THESIS

THE INFLUENCE OF HYDROLOGIC REGIME, VEGETATION, AND LAND USE ON CARBON FLUXES OF NORTHERN SIERRA NEVADA FENS

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ABSTRACT

THE INFLUENCE OF HYDROLOGIC REGIME, VEGETATION, AND LAND USE ON CARBON FLUXES OF NORTHERN SIERRA NEVADA FENS

Peatlands serve as significant carbon storage reservoirs relative to their abundance on the landscape yet impacts to these important ecosystems are numerous. Studies on the effects of cattle grazing on these systems are few. I measured water table dynamics, vegetation composition, CO_2 fluxes, and impacts due to cattle hoof punching at four fens in the northern Sierra Nevada of California to understand the natural functioning of these peatlands and the effects of cattle grazing on the ecosystem. I compared areas with and without cattle hoof punching and contrasted impacts from cattle to the effects of erosion gully-induced water table drawdown on the potential for CO_2 sequestration. I found that areas without hoof punching are generally carbon accumulating while cattle hoof punching had a negative effect on potential carbon sequestration. Areas with high amounts of hoof punching indicated carbon loss. Areas hoof punched by cattle had 10% the potential for carbon storage as areas without hoof punching in the *Oreostemma alpigenum* vegetation type ($p < 0.0001$) and 20% the potential for carbon storage in *Sphagnum subsecundum* ($p = 0.0009$). While intact fens demonstrate carbon storage potential, my analysis indicates that even small amounts of cattle hoof punching negatively affects this process and greater disturbance results in greater potential for carbon losses. Soil temperature in hoof punched areas was not significantly different than temperatures in areas without hoof punching and CO_2 emissions did not depend on variations in the water table.

Results suggest that cattle hoof punching has a greater negative effect on carbon sequestration than water table drawdown resulting from gully incision in these fens.

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TABLE OF CONTENTS

ABSTRACT II

ACKNOWLEDGEMENTS IV

1. INTRODUCTION 1

2. MATERIALS AND METHODS 4

2.1 SITE DESCRIPTION 4

2.2 STUDY DESIGN 4

2.3 CO_2 FLUXES 6

2.5 VEGETATION AND HOOF PUNCHING 7

2.6 WATER TABLE 7

2.7 SITE CHARACTERISTICS 8

2.8 STATISTICAL ANALYSIS 8

3. RESULTS 11

3.1 VEGETATION AND WATER TABLE 11

3.2 CARBON FLUXES IN AREAS WITHOUT HOOF PUNCHING 12

3.3 EFFECTS OF CATTLE HOOF PUNCHING ON CARBON FLUXES 12

3.4 EFFECTS OF GULLIES ON CARBON FLUXES 13

3.5 SITE CHARACTERISTICS 14

3.6 MODEL VARIANCE 14

4. DISCUSSION 15

4.1 CARBON FLUXES IN DISTINCT VEGETATION TYPES 15

4.2 EFFECTS OF HOOF PUNCHING ON CO_2 FLUXES 15

4.4 HOOF PUNCHING EFFECTS ON VEGETATION 17

4.5 WATER TABLE DRAWDOWN AND SITE CHARACTERISTICS 18

4.6 MANAGEMENT IMPLICATIONS 19

5. TABLES AND FIGURES 21

TABLE 1. 21

FIGURE 1. 22

FIGURE 2. 23

FIGURE 3. 24

FIGURE 4. 25
FIGURE 5. 26
FIGURE 6. 27
FIGURE 7. 28
FIGURE 8. 29
FIGURE 9. 30
FIGURE 10. 31
FIGURE 11. 32
FIGURE 12. 33
FIGURE 13. 34
FIGURE 14. 35
FIGURE 15. 36
REFERENCES 37

1. Introduction

Peatlands are wetland ecosystems in which gross primary production exceeds decomposition over the long term (Rydin and Jeglum 2006). Decomposition and respiration rates are restricted by waterlogging that limits the diffusion of oxygen into the soil (Clymo 1983, Clymo *et al*. 1998). This results in the long-term accumulation of organic matter and the formation of peat soils, typically defined as having greater than 40% organic material (Gorham 1991, Mitsch and Gosselink 2007). A minimum organic soil thickness of 30 cm is required for the site to be classified as a peatland in the United States of America (Rydin and Jeglum 2006, Joosten and Clark 2002). In temperate regions, peat accumulation occurs in low temperature, anoxic conditions. The long-term rate of peat accumulation in mountain regions of the western United States averages approximately 20 cm per 1000 years (Cooper 1990, Chimner *et al*. 2002).

Peatlands cover approximately three percent of Earth's terrestrial surface, but store more than one third of global soil carbon (Clymo *et al*. 1998, Gorham 1991, Madgwick and Parish 2008, Yu *et al*. 2010). When degraded, peatlands can shift from sinks of soil carbon to sources of carbon emissions to the atmosphere. Net ecosystem production (NEP) refers to the net flux of carbon in an ecosystem over time. It is the difference between gross primary productivity (GPP), carbon fixed via photosynthesis in living plants, and ecosystem respiration (ER), the sum of plant and microbial respiration [eq. 1] (Chapin *et al*. 2006, Lovett *et al*. 2006, Woodwell and Whittaker 1968).

$$NEP = GPP + ER \qquad \text{[eq.1]}$$

Carbon is stored in an ecosystem when NEP is negative, and lost from an ecosystem to the atmosphere when NEP is positive (Chapin *et al*. 2006, Rydin and Jeglum 2006). NEP is

typically assumed to be negative in peatlands. Fens are peatlands supported primarily by groundwater that has been in contact with mineral sediment. They are especially susceptible to degradation because their persistence relies on long-term, perennially anoxic and undisturbed conditions (Chimner *et al*. 2010, Schimelpfenig *et al*. 2014). Globally, anthropogenic activities such as livestock grazing cause physical disturbance, biomass removal, and changes in plant species within fens (Urbina & Benavides 2015, Renou-Wilson *et al.* 2016, Sanchez *et al*. 2017). This can have profound effects on the potential carbon storage capacity of these ecosystems.

In the Sierra Nevada of California, domestic livestock grazing is concentrated in fens and wet meadows due to the lack of suitable forage in the surrounding conifer forests (Kie and Boroski 1996). Wet meadows are defined as having waterlogged soils near the ground surface for most of the year (Mitsch and Gosselink 2007). Shifts in species composition, erosion, and gully formation in wet meadows since the 1850s are hypothesized to have resulted from historic grazing (Dull 1999, Odion *et al*. 1998). Of the dry meadows in the southern Sierra Nevada in need of restoration, 50-80% were previously wetlands (Odion *et al*. 1988). There have been no previous analyses of the impact of cattle on Sierra Nevada fens, however Urbina & Benavides (2015) found that grazing tripled fen peat decomposition rates compared to controls in the Andes of Colombia. This resulted in high carbon dioxide emissions and reduced soil water holding potential. Heavy grazing reduced or reversed the greenhouse gas benefits expected from mountain peatlands in the Ecuadorian Andes (Sanchez *et al.* 2017). Removing grazing increased plant diversity and GPP, shifting carbon losing sites to areas of neutral carbon flux or carbon storage in Ireland (Renou-Wilson *et al.* 2016).

Mature cattle exert a static ground pressure of approximately 1.7 kg/cm^2 which can increase up to four times during movement as body weight is distributed over smaller surfaces or

fewer than four hooves (Lull, 1959). This compaction results in distinct hoof punching where sod is fragmented and pushed below the vegetated ground surface, bare peat is exposed, and vegetation cover is reduced (Figure 1).

Fen carbon dynamics have been analyzed in the Rocky Mountains of the United States (Chimner *et al*. 2002, Chimner and Cooper 2003*a, b*, Millar et al. 2016). However, there have been no in depth analyses of the effects of disturbance on carbon fluxes in Sierra Nevada fens. The primary goal of this research is to understand the carbon fluxes (GPP, ER, NEP) in fens in the northern Sierra Nevada of California and investigate the potential effects of cattle grazing and variation in water table depth on these ecosystems. To address this goal, I ask the following questions: (1) Do different fen vegetation types have distinct carbon dynamics? (2) Does cattle grazing decrease carbon sequestration potential? (3) Does variation in water table depth influence carbon sequestration potential?

2. Materials and Methods

2.1 Site Description

I worked in four fens in the Mount Pleasant Research Natural Area (MPRNA) on the Mount Hough Ranger District of the Plumas National Forest in the northern Sierra Nevada in California (Figure 2). The MPRNA is approximately 21 km west of the town of Quincy in the Bucks Lake Wilderness. Northern California has a Mediterranean climate with dry, warm summers and cold, wet winters. The study sites Rocky Knoll, Bucks, Quaking, and Aster, are sloping fens formed in watersheds composed of igneous granite bedrock located between 1832-2042 m elevation. They are 0.71 to 2.07 hectares in size and within two km of each other (Table 1). The area received an annual average of 1940 mm of precipitation in water years 2011-2015 (October 1-September 30). Precipitation data are from the Bucks Lake Data Station (BKL) operated by the California Department of Water Resources and located at latitude 39.850000 and longitude -121.242000. The study sites occur in an active grazing allotment. Ranching activities in this area began in the 1850's with 3,000 cattle reported in 1904. The current allotment began in 1946 and allows seasonal cattle grazing of two hundred cow/calf pair from August 1-September 30 of any given year (Kyle Merriam, personal communication, May 15, 2018). All sites have varying sized gullies and channels cutting through the fen. These ranged from small incisions that are a few inches in diameter, to much larger ditches that are a meter wide and just as deep.

2.2 Study Design

Stands of vegetation with similar species composition were delineated in the field before flux data was collected and vegetation types were validated after data collection using cluster and

indicator species analyses. Vegetation types were defined by four characteristic species: *Sphagnum subsecundum* (SPSU), *Eleocharis quinqueflora* (ELQU), *Oreostemma alpigenum* (ORAL), and *Carex aquatilis* (CAAQ) and each was replicated 3-4 times across the study fens. CAAQ was the only type replicated within fens (Bucks and Rocky Knoll) but the sites differed hydrologically because they were separated by gullies and were more than 25 m apart.

