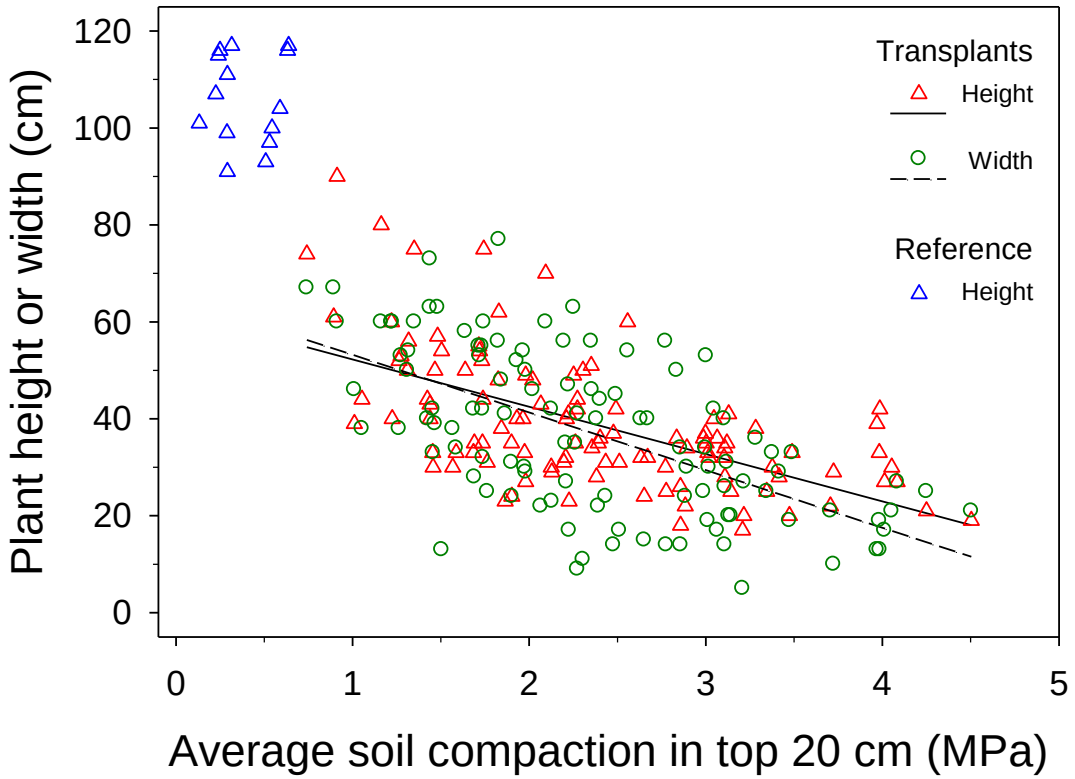

Figure 26. Soil compaction in Upper Halstead Meadow was significantly correlated with the height (red triangles, solid trend line) and width (green circles, dashed trend line) of 110 Scirpus microcarpus transplants. The soil compaction and maximum height (blue triangles) for 14 plants within non-filled and non-compacted natural reference areas are shown but not included in the regression analysis.

Soil compaction and organic matter amendments in a test trench

An equally-applied compaction effort across the test trench cells resulted in a significant negative correlation between the proportional volume of wood chips added and soil compaction ($p << 0.0001$). The estimated linear regression parameters were: y-intercept of 2.624 MPa and a slope of -0.174 MPa per 0.1 volume-proportion-addition of wood chips, with an adjusted-R^2 of 0.743 (Figure 27). At the 0.75-proportion wood chip treatment level, the average soil compaction in the test trench (1.40 MPa) was more than 3 times higher than the average Upper Halstead Meadow reference site (0.391 MPa), where the average volumetric organic matter content is 0.64 and no mechanical compaction occurred.

