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Montane Meadows: A Soil Carbon Sink or Source?

Cody C. Reed,^{1*}  Amy G. Merrill,² W. Mark Drew,³ Beth Christman,⁴ Rachel A. Hutchinson,^{5,6} Levi Keszey,⁷ Melissa Odell,⁸ Sherman Swanson,⁹ Paul S. J. Verburg,¹ Jim Wilcox,¹⁰ Stephen C. Hart,¹¹  and Benjamin W. Sullivan^{1,12} 

¹Department of Natural Resources and Environmental Science, The University of Nevada, Reno, 1664 N. Virginia St. Mail Stop 186, Reno, Nevada 89557, USA; ²American Rivers, 2150 Allston Way, Suite 320, Berkeley, California 94704, USA; ³California Trout, Inc., Sierra Headwaters Program, P.O. Box 3442, Mammoth Lakes, California 93546, USA; ⁴Truckee River Watershed Council, PO Box 8568, Truckee, California 96162, USA; ⁵South Yuba River Citizens League, 313 Railroad Ave Suite 101, Nevada City, California 95959, USA; ⁶Tahoe National Forest, 10811 Stockrest Springs Rd., Truckee, California 96161, USA; ⁷VHB, 40 Idx Dr 100 #200, South Burlington, Vermont 05403, USA; ⁸Sierra Foothill Conservancy, P.O. Box 691, Mariposa, California 95338, USA; ⁹Department of Agriculture, Veterinary and Rangeland Sciences, The University of Nevada, Reno, 1664 N. Virginia St., Reno, Nevada 89557, USA; ¹⁰Plumas Corporation, 47 Trilogy Lane, Quincy, California 95971, USA; ¹¹Department of Life and Environmental Sciences and Sierra Nevada Research Institute, University of California Merced, 5200 North Lake Rd., Merced, California 95343, USA; ¹²The Global Water Center, The University of Nevada, Reno, 1664 N. Virginia St., Reno, Nevada 89557, USA

ABSTRACT

As the largest biogeochemically active terrestrial reserve of carbon (C), soils have the potential to either mitigate or amplify rates of climate change. Ecosystems with large C stocks and high rates of soil C sequestration, in particular, may have outsized impacts on regional and global C cycles. Montane meadows have large soil C stocks relative to surrounding ecosystems. However, anthropogenic disturbances in many meadows may have altered the balance of C inputs and outputs, potentially converting these soils from net C sinks to net sources of C to the atmosphere. Here, we quantified ecosystem-level C inputs and outputs to

estimate the annual net soil C flux from 13 montane meadows spanning a range of conditions throughout the California Sierra Nevada. Our results suggest that meadow soils can be either large net C sinks ($577.6 \pm 250.5 \text{ g C m}^{-2} \text{ y}^{-1}$) or sources of C to the atmosphere ($-391.6 \pm 154.2 \text{ g C m}^{-2} \text{ y}^{-1}$). Variation in the direction and magnitude of net soil C flux appears to be driven by belowground C inputs. Vegetation species and functional group composition were not associated with the direction of net C flux, but climate and watershed characteristics were. Our results demonstrate that, per unit area, montane meadows hold a greater potential for C sequestration than the surrounding forest. However, legacies of disturbance have converted some meadows to strong net C sources. Accurate quantification of ecosystem-level C fluxes is critical for the development of regional C budgets and achieving global emissions goals.

Key words: Carbon budget; Carbon sequestration; Carbon loss; Climate change; Montane meadow; Peatland; Subalpine; Wetland.

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*Corresponding author; e-mail: codyreed@unr.edu

HIGHLIGHTS

- Montane meadows contain high densities of soil carbon (C).
- Montane meadow soils can be large net sinks or sources of C depending on disturbance levels.
- The direction and magnitude of annual net soil C flux is driven by belowground C inputs.