Ground water monitoring wells were installed in the center of each vegetation type in each fen. Sample points refer to the location of each chamber measurement on the landscape. Sample points were selected during each measurement period within a 3-meter radius plot centered around ground water monitoring wells and no sample points overlapped during each round of measurements. Four sample points were measured during each measurement period in every *Eleocharis quinqueflora* and *Carex aquatilis* vegetation type at each site because there were no visual effects of hoof punching in these vegetation types. Eight sample points were measured during each measurement period in *Oreostemma alpigenum* and *Sphagnum subsecundum* vegetation types. Four of the eight sample points captured a gradient of percent hoof punching that ranged from 15-100% and four sample points did not show signs of hoof punching.

Each measurement period included one complete round of data collection in every plot across all sites within a two-week period and is defined by the first day of data collection for that period. CO_2 measurements were made approximately bi-weekly 5-6 times during the growing season (June-September 2016). Four hundred fifty-eight unique sample points were measured in 14 plots during the study.

2.3 CO_2 Fluxes

CO_2 fluxes were measured using a PP Systems EGM-4 Infrared CO_2 Gas Analyzer (IRGA, Amesbury, MA, USA). The IRGA was connected to an air-tight clear plastic chamber 19 cm in diameter and 40.5 cm in height and outfitted with battery-powered air circulating fans. The chamber volume was 11,483 cm^3 with a ground surface area of 284 cm^2. CO_2 concentrations within the chamber were measured every 5 seconds during a 2-minute interval until a linear rate of change was established. After the chamber was set on the ground surface, a 10 second delay allowed mixing and equilibration of air before CO_2 concentration measurements began. Net ecosystem production (NEP) was measured in full sunlight, between the hours of 10 am and 4 pm, when photosynthetically active radiation (PAR) was above 2000 μmol $m^{-2}s^{-1}$ and availability of sunlight was assumed to no longer limit the rate of photosynthesis. Ecosystem respiration (ER) was similarly measured immediately following NEP measurements after the chamber was flushed with fresh air to ensure gas concentrations returned to ambient levels. When measuring ER, the chamber was covered by an opaque cloth to inhibit sunlight and halt photosynthesis. Measurements made under opaque conditions represent the sum of heterotrophic and autotrophic respiration. Gross primary productivity (GPP) was then found by subtracting ER from NEP (Alm *et al.* 2007, Wilson *et al.* 2016).

Permanent soil collars were not installed for this study because they were not permitted in the wilderness area. Furthermore, collar insertion severs shallow roots, especially in peatlands dominated by clonal rhizomatous species, significantly affecting gas flux (Heinemeyer *et al.* 2011). Saturated areas created an airtight seal between the soil surface and bottom of the chamber. In dry locations, clay was placed around the chamber to ensure a tight seal with the ground.

2.5 Vegetation and Hoof Punching

Percent cover of each plant species estimated visually at each sample point where CO_2 measurements were taken. Ground disturbance caused by cattle hoof punching was apparent in the *Sphagnum subsecundum* and *Oreostemma alpigenum* vegetation types. CO_2 fluxes were measured at four sample points with hoof punching and four sample points without hoof punching during every measurement period. Percent hoof punching was visually estimated at each sample point. *Eleocharis quinqueflora* and *Carex aquatilis* vegetation types were not included in the cattle impact analysis. The *Eleocharis quinqueflora* vegetation type occurred on floating mats of peat that had perennial standing water. While severed rhizomes and indentations the size and shape of cattle hooves could be felt, it was not possible to estimate the extent of hoof punching below the ponded water that supported dense algae cover in mid-summer. The *Carex aquatilis* vegetation type occurred in areas where the peat dried and hardened during the summer and cattle hooves did not leave obvious indentations.

2.6 Water Table

Ground water monitoring wells were constructed of fully slotted 3.8 cm diameter PVC pipe inserted into holes made with a 7.6 cm soil auger and backfilled with native soil. Data loggers were installed in wells for the period June through September 2016 and recorded water level every four hours (Rugged TROLL 100, InSitu Inc. Fort Collins, CO, USA). Logged water table levels were corrected for barometric pressure using an In-Situ BaroTROLL logger (Fort Collins, CO, USA) which also measured air temperature. Water table levels were measured manually in wells without data loggers from June-October 2016.

2.7 Site Characteristics

Soil temperature at 5 and 10 cm, air temperature, and photosynthetically active radiation (PAR) were recorded at the sample point during each CO_2 measurement. Soil temperature was measured with a Taylor Precision Products (Oak Brook, IL, USA) digital thermometer while PAR and air temperature was captured on the IRGA. PAR was also logged every 30 seconds and averaged over 30 minute intervals on an Arduino circuit board connected to an Apogee Instruments SQ-110 quantum sensor (Logan, UT, USA) between June and September, 2016.

Samples for soil organic matter analysis were collected in each vegetation type across all sites. One sample was taken from each layer where a difference in color or texture was observed, up to 30 cm depth. Percent organic matter was determined by weighing oven-dried soil samples before and after subjecting them to high heat (288 °C) following the standard loss on ignition (LOI) protocol [eq. 2] (Nelson and Sommers, 1996).

$$LOI, \% = \frac{W_{BI} - W_{AI}}{W_{BI}} * 100 \qquad \text{[eq. 2]}$$

Where W_{BI} is weight of dried soil before ignition and W_{AI} is the weight of soil after ignition at 288 °C.

2.8 Statistical Analysis

Vegetation composition, gas fluxes, and environmental variables were sampled 5-6 times in each vegetation type between June 20 and September 3, 2016. The ORAL vegetation type included 182 point measurements, SPSU 134, CAAQ 75, and ELQU 67 which were averaged across condition (hoof punched or not), vegetation type, site, and date. Data are presented as the mean ± standard error (se). Statistical significance was determined at an alpha of 0.05 or lower. All statistical analyses were performed using R statistical software version 3.3.1 (R Core Team 2016).

'Rare' species occurring in less than 3% of observations were removed from the vegetation analysis. The vegdist() function in the vegan package in R statistical software version 3.3.1 by Oksanen *et al*. (2016) created a Bray-Curtis dissimilarity matrix and a cluster analysis was conducted using the agnes() function in the cluster package (Maechler *et al*. 2016). I employed a flexible beta clustering method ($\beta = -0.25$; McCune and Grace 2002). The resulting dendrogram was evaluated and pruned at the most natural break where stem length was longest. The adonis() function from the vegan package (Oksanen *et al*. 2016) was used to perform a permutational multivariate analysis of variance (PERMANOVA) to test whether the four clusters identified by the dendrogram were significantly different in species composition and multiple comparisons were corrected using the Bonferroni method.

An indicator species analysis was conducted on the four clusters using the multipatt() function from the indicspecies package in R (De Caceres and Jansen, 2016). After data were grouped by vegetation type, differences in hydrologic regime within each vegetation type were analyzed. Average water table depth within each vegetation type that differed by more than 25 cm were separated into wet (W) and dry (D) groups and analyzed separately.

A mixed model was evaluated using lme4 (Bates *et al*. 2015), lmertest (Kuznetsova *et al*. 2016), and lsmeans (Lenth 2016) packages. Fixed effects include 4 vegetation types (ELQU, CAAQ, ORAL, SPSU), 6 sample dates (June 20, July 5, July 20, August 2, August 17, September 3, 2016), and two levels of condition (hoof punched or not), plus all interactions. Random effects included site (Aster, Bucks, Quaking, Rocky Knoll), and vegetation IDs to account for repeated measures of the same vegetation type in both hoof punched and non-hoof punched areas. Sample points with hoof punching were analyzed as both categorical and

numerical predictors. Variance in the model was investigated using the Kenward-Roger method (Edwards 2008) in the r2glmm package (Jaeger 2017).

Differences between soil temperature in sample points with and without hoof punching were analyzed using a Wilcoxon paired signed-rank test in the coin package (Hothorn *et al*. 2016) because data were not normally distributed. The effects of hydrologic modification due to gully induced water table draw down and impacts from cattle hoof punching were compared using the same mixed model ANOVA described above. Means of CO_2 fluxes in areas affected by water table draw down were compared to means of areas affected by cattle hoof punching. Linear regression on NEP and water table depth was performed.

3. Results

3.1 Vegetation and Water Table

A total of 27 species of vascular plants and mosses occurred across all sample points. Ten species occurred in less than 3% of sample points and were removed from the vegetation analysis. The flexible beta clustering method resulted in natural break with long stem length at k(groups) = 4. A PERMANOVA of the cluster analysis indicated the four clusters were significantly different from one another (F model = 165.35; p = 0.001). Pairwise comparisons, corrected for multiple comparisons using the Bonferroni Method, showed that all four clusters were significantly different in species composition (Figure 3; adjusted p = 0.006 for all clusters).

The indicator species analysis identified *Oreostemma alpigenum* as the top species for cluster 1 with a test statistic of 0.809. *Carex aquatilis* is the only indicator species for cluster 2 (0.998). Cluster 3 is characterized by *Eleocharis quinqueflora* (0.624), and cluster 4 by *Sphagnum subsecundum* (0.966). All indicator species had a p-value of 0.005. These indicator species matched the *a priori* vegetation type delineation and validated the placement of monitoring wells.

Carex aquatilis was the only vegetation type where water table averages between plots differed by more than 25 cm. These plots were separated into two water table depth groups, “wet” areas with an average water table 10 cm below ground, and “dry” areas with an average water table 50 cm below the ground surface. Differences in water table between wet and dry sites was significant (ANOVA estimate = -47.29; p = 0.02) with differences in water table between wet and dry sites becoming more pronounced later in the growing season (Figure 4). Average

water table depth was 8 cm below ground in ORAL, 3 cm below ground in SPSU, and 5 cm above ground level in ELQU.