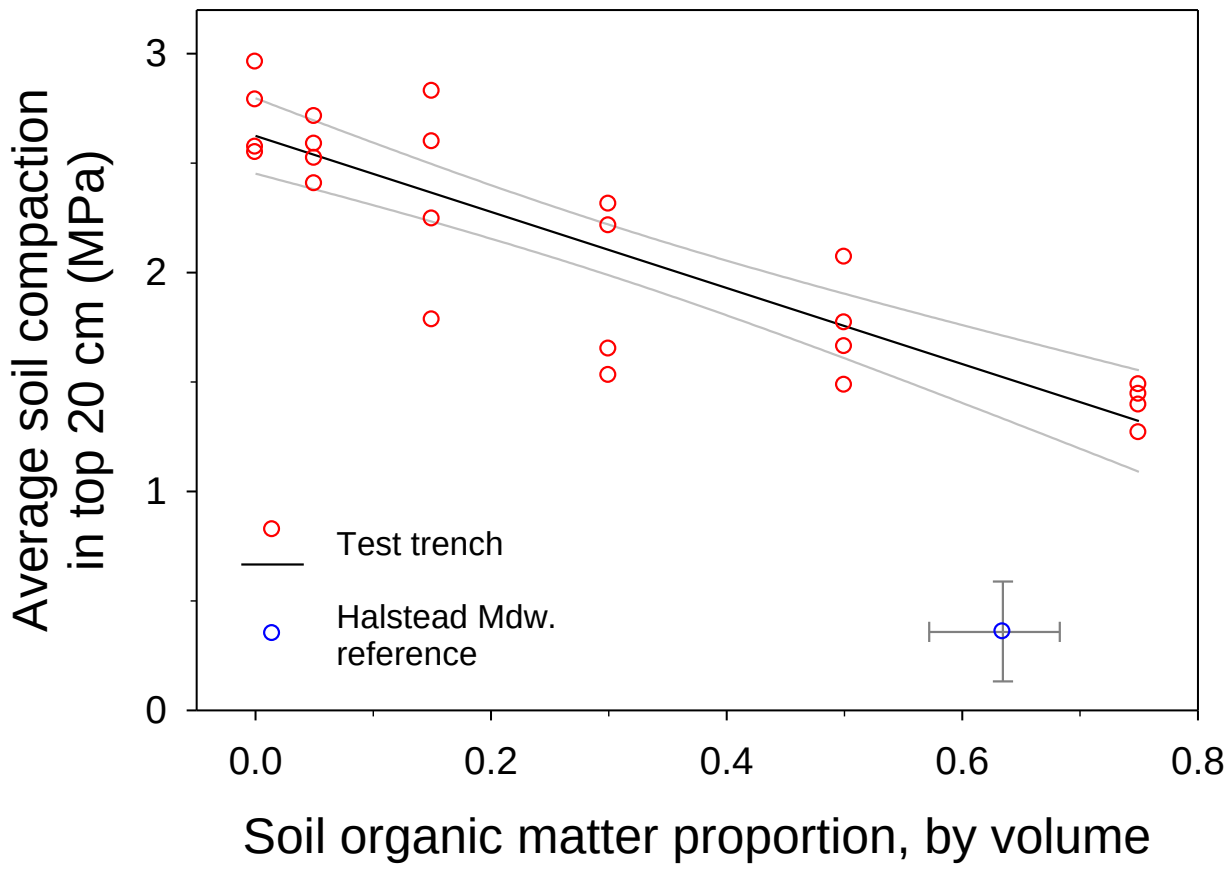

Figure 27. Soil compaction at different treatment levels (4 replicates each of 6 levels) of organic matter additions in a test trench, compared to the measured compaction and soil organic content of the non-filled and non-compacted natural reference areas in Upper Halstead Meadow. Black line shows the linear regression of the test trench data, with 95% confidence intervals.