INTRODUCTION

International climate change mitigation agreements and the commensurate rise of voluntary and compliance C markets have increased interest in terrestrial C dynamics and biotic opportunities for C sequestration. To achieve the 2 °C limit to global warming set by the Paris Agreement or regional emissions goals [for example, legislation passed by the state of California to decrease greenhouse gas (GHG) emissions to 40% below 1990 levels by 2030], changes in land-use will be required along with technological advances and transformation of the energy system (Goodwin and others 2018; van Vuuren and others 2018). Carbon offsets that trade emissions in one area for reductions or sequestration in another have become a key element of market-based climate policies worldwide. Forest C sequestration projects dominate land-use-based offsets in many parts of the world, but recognition of the impermanence of aboveground C stocks (Galik and Jackson 2009) has led to increased interest in soil C sequestration (Minasny and others 2017).

Soils contain four times as much C as vegetation biomass worldwide (Jobbagy and Jackson 2000; Saugier and others 2001). Carbon sequestration in soils occurs when C inputs from organic matter exceed losses from leaching and microbial respiration. A net positive flux of C to the soil can occur as a result of high rates of vegetative C input or environmental conditions that restrict C losses (for example, low temperature or saturated soils). Perturbations that decrease rates of net primary productivity or increase C losses from leaching and microbial respiration can convert ecosystems from net C sinks to net sources of C to the atmosphere.

Variation in soil forming factors and associated biogeochemical activity result in a heterogeneous distribution of global soil C stocks and ecosystems with disproportionately higher soil C relative to the surrounding areas. Disturbances in ecosystems with large stocks of soil C can have outsized impacts on regional and global C cycles. Peatlands, for

example, cover only 3% of terrestrial land area but may contain up to 30% of soil C stocks (Limpens and others 2008). Drainage of peatlands results in increased heterotrophic respiration under aerobic soils and a net loss of soil C. Greenhouse gas emissions from drained tropical peatlands in Southeast Asia alone are equivalent to almost 8% of global fossil fuel emissions annually (Hooijer and others 2006). Managing global GHG emissions will require identifying and conserving ecosystems that have high rates of soil C sequestration, while quantifying C losses from degraded ecosystems and exploring the potential of restoration to mitigate C losses from those that are presently net sources.

Montane meadows are predominately mineral soil wetlands (Bridgham and others 2006) that contain high densities of soil C relative to the surrounding forests. In the Sierra Nevada mountains of California and Nevada, meadows make up less than 2% of the geographic land area (National Fish and Wildlife Foundation 2010) but are estimated to contain 12–31% of soil organic C stocks (Norton and others 2011, 2014). Montane meadows may contribute disproportionately to C fluxes in mountainous regions, but limited knowledge of meadow C dynamics has precluded their inclusion in regional C budgets (Sleeter and others 2019), wetland assessments (Nahlik and Fennessy 2016), and C offset initiatives.

Montane meadows form in alluvial reaches and low-gradient valleys where sediment and water accumulate from the surrounding uplands (Wood 1975; Chambers and others 2011; Weixelman and others 2011). Shallow water tables throughout the growing season support emergent vegetation and limit the presence of shrubs and trees. The dense root mats of these herbaceous species stabilize stream channels and dissipate high flows throughout the floodplain, building resistance to erosive forces and maintaining extended periods of saturated soils. Large extant soil C stocks in montane meadows (Norton and others 2011, 2014) also point to high rates of soil C sequestration. Positive fluxes of C to the soil in montane meadows may be driven by high rates of vegetative C inputs that are rapidly stabilized through physico-chemical protection by mineral soil (Newcomb and others 2017) or restricted microbial decomposition of organic matter under anoxic soils and seasonally low temperatures (Whiting and Chanton 2001).