3.2 Carbon Fluxes in Areas Without Hoof Punching

Mean GPP in areas without hoof punching was -4.11 g CO_2 m^{-2} hr^{-1} in the ORAL vegetation type, -2.53 in SPSU, -1.21 in ELQU, -4.25 in CAAQ wet, and -4.13 in CAAQ dry sites (Figure 5). When averaged over the measurement periods, ELQU stands had significantly lower GPP than ORAL (estimate = 2.90; p = 0.0007), CAAQ wet (estimate = 2.95; p = 0.002), CAAQ dry (estimate = 2.83; p = 0.003) vegetation types while SPSU had lower GPP than ORAL (estimate = 1.58; p = 0.02; Figure 6). Mean ER in sample points that were not affected by cattle hoof punching averaged 1.80 g CO_2 m^{-2} hr^{-1} in the ORAL vegetation type, 0.82 in SPSU, 1.11 in ELQU, 2.36 in CAAQ wet, and 2.57 in CAAQ dry sites (Figure 7). When averaged over all measurement periods, the ORAL vegetation type had significantly greater ER than SPSU (estimate = 0.98; p = 0.02). Both CAAQ wet and dry had greater ER than SPSU (Wet: estimate = 1.48; p = 0.005. Dry: estimate = 1.70; p = 0.003) and ELQU (Wet: estimate = 1.44; p = 0.006. Dry: estimate = 1.66; p = 0.003; Figure 8). Mean NEP in areas without hoof punching was -2.31 g CO_2 m^{-2} hr^{-1} in the ORAL vegetation type, -1.67 in SPSU, -0.08 in ELQU, -1.91 in CAAQ wet, and -1.57 in CAAQ dry sites (Figure 9). When averaged over the entire growing season, ELQU had significantly higher NEP than both ORAL (estimate = 2.23; p = 0.004) and SPSU (estimate = 1.59; p = 0.03) vegetation types (Figure 10).

3.3 Effects of Cattle Hoof Punching on Carbon Fluxes

GPP was significantly lower in sample points with hoof punching than in sample points without hoof punching over the growing season in both ORAL (estimate = 3.29 g CO_2 m^{-2} hr^{-1}; p < 0.0001) and SPSU vegetation types (estimate = 1.70 g CO_2 m^{-2} hr^{-1}; p = 0.0006; Figure 11).

ER in hoof punched areas was significantly lower than areas without hoof punching in both ORAL (estimate = -0.74 g CO_2 m^{-2} hr^{-1}; p = 0.0005) and SPSU (estimate = -0.36 g CO_2 m^{-2} hr^{-1}; p = 0.02) vegetation types (Figure 12). In ORAL, hoof punched areas (0.24 g CO_2 m^{-2} hr^{-1}) had 10% the carbon storage potential of areas without hoof punching (-2.30 g CO_2 m^{-2} hr^{-1}; p < 0.0001). In SPSU, hoof punched areas (-0.32 g CO_2 m^{-2} hr^{-1}) had 20% the carbon storage potential of areas without hoof punching (estimate = -1.65 g CO_2 m^{-2} hr^{-1}; p = 0.0009; Figure 13).

Areas without hoof punching had greater carbon storage potential (lower NEP) than hoof punched areas (Figure 13). While areas without hoof punching had greater GPP, ER also increased with greater plant cover. For example, in the SPSU vegetation type, areas without hoof punching had 3 times more GPP than hoof punched sample points (p = 0.0006) and 2 times more ER (p = 0.02). In ORAL, this effect was even greater because areas without hoof punching had 5 times greater GPP than hoof punched sites (p < 0.0001) and 2 times more ER (p = 0.0005).

Observations in areas impacted by cattle trampling ranged from 0-100% hoof punching (Figure 14). In the ORAL vegetation type, for every 1% increase in impact, 0.03 grams of CO_2 m^{-2} hr^{-1} was lost from the system and NEP shifted from carbon storage to carbon loss at 77% impact. In SPSU, 0.02 grams of CO_2 m^{-2} hr^{-1} is respired from the system with every 1% increase in impact and NEP shifted from sequestration to respiration at 85% impact.

3.4 Effects of Gullies on Carbon Fluxes

In CAAQ, dry sites had a mean NEP of -1.63 g CO_2 m^{-2} hr^{-1}, which was not significantly different than hydrologically intact areas (-1.98 g CO_2 m^{-2} hr^{-1}; p = 0.41; Figure 9). GPP (estimate = 0.14; p = 0.82; Figure 5) and ER (estimate = 0.20; p = 0.55; Figure 7) were not significantly different between wet and dry CAAQ plots. Linear regression of NEP and water

table depth was not significant (slope = -0.002; p = 0.61) and had a low R^2 value of -0.01 (Figure 15). Differences in carbon fluxes due to hoof punching were compared to impacts from erosion gully induced water table decline.

3.5 Site Characteristics

Soil temperatures at 10 cm in areas without hoof punching averaged 14.4 °C, which was 0.3 °C more than in hoof punched areas (p = 0.03). When separated by vegetation type, areas without hoof punching averaged 0.5 °C warmer than hoof punched areas (p < 0.001) in ORAL and differences in temperature were insignificant in the SPSU vegetation type. Differences in soil temperature between sample points with hoof punching and sample points without hoof punching were not significant at 5 cm and averaged 16.1 and 16.0°C.

Percent organic matter (OM) in the ELQU vegetation was 66-82%, 49-86% in ORAL, 39-88% in SPSU, and 42-78% in CAAQ dry. The CAAQ wet vegetation type ranged from 5-60% OM with one location ranging from 5-26% in the top 30 cm. All other sites ranged from 39-88% OM.

3.6 Model Variance

In areas without hoof punching, community type was the most important variable explaining NEP with a partial R squared value of 0.83. The overall model fit was 0.75 and date explained 0.42 NEP variance. When areas with hoof punching were included, condition (hoof punched or not) was a significant predictor of NEP with an R squared value of 0.97. Model fit was 0.91 and the interaction of vegetation type and condition was significant, explaining 0.77 of the variance. The interaction between site and vegetation type was not significant and was dropped from the model. Similarly, water table was not a significant covariate and was not included in the model.

4. Discussion

4.1 Carbon Fluxes in Distinct Vegetation Types

Globally, intact fens are carbon accumulating ecosystems (Alm et al. 1997, Clymo *et al*. 1998, Gorham 1991, Robinson & Moore 1999). In this study, NEP in areas without hoof punching demonstrated carbon storage potential during peak sunlight hours throughout the growing season. Rates of carbon accumulation in this study are similar to ranges observed in high elevation fens in Colorado and Wyomming (Millar *et al.* 2017), sites in the Ecuadorian Andes (Sanchez *et al.* 2017) and peatlands in southern Germany (Otieno *et al.* 2009).

Although ELQU and ORAL vegetation types were significantly different in NEP and GPP throughout the growing season, carbon fluxes varied seasonally without significant distinction across all other vegetation types. Similarly, vegetation type was not an important factor in predicting carbon flux between sedge (*Cyperaceae*) and *Sphagnum* dominated stands in northern Minnesota peatlands (Updegraff *et al.* 2001) nor were CO_2 efflux rates significantly different between *Sphagnum* and *Eriophorum* species in peat monoliths in Scotland (Thomas *et al.* 1996). However, vegetation type strongly influenced carbon fluxes when comparing between woody and herbaceous communities in tussock tundra, wet sedge (*Carex aquatilis)*, and shrub (*Salix* spp. and *Betula nana)* tundra (Neff and Hooper, 2002).

4.2 Effects of Hoof Punching on CO_2 Fluxes

Studies from the globe found the same trend that is reported here: a decrease in NEP in grazed areas (Cahoon 2012, Enriquez *et al.* 2014, Falk *et al* 2014, Sanchez *et al.* 2017). Potential CO_2 sequestration was significantly influenced by cattle hoof punching, suggesting that CO_2 emissions in this study area will increase with increased grazing. Hoof punching by cattle was

linearly correlated to reduced carbon storage potential with plant communities shifting to carbon loses at high cover of hoof punching. This negative effect on carbon storage was significant in both SPSU and ORAL vegetation types throughout the growing season and is due to the lower GPP in sample points with hoof punching (Figure 11).

Carbon accumulation in northern peatlands is assumed to be controlled by substantial plant production during warm summer growing months (Jones & Yu 2010) and hoof punching directly inhibits this process. The lower ER found in areas with hoof punching follows trends reported in Falk *et al.* 2014 and is not surprising as autotrophic respiration declines with reduced vegetation cover (Cahoon 2012).

In a simulated grazing experiment in Greenland, Falk *et al.* (2014) found a 113% decrease in mean CO_2 uptake, leading to C loss, when vascular plants were removed. In the Andean páramo Sanchez *et al.* (2017) found that ungrazed peatlands stored approximately 2.5 times more carbon than grazed peatlands, and Enriquez *et al.* (2014) reported that grazing at levels beyond the natural capacity of the system reduced ecosystem carbon storage by 35%.

The difference in NEP between areas with and without hoof punching is greater for ORAL than the SPSU vegetation type, suggesting that the ORAL vegetation type is less resilient to cattle hoof punching (Figure 13). While *Sphagnum* that has been impacted by cattle hoof punching and is brown in color may still be photosynthesizing (Rydin and Jeglum 2006) this is not typical in vascular plants. The ability to photosynthesize, even when brown may contribute to greater resilience of the SPSU vegetation type.

Although cattle hoof punching also occurs in ELQU, this vegetation type was covered by surface water and algae that limited visual observation. Percent hoof punching could not be quantified for the ELQU vegetation but distinct depressions the size and shape of cattle hooves

and broken rhizomes were present, indicating that cattle hoofs penetrate the organic soils and plants in this vegetation type. While NEP in ELQU maintained near net neutral carbon fluctuations throughout the growing season, it is possible that cattle have negatively affected the ELQU vegetation type by severing their rhizomes, limiting reproduction, and reducing GPP. In the Rocky Mountains, fens dominated by ELQU were determined to be susceptible to disturbance and most in need of protection and restoration (Chimner 2010).