Phenolics, plant growth, and PPO production in a greenhouse experiment

Leachate from soaking chipped Sierra Nevada mixed-conifers was 11.6 mg/L and 210.6 mg/L for wood and bark respectively. Samples of soil water from Upper Halstead Meadow yielded a maximum phenol concentration of 6.5 mg/L (4-sample average: 3.5 mg/L).

We exhaustively tested models for proportional plant growth (change in plant mass / initial plant mass), as a function of four primary variables, their six two-way interactions, and an intercept. The proportional growth model with the lowest AICc contained three terms: phenol concentration, interaction of phenol with initial plant mass, and interaction of phenol with Hoagland treatment. No other AICc-equivalent models contained fewer terms, so we selected this as the best model. The estimated model parameter values and statistics are shown in Table 8.

Table 8. Parameters and statistics for the best proportional growth and PPO activity models.

Proportional growth			PPO activity		
Best-model terms	Parameter estimate	P-value	Best-model terms	Parameter estimate	P-value
Intercept	0.664900	0.000000	Intercept	0.046080	0.000000
Phenol	-0.004828	0.000001	Hoagland	-0.047190	0.004190
Phenol:Initial mass	0.000074	0.035340	Hoagland:Initial mass	0.001720	0.003390
Phenol:Hoag	0.002055	0.005250	Phenol:Hoagland	0.000187	0.020520
			Phenol:shoot-root ratio	0.000101	0.000009
			Phenol:Initial mass	-0.000013	0.003470
	Full-model P-value	0.000001		Full-model P-value	0.000000
	Adjusted R^2	0.396800		Adjusted R^2	0.493400
	Cross-validated prediction error	0.116200		Cross-validated prediction error	0.001389

The phenol effect on proportional plant growth was contingent on both the initial plant mass and the Hoagland treatment. At the lowest two phenol treatment levels (0 and 12 mg/L), initial plant mass did not significantly change proportional growth. At the highest phenol level (211 mg/L), however, plants that were initially smaller grew proportionally less (Figure 28).