The vegetative, hydrologic, and geomorphic conditions that characterize montane meadows also make them highly sensitive to disturbance. In the Sierra Nevada, it is estimated that up to 70% of meadows have been degraded by anthropogenic

activities, including channelization, road construction, logging, grazing, and recreational activities (Hunsaker and others 2015). These activities can destabilize stream banks and increase erosive forces resulting in channel incision and disconnection of floodplain hydrology. Altered hydrologic regimes lead to prolonged periods of aerobic soils, changes in vegetation community composition, and decreased rates of net primary productivity (Allen-Diaz 1991; McIlroy and Allen-Diaz 2012). Research in other wetlands has shown that increased depth to groundwater following hydrologic change leads to a net loss of soil C previously preserved under low soil oxygen conditions (Chivers and others 2009; Hooijer and others 2010; Millar and others 2017). Changes in vegetation community composition and lower above- and belowground biomass following grazing have also been linked to loss of soil C in alpine meadows and grasslands (Sun and others 2011; Ma and others 2018). Similar patterns in montane meadows could lead to the depletion of extant soil C stocks with implications for water storage, soil fertility, and atmospheric chemistry, but the direction and magnitude of net C fluxes remain unknown.

In this study, we measured the annual net soil C flux in 13 montane meadows across the Sierra Nevada that ranged from lightly disturbed to severely degraded. We sought to address the following questions: (1) What are rates of annual net soil C flux in Sierra Nevada montane meadows?; (2) Is variation among sites driven primarily by differences in C inputs or C outputs from the ecosystem?; (3) Given the link between meadow hydrology and vegetation, can vegetation metrics be used to elucidate patterns in C fluxes?; and (4) Do watershed and climatic characteristics influence the direction and magnitude of C flux in montane meadows?

Given large extant soil C stocks, we expected that soils in montane meadows with functioning floodplain hydrology, indicated by productive emergent plant communities, would be net sinks of atmospheric C. However, in meadows with disconnected floodplain hydrology, denoted by decreased primary productivity and upland plant communities, we expected heterotrophic decomposition of soil C to outpace vegetative C inputs resulting in a net loss of extant soil C to the atmosphere. Based on established relationships between depth to groundwater and vegetative community composition in montane meadows (Allen-Diaz 1991; McIlroy and Allen-Diaz 2012), we hypothesized that vegetative metrics may serve

as indicators of meadow disturbance levels and the direction of net soil C fluxes. Finally, as we expected seasonally low temperatures and extended periods of anoxic soils to create conditions for soil C sequestration, we hypothesized that the strongest net C gains would be in sites with watershed and climate characteristics that increase the duration of frigid and anoxic soil conditions.

MATERIALS AND METHODS

Site Descriptions

To quantify annual net soil C flux, we estimated gross C inputs and outputs by combining measurements of carbon dioxide (CO₂) and methane (CH₄) fluxes, above- and belowground biomass, and soil C stocks with a ¹³CO₂ pulse-labeling experiment. The 13 meadows in this study were located throughout the Sierra Nevada (Figure S1) and classified as either discharge slope peatlands or riparian low- to mid-gradient meadows (Weixelman and others 2011). Meadows were under both private and public management with diverse land-use histories. Most meadows were actively grazed and some were influenced by road construction, channelized, or historically cultivated. Ecological function at each site ranged from lightly impacted (native plant communities and undisturbed hydrology) to severely degraded (incised stream channels and predominately upland vegetation; see Table S1 for dominant vegetation species in each meadow and Table S2 for historic and current land-use practices). The 13 meadows we sampled represented a range of disturbance levels and state factors in the montane zone of the Sierra Nevada. The meadows were identified by members of the Sierra Meadows Research and Restoration Partnership, a collaboration of public and private institutions with the goal of advancing understanding of meadow C cycling following disturbance and restoration. Five of the 13 meadows were slated for restoration in 2016 or 2017, four were used as unrestored degraded control sites, and the remaining two (Upper Loney and Bonita) were selected as undisturbed reference sites. The region is characterized by a Mediterranean climate with warm, dry summers and cool, wet winters. Thirty-year averaged mean annual temperature ranged from 4.8 to 12.9 °C and mean annual precipitation from 60.4 to 190.8 cm (PRISM Climate Group 2010). Sites were located on both the east and west slopes of the Sierra Nevada at elevations from 928 to 2650 m asl (Table S3).