Carbon flux data were collected during peak sunlight hours during the height of the growing season. Therefore, these measurements represent best case scenarios with respect to potential carbon storage. Potential for carbon storage is expected to be at maximum during these times because CO_2 uptake is greatest during the summer months and daylight hours (Lafleur *et al.* 2003). Higher summer temperatures increase GPP with primary productivity peaking in mid-summer in North American ecosystems and little GPP occurring during winter months (Sims 2008). This is largely due to enhanced PAR during summer months, one of the most important drivers of GPP (Mercado *et al.* 2009, Hashimoto *et al.* 2010).

4.4 Hoof Punching effects on Vegetation

Hoof punching negatively influences ecosystem function in fens beyond hindering carbon storage. It reduces plant cover, causes erosion, compacts soils, and severs the rhizomes of clonal peat-forming plants, inhibiting growth and reproduction (Ratliff 1985). Increased disturbance may cause vegetation composition to shift from rhizomatous vascular plant and moss species typically found in fens to upland and wetland species with shallow root systems (Cole *et al.* 2004, Dull 1999, Kauffman *et al.* 2004, Ratliff 1985, Urbina & Benavides 2015) and woody species (Ratliff 1985, Middleton 2002) that may not adequately contribute to peat formation.

Arnesen (1999) and Cole *et al.* (2004) found that hoof punching from cattle negatively affected vegetation composition by reducing *Sphagnum* and vascular plant species cover while increasing bare ground. Hoof punching and the associated fertilization due to nitrogen in cattle fecal matter can negatively affect soil bulk density, water holding capacity (Kauffman *et al*. 2004), and soil-forming processes (Ratliff 1985) while increasing the establishment of invasive species and rates of decomposition (Urbina & Benavides 2015). Germination, seedling survival and clonal spreading of vegetation into hoof prints may take decades following hoof punching in fens (Stammel and Kiehl 2004, Arnesen 1999).

4.5 Water Table Drawdown and Site Characteristics

Water table drawdown due to the existing gullies surprisingly did not significantly influence carbon storage potential in the CAAQ vegetation type. In contrast, previous researchers have found that water table position had a significant influence on fen carbon storage (Chimner *et al*. 2017, Chimner and Cooper 2003*a*, Moore and Dalva 1993, Moore and Knowles 1989, Riutta *et al.* 2007, Schimelpfenig *et al*. 2014, Silvola *et al*. 1996). Experimental lowering of the water table in a laboratory setting resulted in a strong linear relationship with larger carbon dioxide emissions occurring at lower water table positions (Moore and Knowles 1989). Similarly, depth of the aerated zone determined CO_2 efflux in Alaskan tussock tundra (Tenhunen *et al.* 1995). However, Updegraff *et al*. 2001 found that CO_2 emissions were not affected by differences in water table level.

An experimental lowering of the water table in a Rocky Mountain fen found that CO_2 emissions were lowest at the highest water tables (6-10 cm above ground surface) and tripled when the water table dropped 0-5 cm below ground level (Chimner and Cooper 2003*b*). Further lowering of the water table (40 cm below ground level) had little effect on CO_2 emissions. It is

possible that a significant change in NEP was not found in hydrologically modified sites because the dry CAAQ vegetation type had water tables lower than the near surface labile soil carbon pool (Chimner and Cooper 2003*b*) throughout most of the season.

While differences in soil temperature at 10 cm were statistically different between hoof punched and non-hoof punched areas, there is likely little ecological difference between 0.5 and 0.3 degrees Celsius. In contrast, Updegraff *et al.* 2001 found that CO_2 respiration in peatland mesocosms was largely controlled by soil temperature and unrelated to other measured variables. All sites had peat soils of greater than 40% OM in the top 30 cm except for one location in the CAAQ wet vegetation type which ranged from 5-26% OM (Table 1). In this location, there were visible layers of sand and other fine mineral particles mixed into the soil column which could be due to sediment deposition following a previous erosion event after a wildfire in the surrounding forest.

4.6 Management Implications

In the Sierra Nevada, little herbaceous plant biomass occurs in the forest understory compared to meadows (Allen 1989, Bartlett and Betters 1983). This lack of forage leads to livestock grazing being concentrated in meadows, including fens, wet meadows, and riparian areas (Kie and Boroski 1996). These ecosystem types are rare with wet meadows and fens comprising only 1% of the Sierra Nevada landscape (Davis & Stoms 1996). Furthermore, peat accumulation in the mountain west of the United States is slow, averaging just 20 cm per 1000 years in the Rocky Mountains (Cooper 1990, Chimner *et al.* 2002).

While hoof punched areas had significantly less carbon storage potential than areas without hoof punching, NEP in plots with water table draw down was not different than hydrologically intact areas. This suggests that cattle hoof punching had a greater negative effect

on NEP than water table decline. Differences in GPP determine this pattern. While GPP is significantly reduced in hoof punched areas, plots experiencing water table drawdown still support high levels of primary production, offsetting their higher levels of ER and leading to negative NEP.

Reducing the carbon storage potential of these mountain ecosystems is a fundamental change that may affect their persistence on the landscape. This analysis shows that all vegetation types in which impacts from cattle were measured are negatively impacted by hoof punching in the study fens. Therefore, any amount of hoof punching and removal of plant biomass is expected to decrease fen carbon storage potential regardless of season-based grazing restrictions. With continued or increased grazing in these fen ecosystems, we expect a decline in many ecosystem services offered by mountain peatlands.

5. Tables and Figures

Table 1. Site overview including fen name, elevation, area, vegetation types, number of repeated measures, percent organic matter, and average water table. Samples for soil organic matter were collected in the upper 30 cm every time a difference in color or texture was observed.

Fen	Elev. (m)	Area (ha)	Vegetation	Dates Sampled	OM (%)	Ave. WT (cm)
Aster	2042	.47	ORAL	6	81	+2
Bucks	1847	2.07	CAAQ wet	5	5-26	-14
			CAAQ dry	5	42-78	-52
			ORAL	5	70-85	-10
			SPSU	5	79-88	-4
			ELQU	5	79-83	-5
Quaking	1929	.65	ORAL	6	76-86	-20
			SPSU	6	73-81	-3
			ELQU	6	66-78	-6
Rocky Knoll	1832	1.61	CAAQ wet	4	59-60	-5
			CAAQ dry	5	45-50	-48
			ORAL	5	49-79	-2
			SPSU	5	39-87	-2
			ELQU	5	70-80	-4

Figure 1. Hoof punching in Aster fen. Dark areas are exposed, bare peat resulting from cattle hoof punching while vegetated areas are largely comprised of *Oreostemma alpigenum*, *Philonotis fontana*, and small amounts of *Drosera rotundifolia*.

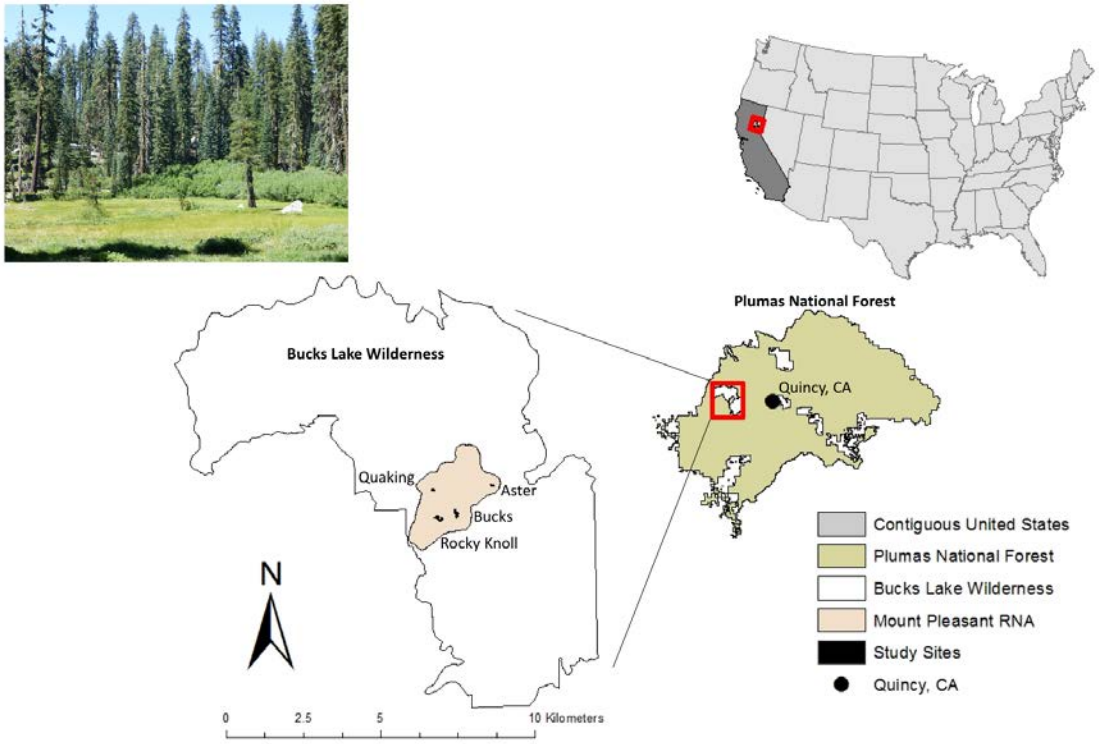

Figure 2. Study sites are located in the Mount Pleasant Research Natural Area in the Bucks Lake Wilderness, Plumas National Forest, California. Sites are named Quaking, Aster, Bucks, and Rocky Knoll. Left photo inset is of Quaking Fen.