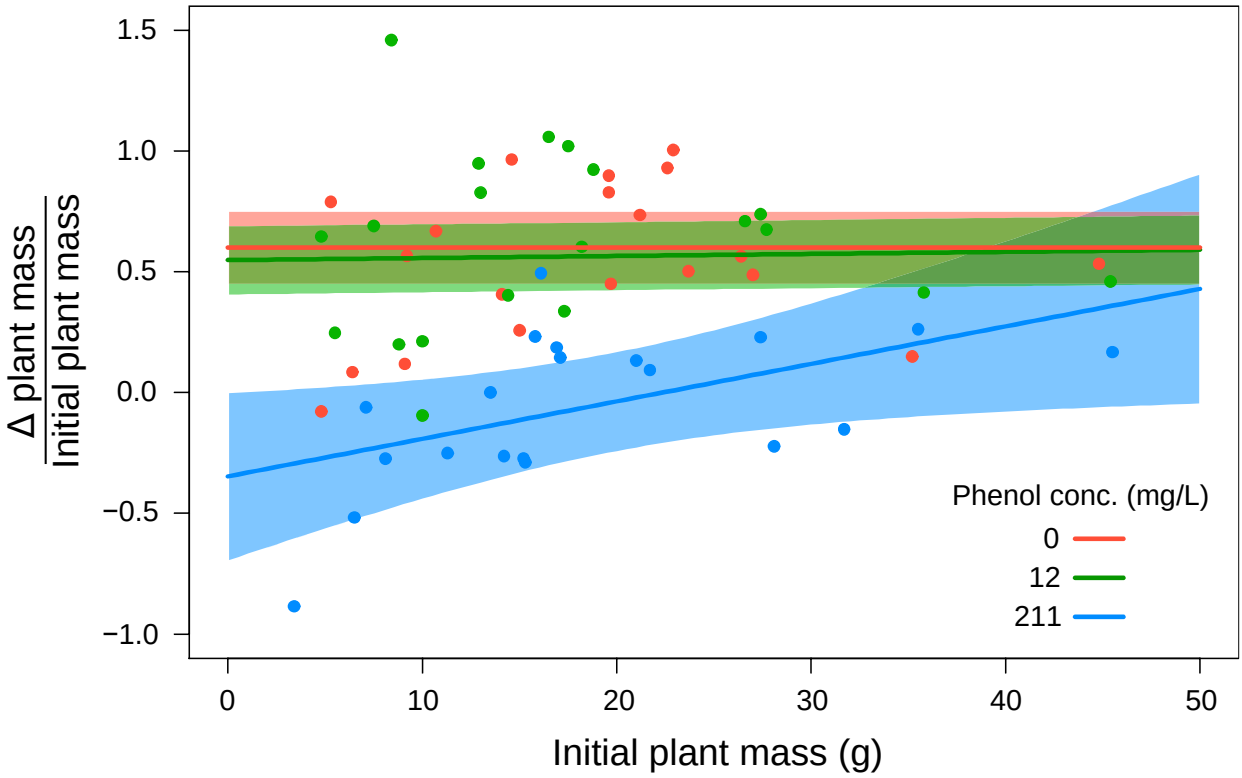

Figure 28. Partial-residual plot of the best model for proportional plant growth. The different effects of the three levels of phenol (red, green, blue) on the relationship between initial plant mass (x-axis) and proportional growth (y-axis) are shown. Solid colored lines depict linear regression on the corresponding-color partial residual points, with shaded 95% confidence intervals.

Similarly, at the lowest two phenol levels, both with and without Hoagland nutrients added, plants gained an average of 62-67% of their initial mass. However, at the highest phenol level, plants with no nutrients added lost an average of 9.8% of their initial mass, while plants provided with Hoagland nutrients gained an average of 33.5% (Figure 29).