Field Sampling

Samples were collected from all 13 meadows in 2015–2016 using a 24-point grid with 30 m between points. Grids were located along the stream channel in each meadow, the area most likely to be impacted by channel incision. In each meadow we measured in situ GHG fluxes, aboveground vegetation biomass, root biomass, soil C concentration, bulk density, and vegetation community composition. The mean value of each variable was calculated for each site and used for the calculation of annual net soil C flux and comparisons at the site level.

To partition the C fluxes and estimate rates of root exudation, we conducted a ^{13}C pulse-labeling experiment during the summer of 2017. The 13 sites were stratified by elevation (low: < 1600 m, medium: 1600–1800 m, and high: > 1800 m) to account for broad differences in climate and vegetation. Five of the sites fell within the low elevation strata, two were medium elevation, and six were high elevation (Table S3). Three sites, one in each stratum, were selected for the labeling study. Values estimated from the labeling study in the representative meadows were applied to the other ten meadows by elevation stratum (see SI Methods for more details). The same three representative meadows were used to measure C concentrations in above- and belowground biomass and rates of litter decomposition during 2017–2018 (see below).

Carbon Flux Estimates

The annual net soil C flux in each meadow was calculated as the difference between gross C inputs and gross C outputs to the soil during the year sampled. Similar to net ecosystem productivity (Woodwell and Whittaker 1968) and net ecosystem C balance (Chapin and others 2006), annual net soil C flux provides an estimate of ecosystem function under current conditions without making assumptions of ecosystem steady state. While this may not equate to long-term rates of soil C change, a comparison of methods in boreal wetlands demonstrated that direct annual measurements of NEP yielded results of the same magnitude as radiocarbon data from soil cores (Trumbore and others 1999).

Carbon Inputs to Soil

Gross C inputs were estimated as the sum of above- and belowground C inputs. Aboveground C inputs were calculated as the amount of C from litter that

was decomposed and converted to either CO_2 or soil C. Litter biomass was sampled at the 24 sampling points in each site following senescence in 2015. We measured senescent biomass by clipping all vegetation to within 1 cm of the ground surface inside a 25-cm² quadrat placed 1 m from each of the 24 sampling points. Biomass was dried at 60 °C to constant mass and weighed to 0.01 g precision. Percent C was measured in the three meadows representative of each elevation strata (see above) on a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). The mean value for each site was applied to all other meadows within that elevation strata (low: 42.1% C, medium: 44.5% C, high: 43.2% C). Litter decomposition constants (k_l) were estimated using litter bags placed in the three meadows used for the ^{13}C pulse-labeling (one in each elevation strata; see SI Methods for more details).

To determine the amount of litter that remained undecomposed at the end of a year, values of k_l for each elevation strata were applied using an exponential decay curve to senescent biomass measured at each of the 13 sites. While much of the remaining litter may eventually decompose and be converted to CO_2 or soil C, it was excluded from these calculations as the aim was to measure the annual net soil C flux. The undecomposed litter was then excluded from calculations of litter C inputs:

$$\begin{aligned} \text{C inputs from litter} \\ &= (\text{Senescent biomass} - \text{Undecomposed litter}) \\ &\quad \times \%C/100 \end{aligned}$$

where

$$\text{Undecomposed litter} = \text{Senescent biomass} \times e^{-k_{\text{litter}} \times 1y}$$