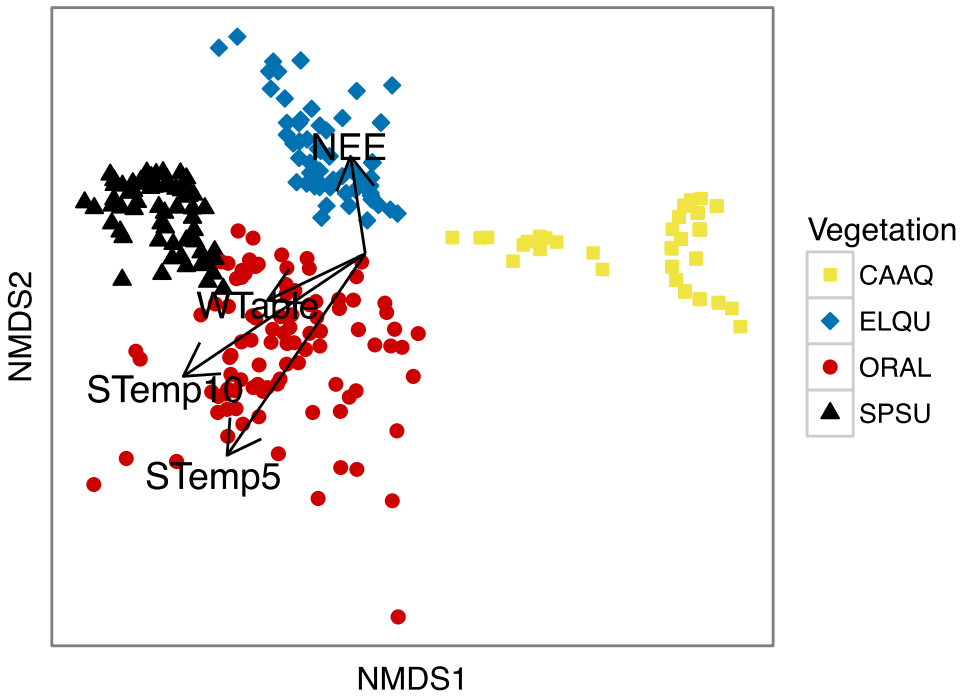

Figure 3. Nonmetric multidimensional scaling ordination of 4 vegetation types matched the *a priori* vegetation type delineation and validated the placement of ground water monitoring wells. All clusters were significantly different (F model = 165.35; p = 0.001) from each other. Pairwise comparisons showed that all clusters (1-4) were significantly different in species composition (adjusted p = 0.006 for all clusters). *Oreostemma alpigenum* was identified as the top indicator species for cluster 1 (0.809), cluster 2 is defined by *Carex aquatilis* (0.998), cluster 3 is characterized by *Eleocharis quinqueflora* (0.624), and cluster 4 by *Sphagnum subsecundum* (0.966). All indicator species had a p-value of 0.005. Environmental data are overlain as vectors where NEP corresponds to net ecosystem production, WTable refers to water table depth, and STemp is soil temperature taken at 5 and 10 cm.

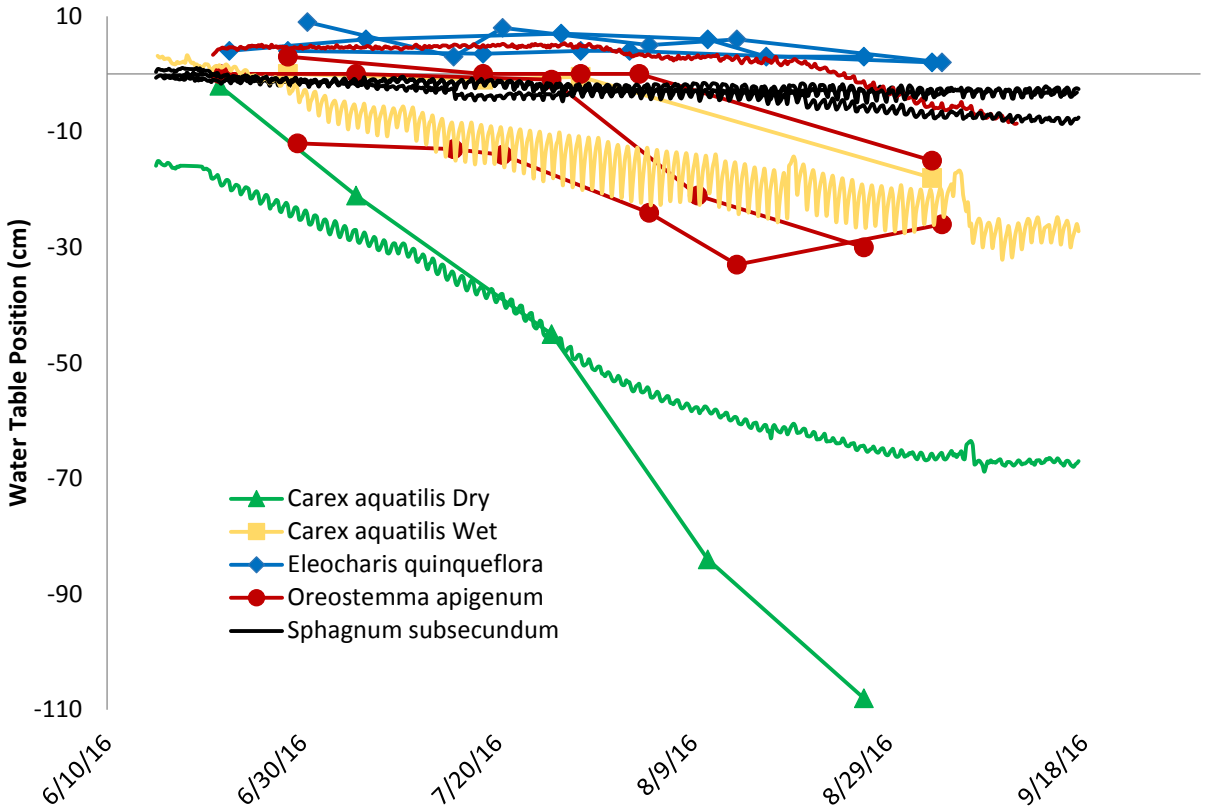

Figure 4. Water table position or each vegetation type in every fen included in the study. Data logged with pressure transducers are indicated by continuous lines and manual measurements are shown as points. Negative numbers on the x-axis indicate cm below ground level.

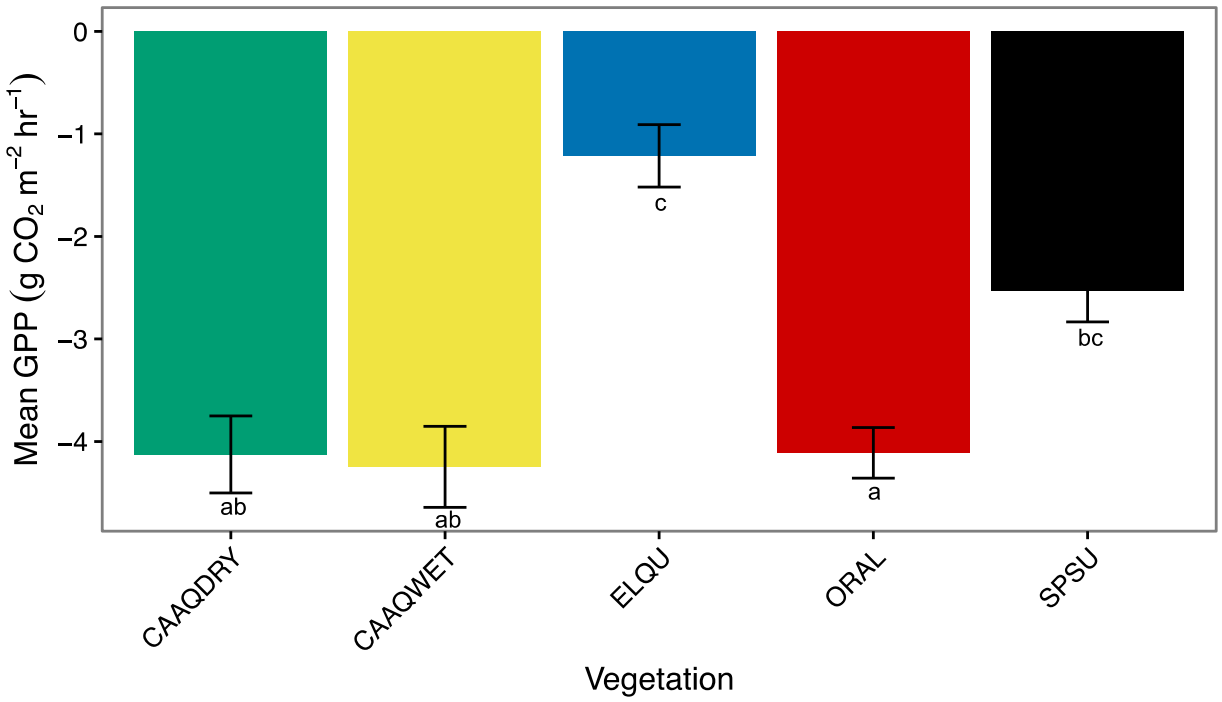

Figure 5. Mean growing season GPP (±1 se) in all vegetation types. Mean GPP in areas without hoof punching was -4.11 g CO_2 m^{-2} hr^{-1} in the ORAL vegetation type, -2.53 in SPSU, -1.21 in ELQU, -4.25 in CAAQ wet, and -4.13 in CAAQ dry sites.