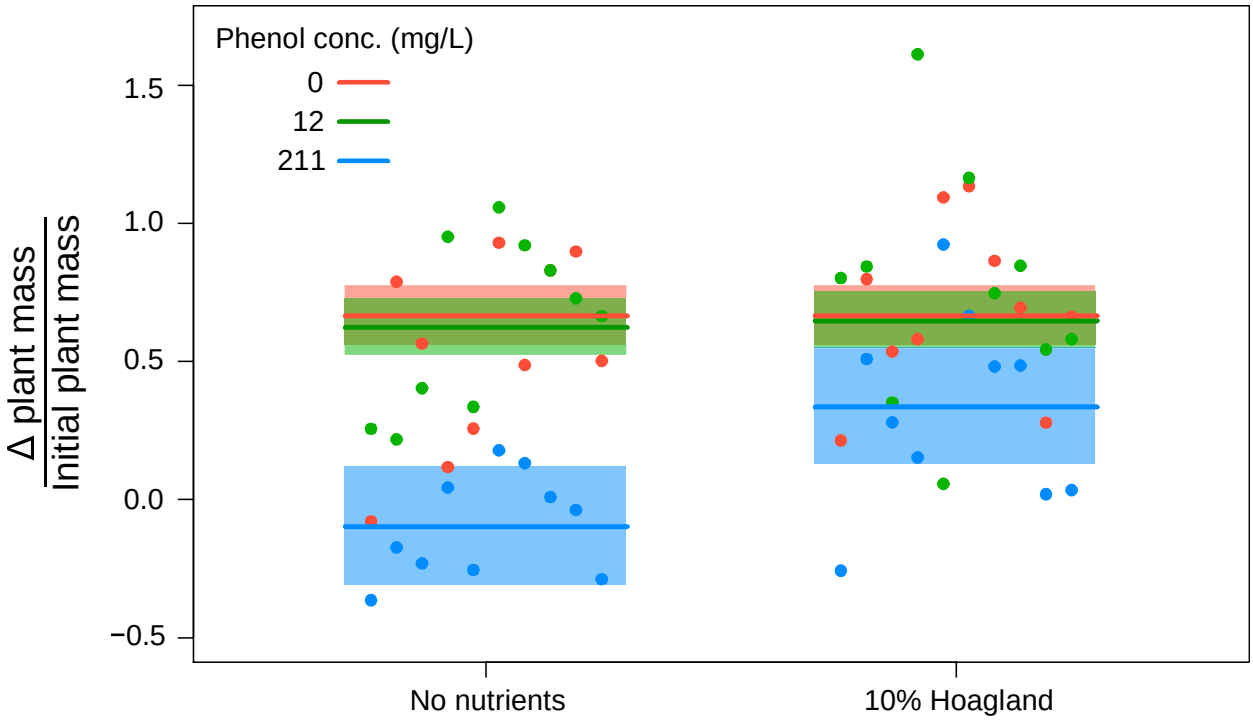

Figure 29. Partial-residual plot showing the interacting effect of phenol concentration level (red, green, blue) and Hoagland nutrient addition (x-axis) on proportional plant growth (y-axis). There is no growth difference at the 2 lower phenol levels (red and green), but at the highest level (blue, 211 mg/L), plants growing with no nutrients lost mass, while those growing in a Hoagland solution maintained significantly higher positive growth. Solid colored lines depict linear regression on the corresponding-color partial residual points, with shaded 95% confidence intervals. Note: the horizonal spread of data points within each nutrient category is solely for visual clarity and conveys no information.

To model PPO production we exhaustively considered the same four primary variables as the growth model, their six two-way interactions, and an intercept. The PPO model with the lowest AICc contained five terms: Hoagland treatment level, and the following four interactions: Hoagland with initial mass, phenol with Hoagland, phenol with above/below ratio, and phenol with initial mass. No other AICc-equivalent models contained fewer terms, so we selected this as the best model. The estimated model parameter values and statistics are shown in Table 8. The phenol treatment effect on PPO production was contingent on the level of Hoagland treatment. When no nutrients were added, all phenol treatment levels resulted in similar PPO activity. In the Hoagland treatment however, PPO

activity was significantly higher in the 211 mg/L phenol level, while the two lower phenol levels had significantly reduced PPO activity (Figure 30).