Belowground C inputs were calculated as the C additions from decomposed dead roots plus root exudates. We sampled root biomass and soil C stocks at 12 of the 24 grid points to a depth of 75 cm using a 5-cm-diameter AMS slide-hammer with a 15-cm corer (AMS Equipment Corp, American Falls, Idaho; Figure S2). To more precisely measure bulk density in rocky meadows, we used a diamond-tipped rotary auger where necessary (Rau and others 2011). Samples were passed through a 2-mm sieve to separate soil and roots. Roots were dried and weighed in similar fashion to aboveground biomass. The biomass of dead roots was calculated as the fractional mortality of total root biomass per year using rates estimated from

literature values from similar ecosystems (mean = 0.49 y^{-1} , CV = 0.06, $n = 3$; see Table S2). The C concentration of roots was measured in the three meadows used for the ^{13}C pulse-labeling experiment in the same way as aboveground biomass. Mean values from each site were applied to other meadows within the strata (low: 35.7% C, medium: 37.2% C, high: 37.5% C). The root decomposition constant (k_r) was estimated from literature values (mean = 0.53 y^{-1} , CV = 0.2, $n = 4$; Table S2). An exponential decay curve using the mean value for k_r was applied to dead root biomass and undecomposed dead roots excluded from calculations of annual root C inputs to the soil.

C inputs from roots

$$= ((\text{Root biomass} \times \text{Annual fractional mortality} \\ - \text{Undecomposed roots}) \times \%C/100) \\ + \text{Root exudates}$$

where

Undecomposed roots

$$= (\text{Root biomass} \times \text{Annual fractional mortality}) \\ \times e^{-k_{\text{roots}} \times \text{ly}}$$

Despite their ecological significance, in situ rates of root exudation remain difficult to estimate (Jones and others 2009). We measured rates of root exudation during the ^{13}C pulse-labeling study using two different methods to develop minimum and maximum estimates for each meadow (see SI Methods for more details).

We measured root exudation near the stream channel in each meadow, but did not explicitly consider species differences nor seasonal variation in rates. Variation in rates of root exudation arising from seasonal fluctuation and species differences are likely to be greatest in degraded meadows with the earliest dry-down and highest percentage of upland plant species (Mou and others 2018). Therefore, by applying root exudation rates at peak productivity to exudate estimates throughout the growing season, we may have overestimated C inputs from root exudates in the more degraded meadows.

The mean hourly rate of root exudation for each elevation strata was applied to the period of active vegetation growth at each site, as described below (see Figure S3 for annual net soil C flux using maximum and minimum estimates of root exudates). The dates of active growth during 2015–2016 were identified using the Normalized Difference Vegetation Index (NDVI) ratio based on

Landsat-8 OLI imagery. Normalized difference vegetation index ratios were standardized for each site and time period by taking the value at each time point minus the minimum annual value divided by the difference between the maximum and minimum NDVI values. As per Yu and others (2010), we interpreted an increase in the NDVI ratio above 0.2 in the spring as the beginning of the growing season and a drop in the ratio below 0.6 as the beginning of senescence and end of the period of active growth.

Carbon Outputs from Soil

Gross C outputs from the soil were calculated as the sum of losses from heterotrophic respiration, C leaching, and methane flux. Autotrophic respiration was not considered a loss as it represents the fraction of photosynthetically fixed C converted to CO_2 by internal plant metabolism rather than the decomposition of organic matter. Heterotrophic respiration was defined as:

Heterotrophic respiration

$$= \text{Total respiration} - \text{Root respiration} \\ - \text{Shoot respiration}$$

Total respiration and CH_4 flux were measured in situ during the 2015–2016 field samplings. We measured GHG fluxes at each of the 24 points every three to six weeks for 12 months using vented static chambers (more details are available in Reed and others, 2018). Gas samples were transported to one of three laboratories for analysis of CO_2 and CH_4 concentrations using a gas chromatograph (GC-2014, Shimadzu Scientific Instruments, Columbia, MD, USA or HP 6890 GC, Hewlett Packard Labs, Palo Alto, CA, USA). Standards were cross referenced between gas chromatographs to ensure no instrument bias. During each GHG sampling and at each sampling point, we measured soil volumetric water content using time domain reflectometry (TDR; FieldScout 100, Spectrum Technologies, Aurora, IL, USA) and soil temperature using an analog or digital thermometer. Both measurements were integrated from 0 to 7.5 cm. We used the standard calibration curve provided by the factory to measure volumetric water content at all sites.