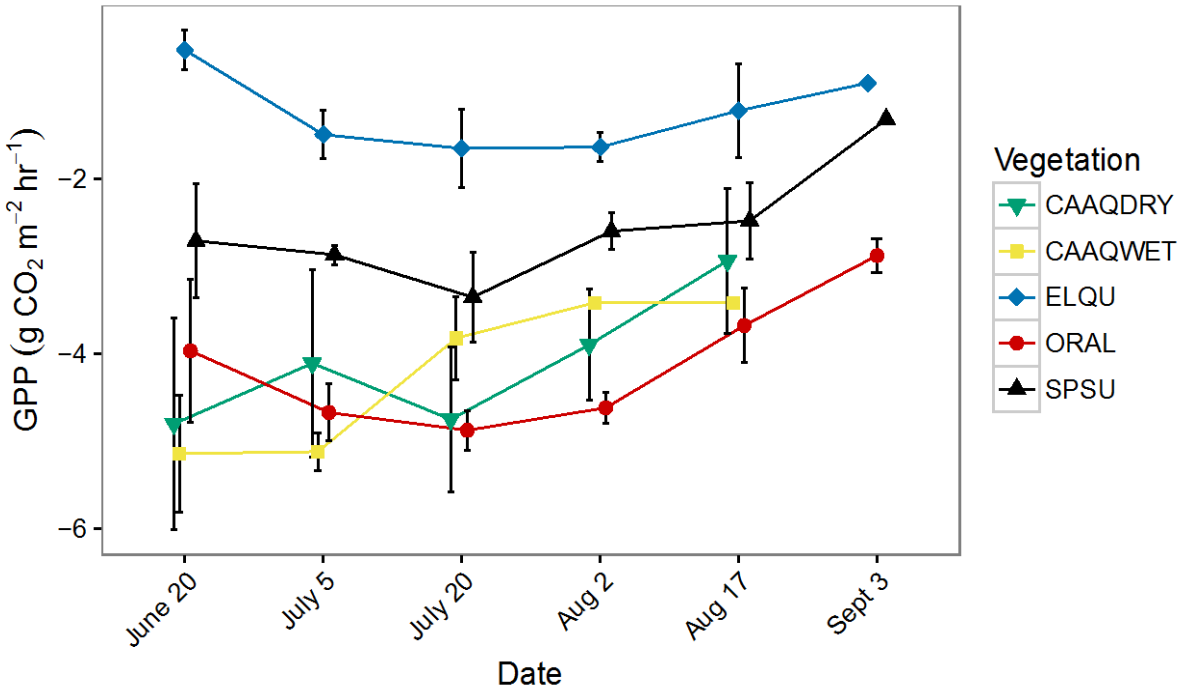

Figure 6. Repeated measures of mean GPP (±1 se) in areas without hoof punching during the 2016 growing season. When averaged over the measurement periods, *Eleocharis quinqueflora* stands had significantly lower GPP than *Oreostemma alpigenum* (estimate = 2.90; p = 0.0007), *Carex aquatilis* wet (estimate = 2.95; p = 0.002), *Carex aquatilis* dry (estimate = 2.83; p = 0.003) vegetation types while *Sphagnum subsecundum* had lower GPP than *Oreostemma alpigenum* (estimate = 1.58; p = 0.02).

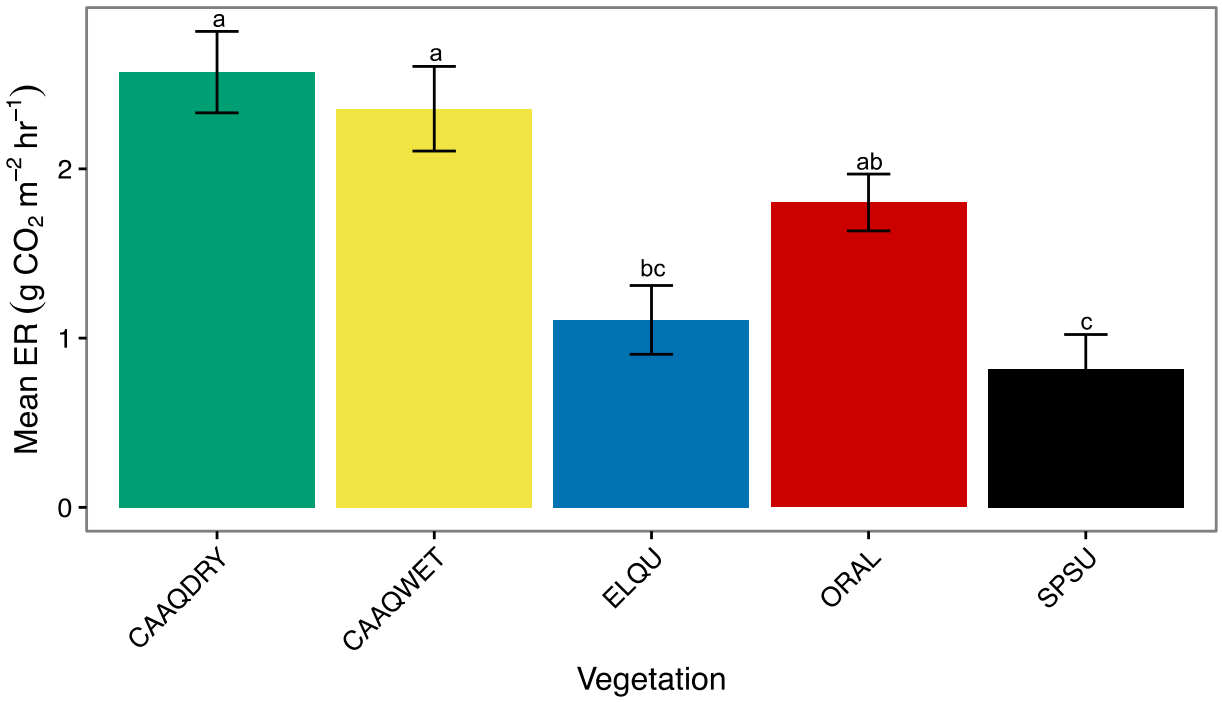

Figure 7. Mean growing season ER (±1 se) in all vegetation types. Mean ER in sample points that were not affected by cattle hoof punching averaged 1.80 g CO_2 m^{-2} hr^{-1} in the *Oreostemma alpigenum* vegetation type, 0.82 in *Sphagnum subsecundum*, 1.11 in *Eleocharis quinqueflora*, 2.36 in *Carex aquatilis* wet, and 2.57 in *Carex aquatilis* dry sites.

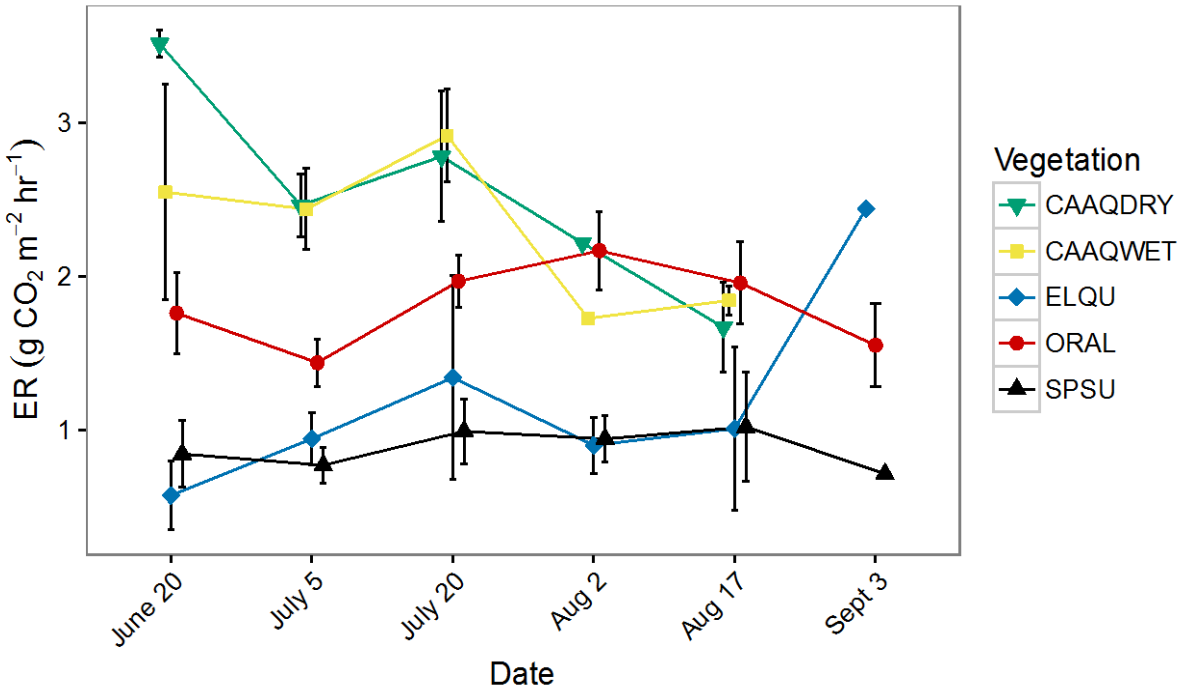

Figure 8. Repeated measures of mean ER (±1 se) in areas without hoof punching during the 2016 growing season. When averaged over all measurement periods, the *Oreostemma alpigenum* vegetation type had significantly greater ER than *Sphagnum subsecundum* (estimate = 0.98; p = 0.02). Both *Carex aquatilis* wet and dry had greater ER than *Sphagnum subsecundum* (Wet: estimate = 1.48; p = 0.005. Dry: estimate = 1.70; p = 0.003) and *Eleocharis quinqueflora* (Wet: estimate = 1.44; p = 0.006. Dry: estimate = 1.67; p = 0.003).