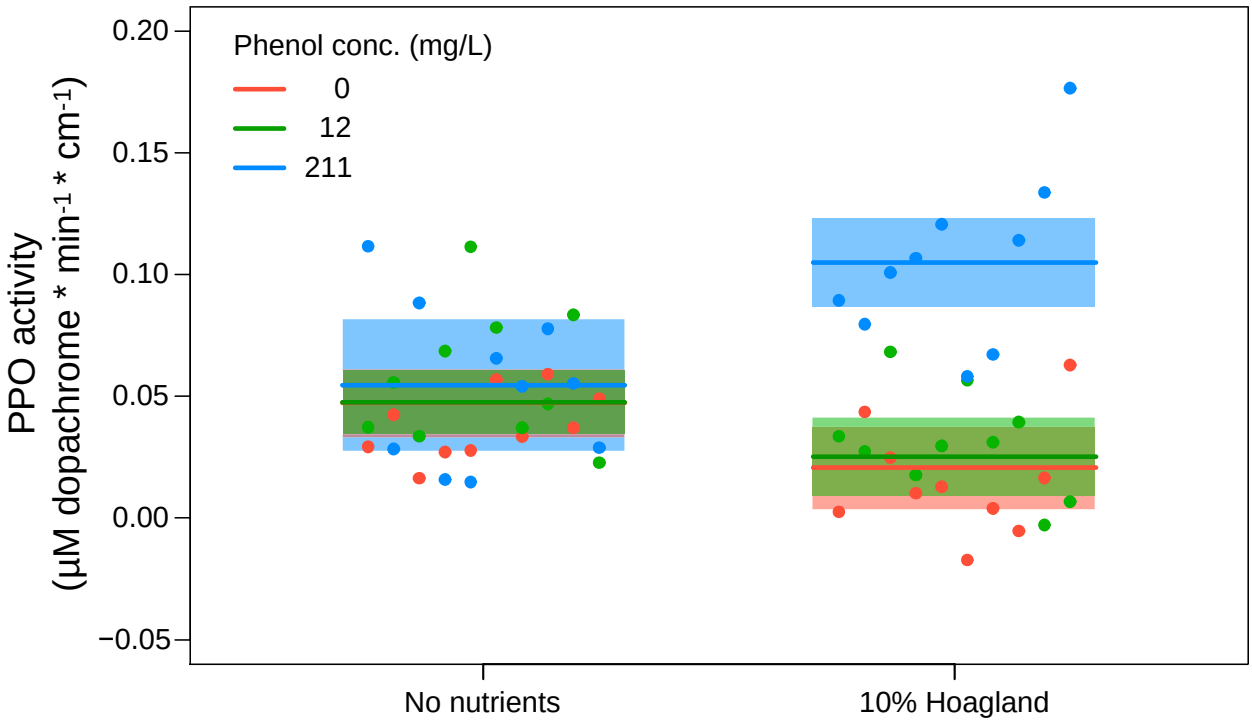

Figure 30. Partial-residual plot showing the interacting effect of phenol concentration level (red, green, blue) and Hoagland nutrient addition (x-axis) on polyphenol oxidase (PPO) activity (y-axis). When no nutrients are added all levels of phenol have similar PPO activity. In a 10% Hoagland solution the highest phenol level (211 mg/L) has significantly higher PPO activity, and the two lowest phenol levels have significantly lower PPO activity. Solid colored lines show mean values, with shaded color 95% confidence intervals. Note: the horizonal spread of data points within each nutrient category is only to prevent point overlap and conveys no information.

DISCUSSION

Soil compaction during the gully-fill restoration of Upper Halstead Meadow significantly reduced plant growth after two growing seasons, leaving placed fill vulnerable to re-erosion. Despite the successful restoration of even and constant sheet-flow hydrology and soil saturation (Cooper *et al., in prep.*), below-ground rhizomatous spread and above-ground leaf height of the wetland obligate, *Scirpus microcarpus*, were reduced by soil compaction. Because this species thrives in saturated soil conditions

in the reference area and throughout its range, it is unlikely that any compaction-related reduction in soil aeration or increase in duration of soil saturation negatively affected growth. Rather, it is probable that the compaction produced a physical impediment to root and rhizome spread, which limited growth. This study demonstrated that *S. microcarpus* seedlings are stunted by the levels of soil compaction (1-4.5 MPa) produced by heavy equipment in wetland gully-fill restoration. However, it should be noted that the naturally propagated plants measured in the reference areas are not directly comparable to our transplants, due to differences in age and in plant community composition. To directly compare plant growth in reference areas (never filled or compacted) to filled areas, all existing plants would need to be removed from reference plots without disturbing the soil, and then test plants could be transplanted at the same spacing as filled plots.

Heavy equipment is necessary in large gully-fill restorations; therefore the ability to reduce soil compactibility, and promote rapid plant growth, is essential for minimizing erosion risk and creating the aboveground biomass that will facilitate a sheet flow hydrologic system. We have shown that soil with a mix of wood chips and mineral sediment is less compactible than unamended soil. Had the fill used in Upper Halstead Meadow been amended with wood chips to match the organic matter content of the reference area, the projected reduction in compactibility, based on the test trench data, would be the difference between 2.72 MPa ave. with no wood chips and 1.51 MPa ave. with 0.64 wood chips = 1.21 MPa . This reduction of compaction would have resulted in an approximate 14 cm increase (from 33 cm to 47 cm) in plant width after two growing seasons, based on the linear regression of Upper Halstead Meadow data. This expanded plant width due to reduced compaction would have equated to a 49% increase in vegetated area: increasing from 855 cm^2 to 1735 cm^2 per plant.