As previous work in a Sierra Nevada meadow (Reed and others 2018) and an eastern Sierra riparian ecosystem (Hart and DiSalvo 2005) has shown no significant diel variation in GHG fluxes, constant flux rates were assumed, summed to produce daily values and converted to g C m^{-2} .

Annual soil GHG budgets were constructed for each site by extrapolating the measured gas flux at each sampling date (mean of 24 chambers) to the midpoint between that date and the previous and subsequent sampling dates.

Restricted winter access prevented sampling in four of the high elevation sites (Bonita, Osa, Partnership, and Upper Loney). To fill the gaps in GHG fluxes, we applied mean fluxes during the snow covered period from the two accessible high elevation sites to the sites that were inaccessible due to snow cover. Fluxes during the snow-covered period accounted for $29.3 \pm 7.2\%$ of the annual GHG budget. Other studies have similarly found that CO₂ fluxes during the snow-covered period accounted 20–30% of annual CO₂ production (Liptzin and others 2009; Merbold and others 2012; Gavazov and others 2017) and were not significantly impacted by snow depth (Li and others 2016; Gavazov and others 2017).

The contribution of shoot respiration to total soil CO₂ flux was measured as the difference between the CO₂ flux from chambers with and without vegetation. During the first GHG sampling of the ¹³C pulse-labeling experiment, we measured CO₂ flux rates simultaneously from two static chambers within each plot. Vegetation was clipped inside one chamber to within 1 cm of the ground surface at least 1 h before sampling. The fraction of the total CO₂ flux contributed by shoots (mean range: 25–61%) was applied to the total CO₂ flux to calculate above- and belowground respiration at each time point during the growing season.

Heterotrophic and root respiration were partitioned during the ¹³C pulse-labeling experiment using the root-regression method, based on the assumption of a positive linear correlation between root biomass and root-derived CO₂ flux (Kucera and Kirkham 1971; see SI Methods for more details). Mean root respiration was 5.7, 8.3, and 14.3% of belowground respiration at the low, medium and high elevation sites, respectively, similar to values reported in a Tibetan montane grassland (Hafner and others 2012). The root and shoot contributions to ecosystem respiration were subtracted from the total CO₂ flux during the period of active vegetative growth to determine rates of in situ heterotrophic respiration.

Dissolved organic C (DOC) losses from leaching were estimated as 1% of total respiration losses based on literature values from a drained wetland in the California San Joaquin Delta (Deverel and Rojstaczer 1996) and restored Canadian peatland (Nugent and others 2018). To account for uncertainty in this estimate of DOC losses, we considered

DOC losses up to 10% of ecosystem respiration in our sensitivity analysis (see below).

Sensitivity Analysis

We performed a sensitivity analysis for all values derived from literature or estimated with a degree of uncertainty. This included litter decomposition rate, rate of root turnover, root decomposition rate, root respiration as a percent of total respiration, rate of root exudation, and soil C losses due to leaching. Annual net soil C flux was calculated using each estimated value and the range plotted.

Vegetation, Climate, Watershed Characteristics

We made ocular assessments of percent bare ground within a 1-m² quadrat and cover of individual plant species within a 25-cm² quadrat placed within 1 m of each of the 24 grid points. Measurements were made at peak productivity in 2015 or 2016 to coincide with the period of GHG sampling. The wetland indicator status of each species was determined based on the USDA PLANTS Database (USDA Natural Resource Conservation Service: <http://plants.usda.gov>).