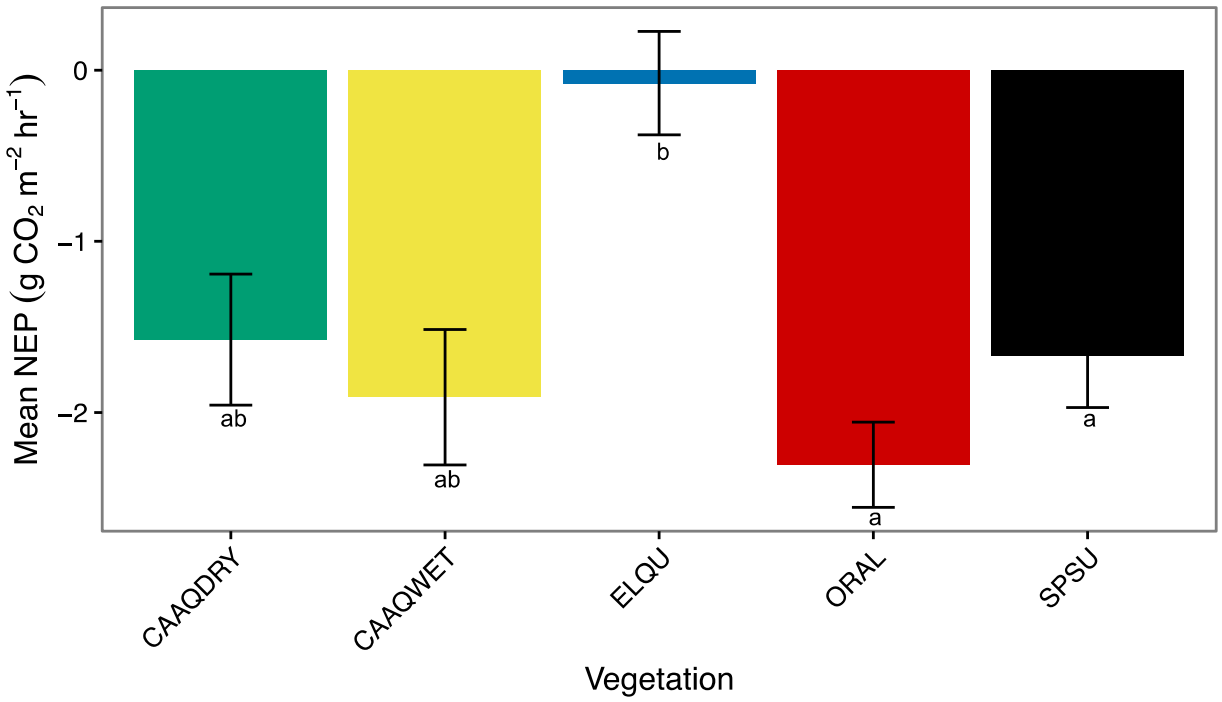

Figure 9. Mean growing season NEP (±1 se) in all vegetation types. Mean NEP in areas without hoof punching was -2.31 g CO_2 m^{-2} hr^{-1} in the ORAL vegetation type, -1.67 in SPSU, -0.08 in ELQU, -1.91 in CAAQ wet, and -1.57 in CAAQ dry sites.

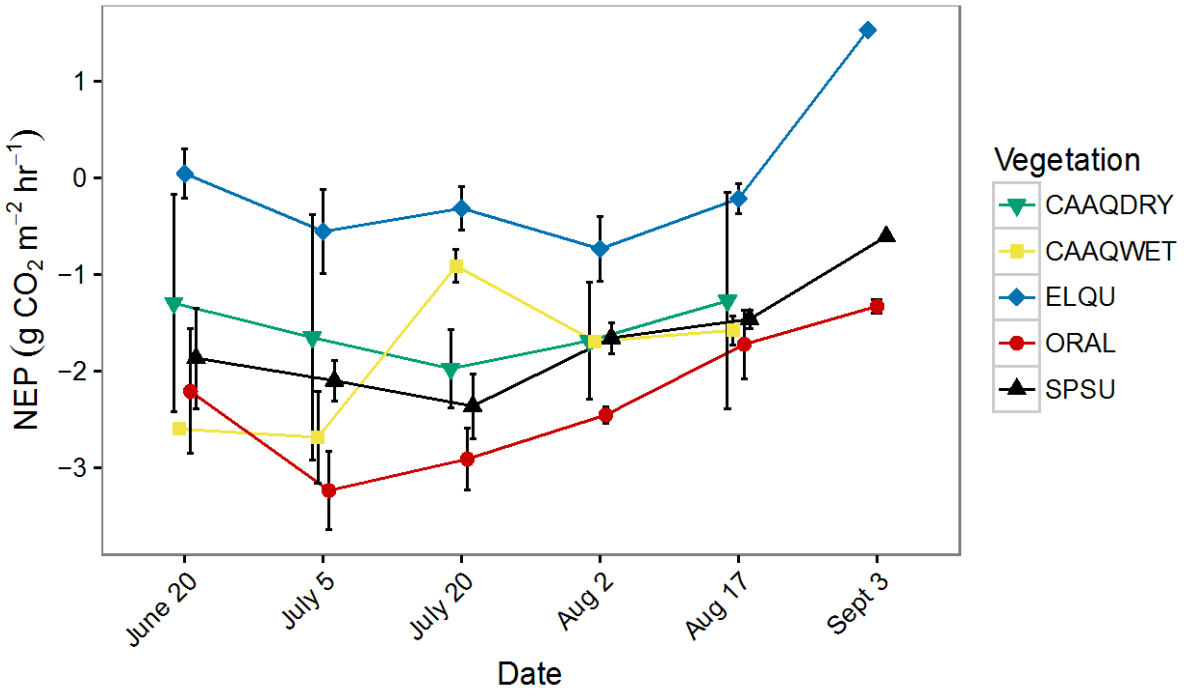

Figure 10. Mean (±1 se) biweekly NEP in areas without hoof punching during the 2016 growing season. When averaged over the entire growing season, *Eleocharis quinqueflora* had significantly higher NEP than both *Oreostemma alpigenum* (estimate = 2.23; p = 0.004) and *Sphagnum subsecundum* (estimate = 1.59; p = 0.03) vegetation types.

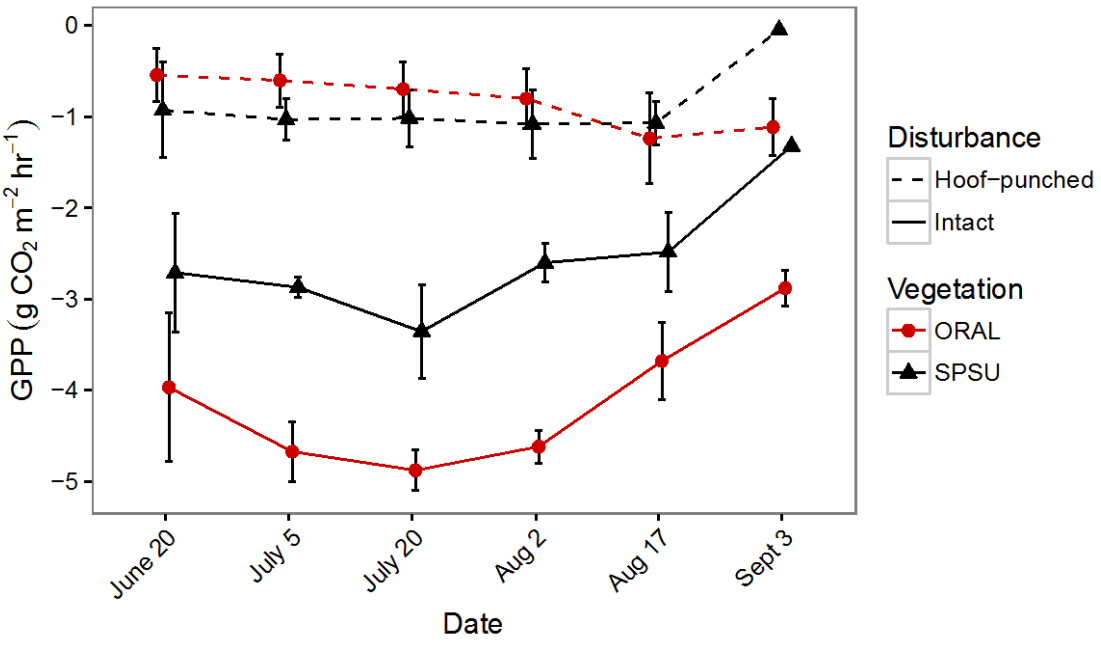

Figure 11. Hoof punched areas in the *Sphagnum subsecundum* vegetation type had 33% the gross primary productivity of areas without hoof punching ($p = 0.0006$). In *Oreostemma alpigenum*, hoof punched areas had 20% the GPP of sample without hoof punching ($p < 0.0001$). Data is presented as mean (±1 se).

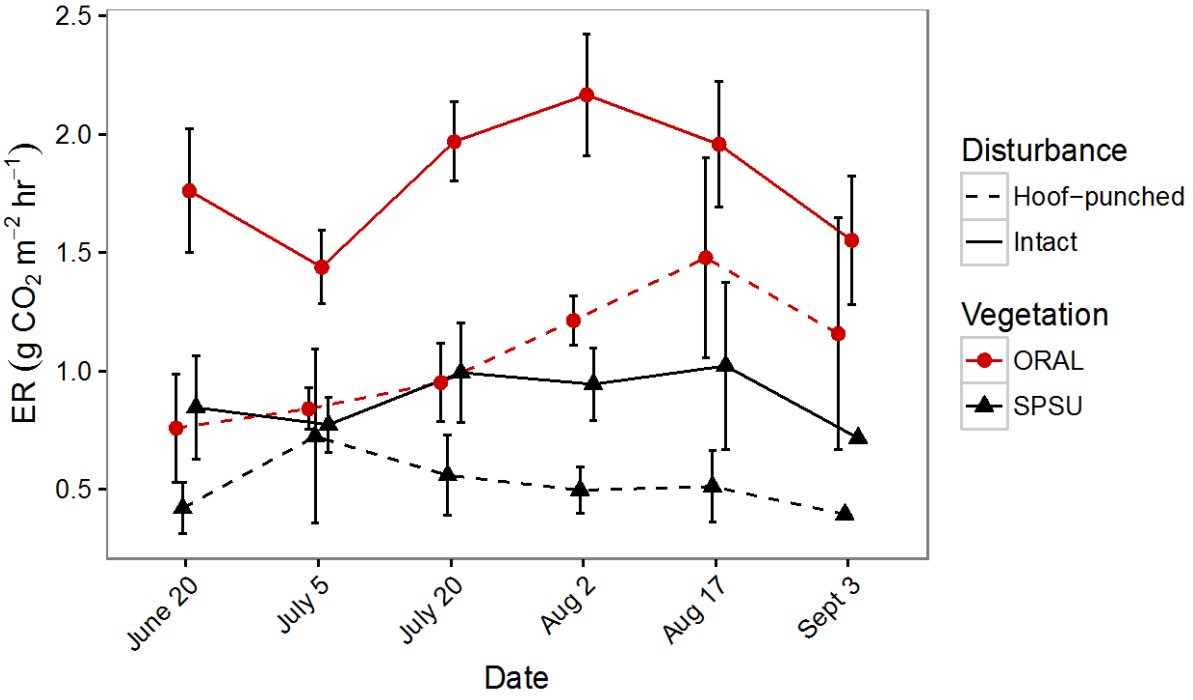

Figure 12. Mean (±1 se) ER in areas with and without hoof punching. ER in hoof punched areas was significantly lower than areas without hoof punching in both *Oreostemma alpigenum* (estimate = -0.74; p = 0.0005) and *Sphagnum subsecundum* (estimate = -0.36; p = 0.02) vegetation types.