In addition to reducing compactibility, soil organic matter increases water holding (Hudson 1994; Saxton & Rawls 2006; Ankenbauer & Loheide II 2017) and nutrient exchange capacity (van Erp, Houba & van Beusichem 2001). Therefore, amending mineral fill to match the organic matter content of

native wetland soil should have benefits beyond reducing compactibility. Another potential benefit of incorporating wood chips into gully fill is cost savings. The relocation of large quantities of mineral fill is expensive, accounting for roughly ¼ of the total $480K Upper Halstead project cost (Cooper *et al., in prep.*). Many areas in the Sierra Nevada are in need of forest thinning to reduce fire risk and severity (Safford *et al.* 2012), or have significant hazard-tree removal needs around infrastructure. These activities generate large quantities of wood, whose disposal expense is generally born by the removal projects. Using this chipped waste wood to improve meadow restoration outcomes could be economical where fuels treatments or hazard tree removal areas are in proximity to gullied meadows.

Before proceeding with large-scale incorporation of chipped wood into gully-fill restorations, it is essential to understand the potential consequences. This study demonstrates that the leachate of Sierra Nevada mixed conifer bark contains ~20-fold higher phenol concentration than similarly prepared wood-only leachate. High levels of phenol (211 mg/L) inhibit the growth of small *Scirpus microcarpus* individuals and those growing in nutrient-limited condition. However, this concentration of phenol does not appear to be typical of field conditions. The highest concentration phenol treatment (211 mg/L) was about 30-times greater than the highest field-measured values (range 0-6.5 mg/L; ave. 3.5 mg/L) in Upper Halstead Meadow and about 7 times higher than a leachate pond (30 mg/L) at an aspen logging operation in Canada (Taylor *et al.* 1996). We found that the lower concentrations of phenol (0-12 mg/L) typical of field conditions do no significantly affect plant growth. But, meadow-specific topography and hydrology could result in stagnant areas of water with elevated phenol concentrations, especially if significant amounts of conifer bark are present.

In the greenhouse phytometer study we found that plants in nutrient-rich conditions modulate their PPO production according to phenol concentration, whereas plants grown without nutrients produce a constant level of PPO regardless of phenol concentration. The nutrient-limited ability to adjust PPO production probably accounts for the different growth rates at high phenol concentrations

between nutrient treatments. Therefore, the nutrient status of wetlands will be an important determinant in how plants will respond to increased levels of phenol. The majority of meadows in the Sierra Nevada have very low dissolved ion and nutrient concentrations due to dominance of silica-rich low-metal-content granodiorite bedrock (Wolf & Cooper 2015). However, local conditions and land management (e.g. grazing) can significantly affect nutrient dynamics. Each polyphenol oxidase molecule contains four atoms of copper, a plant micronutrient whose importance in phenol tolerance could be tested more specifically in a follow-up phytometer experiment. The standard Hoagland nutrient solution used in this study contains copper, but it could be prepared without copper to determine the relative importance of copper-specific PPO production compared to the supply of other important plant nutrients. Additionally, the presence of phenolics deactivates cellulolytic enzymes that break down soil organic matter (Ximenes *et al.* 2011), an important source of plant nutrients. Therefore, high levels of dissolved phenolics can promote the nutrient poor conditions that limit their own decomposition.

The negative relationship between soil compaction and Upper Halstead Meadow plant growth, the test trench results showing lower soil compactibility with increased organic matter content, and the phytometer experiment linking phenol concentration to plant growth and PPO production, describe a set of ecologically important relationships that will guide the design, implementation, and success of gully-fill restorations throughout the Sierra Nevada and wherever gullied wetlands need repair.

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