The watershed area upstream from the meadow (upland accumulated area) was calculated from the lowest elevation point of each sample grid using the Watershed tool in ArcGIS based on 1/3 arc-second Digital Elevation Models (data available from U.S. Geological Survey, National Geospatial Program). Watershed relief was then measured as the difference between the maximum and minimum elevations within each upland accumulated area. We measured the percent cover of forest and wetland species within each upland accumulated area in ArcGIS using the National Land Cover Database vegetation classification (Homer and others 2015). Coniferous, deciduous, and mixed forest types were combined to provide one estimate of forest cover across forest types. Depth to groundwater (up to 2 m below surface) was measured monthly throughout the sampling period in 11 of the 13 sites using a combination of manual measurements and data loggers. Watershed characteristics for each site are provided in Table S3.

To compare general climate differences among sites that arise as a result of elevation and latitude, we used 4-km resolution, thirty-year normal temperature, precipitation and actual evapotranspiration data. Mean monthly minimum temperature (Min Temp), mean monthly maximum temperature (Max Temp), and mean annual precipitation (MAP) were sourced from the PRISM Climate Da-

tabase (PRISM Climate Group 2010) and actual evapotranspiration was sourced from the TerraClimate Database (Abatzoglou and others 2018). Values for each site are provided in Table S4. All sites were drier and warmer in 2015 than the 30-year mean (MAP: 43–63% of average, Min Temp: 81–259% of average, Max Temp: 110–136% of average). In 2016, precipitation was higher across the region (MAP: 90–137% of average), but temperatures were similar to 2015 (Min Temp: 81–208% of average, Max Temp: 102–120% of average). Actual evapotranspiration during the growing season (April–October) was 81–101% of average in 2015 and 97–130% of average in 2016.

Statistical Analysis

All data were analyzed using R statistical software (R Core Team 2017). The annual net soil C flux was calculated for each site and a sensitivity analysis was conducted, as described above. Differences in vegetation community composition and functional groups among sites were analyzed by Nonmetric Multidimensional Scaling (NMDS) to account for non-normally distributed community data ('metaMDS' function in the 'vegan' package; Oksanen and others 2018). Percent cover of individual species were multiplied by vegetation biomass to get biomass of each species and functional group. Plot-level data were then summed to generate site-level values. Given unequal sample size and variance, we selected Welch's T-test to identify significant differences between groups of meadows. Welch's T-test estimates the variance of each group, resulting in fractional degrees of freedom in cases of heteroscedasticity. We assessed the relationships of heterotrophic respiration with soil temperature and soil moisture using generalized linear models with a gamma distribution ('glm' function). The amount of deviance accounted for by each general liner model (D^2) was calculated using the 'Dsquared' function in the 'modEVA' package (Barbosa and others 2016). The slopes of the heterotrophic respiration models were compared using a Chi-squared test ('anova' function). Stepwise linear regression, using bidirectional elimination, was used to elucidate which biophysical characteristics best explained variation in annual net soil C flux between sites ('step' function). Statistical significance was designated a priori to $\alpha = 0.05$. Summary data for groups are reported as the mean \pm standard deviation and $n = 13$ for all analyses unless specified otherwise. Pairwise relationships among net soil C flux, vegetation, watershed, and climate

characteristics were assessed using Pearson correlation coefficients.

RESULTS

Three meadows gained soil C at rates ranging from 371.4 to 847.7 $\text{g C m}^{-2} \text{y}^{-1}$ (mean: $577.5 \pm 244.5 \text{ g C m}^{-2} \text{y}^{-1}$; Figure 1). Soil C stock in these meadows ranged from 22.1 to 31.0 kg C m^{-2} (mean: $26.2 \pm 4.3 \text{ kg C m}^{-2}$; upper 75 cm soil) and increased by $2.3 \pm 1.2\%$ in the year measured (Figure 2). In contrast to the three meadows that were large C sinks, ten meadows had high rates of annual net soil C loss ($-391.6 \pm 152.9 \text{ g C m}^{-2} \text{y}^{-1}$; Figure 1). Meadows losing soil C had smaller soil C stocks ($18.8 \pm 4.5 \text{ kg C m}^{-2}$; Figure 2) and lost $2.2 \pm 1.0\%$ of the soil C stock during the year sampled. Among the 13 meadows, mean C concentration in the surface soils (0–15 cm) ranged from 3.1% (Bean) to 13.6% (Upper Loney) and decreased with depth at all sites (Figure S2). Differences between the sink and source meadows were significant for annual net soil C flux ($p = 0.01$, $t = 6.36$, $df = 2.47$; Figure 1) and annual C fluxes as a percent of the soil C stock ($p = 0.01$, $t = 5.43$, $df = 2.77$; Figure 2), but not for soil C stocks ($p = 0.15$, $t = 2.12$, $df = 2.28$; Figure 2). Meadows that were net C sources had 76% higher soil bulk density