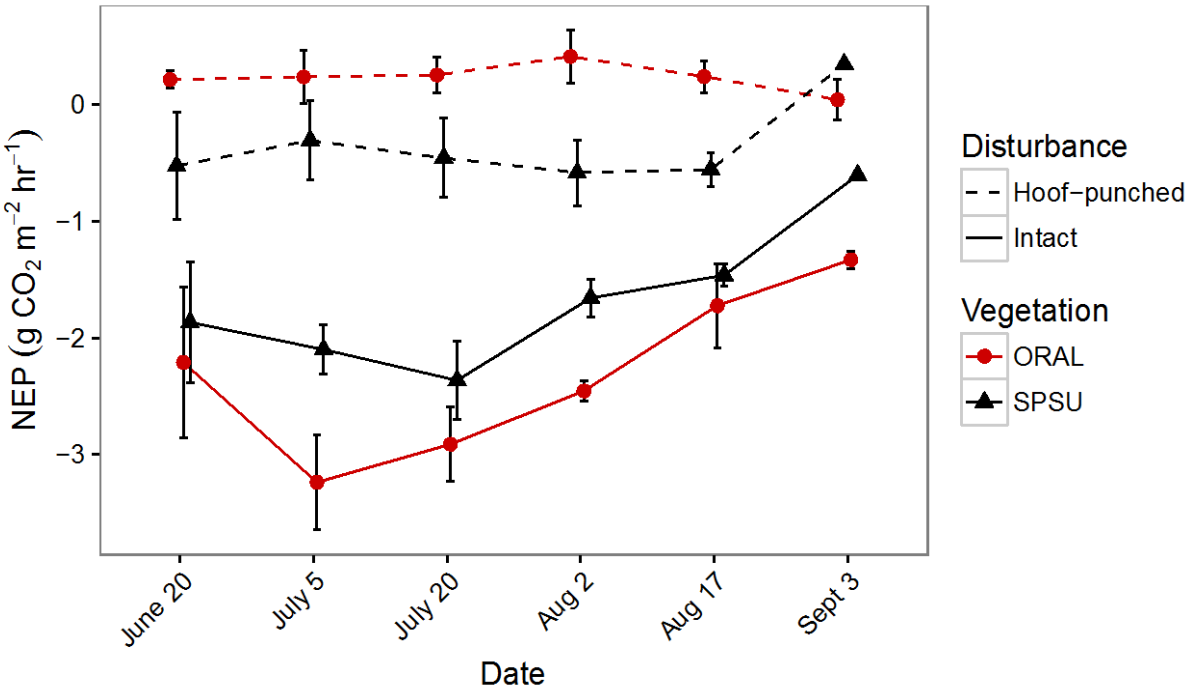

Figure 13. NEP in areas with and without hoof punching. Areas affected by cattle hoof punching had 10% the carbon storage potential of areas without hoof punching in the *Oreostemma alpigenum* vegetation type ($p < 0.0001$) and 20% the carbon storage potentials in *Sphagnum subsecundum* ($p < 0.001$) over the growing season.

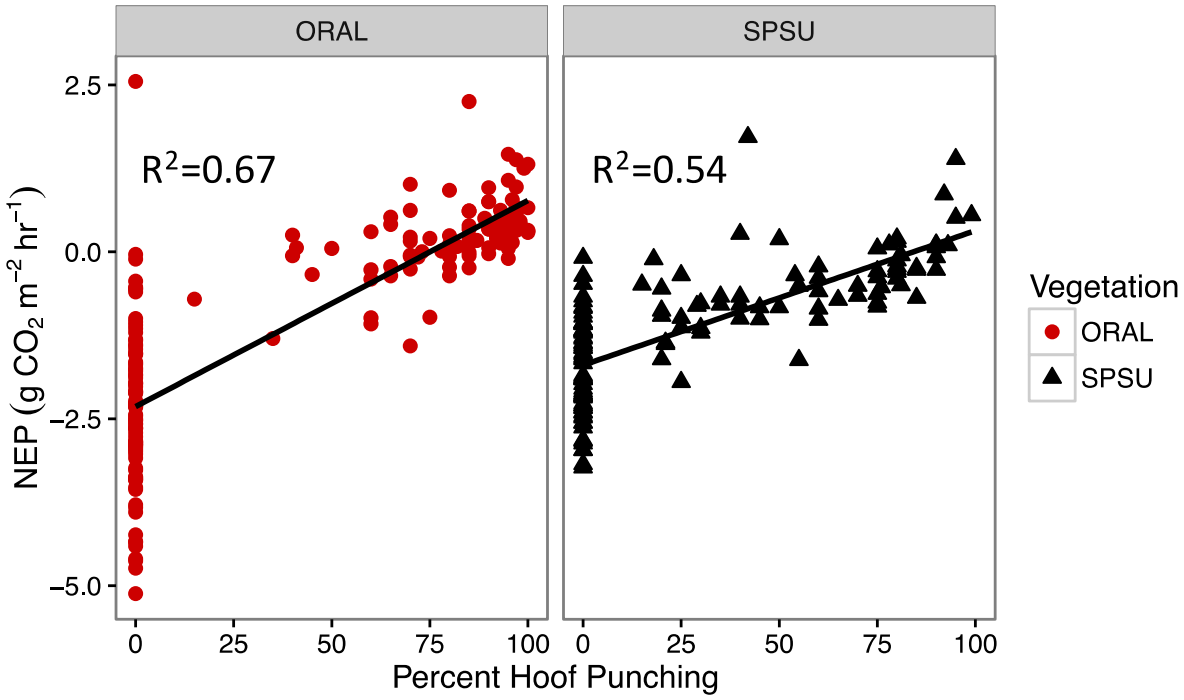

Figure 14. Linear regression of cattle hoof punching and NEP. Percent hoof punching ranged from 0-100%. Increased hoof punching is linearly correlated to greater potential for carbon loss. In areas with high amounts of hoof punching NEP is positive, indicating carbon loss. In the *Oreostemma alpigenum* vegetation type, for every 1% increase in impact, 0.03 grams of CO_2 m^{-2} hr^{-1} was lost from the system and NEP shifted from carbon storage to carbon loss at 77% impact during measurements taken at mid-day. In *Sphagnum subsecundum*, 0.02 grams of CO_2 m^{-2} hr^{-1} is respired from the system with every 1% increase in impact and NEP shifted from sequestration to respiration at 85% impact. Please see discussion about these values representing conservative estimates in section 4.2 above.

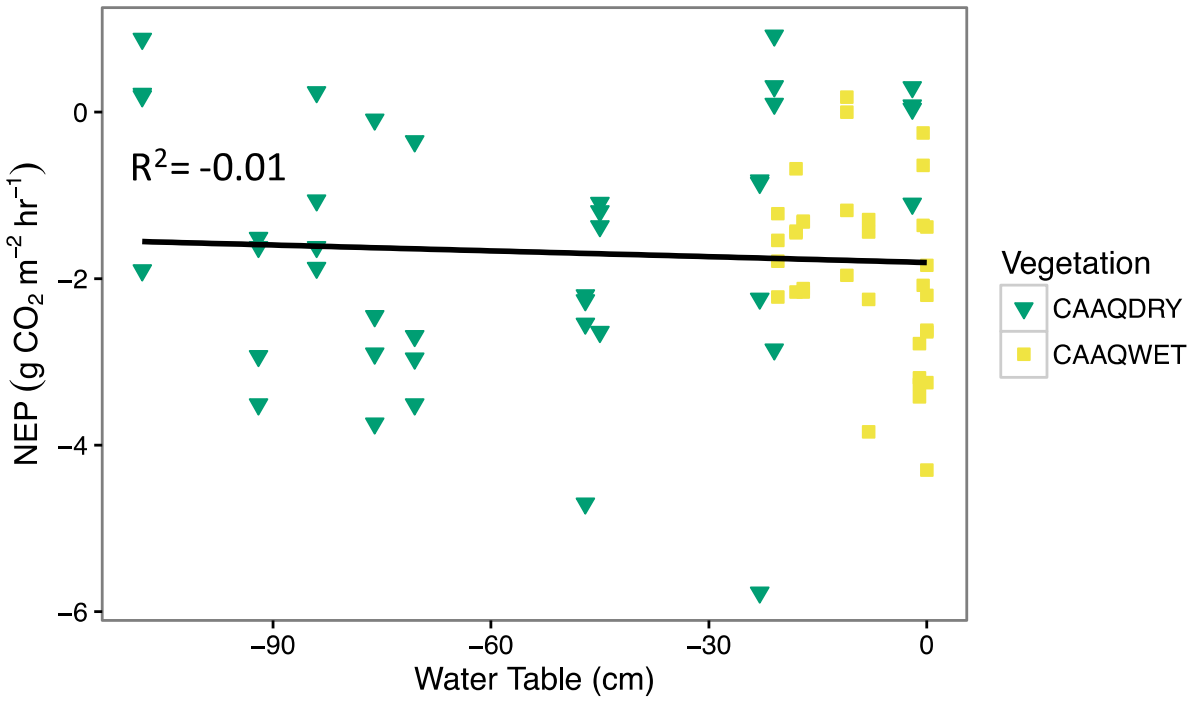

Figure 15. Linear regression of NEP and water table depth was not significant (slope = -0.002; R^2 = - 0.01; p = 0.61) across all sample points in both wet and dry *Carex aquatilis* vegetation types. CO_2 fluxes were not significantly different between wet and dry areas indicating that NEP not dependent on water table position.

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