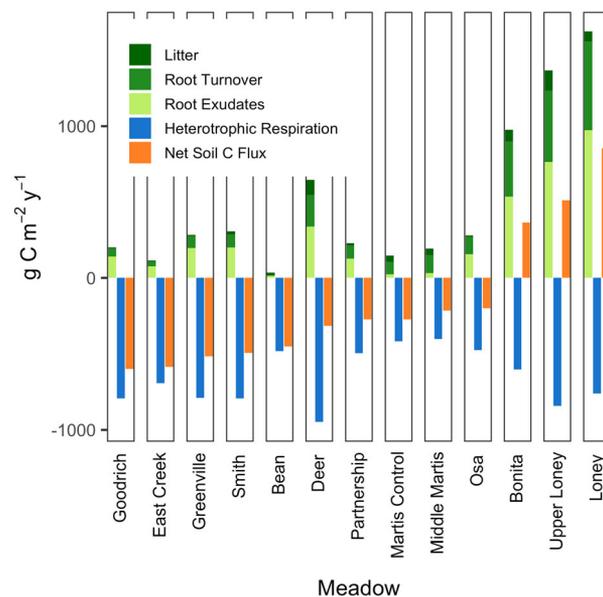


Figure 1. Annual net soil carbon (C) flux. Total C inputs (green) and losses (blue) separated by type. Annual net C flux for each site is represented by the orange bars. Meadows are arranged in order of lowest to highest net C flux. Methane-C flux and C losses by leaching are not shown on this graph due to their small contribution but are included in the net soil C flux values.

($1.09 \pm 0.25 \text{ Mg m}^{-3}$) than meadows that were net C sinks ($0.62 \pm 0.11 \text{ Mg m}^{-3}$; mean values from 0 to 75 cm). The mean depth to groundwater over the 12-month period was also greater for meadows losing C ($1.10 \pm 0.44 \text{ m}$) than those gaining C ($-0.25 \pm 0.34 \text{ m}$; Table S3). The difference between source and sink meadows was significant for both bulk density ($p = 0.001$, $t = -4.67$, $df = 8.60$) and mean depth to groundwater ($p = 0.05$, $t = 4.78$, $df = 1.81$).

Variation in the estimated values (litter k , root k , root turnover, root respiration, root exudates, and DOC losses due to leaching) altered the annual net C flux values but not the overall source/sink pattern (Figure 3). The standard deviation of the annual net C flux due to variation in estimated values was less than 90 g C m^{-2} for all sites and variables with the exception of rate of root exudation in the three meadows that were net C sinks (Bonita = 162, Loney = 259, Upper Loney = 236 g C m^{-2}). Although variation in estimates of root exudates had the greatest effect on annual net soil C flux, the difference between source and sink meadows remained significant under both high ($p = 0.02$, $t = 6.20$, $df = 2.34$) and low ($p = 0.01$, $t = 6.51$, $df = 2.77$) estimates of root exudation (Figure S3).

Total C inputs explained more of the variation in annual net soil C flux than total C losses, as demonstrated by lower variance in the residuals of the linear model (inputs: $171.90 \text{ g C m}^{-2}$; outputs: $473.60 \text{ g C m}^{-2}$). Differences between source and sink meadows were significant for belowground C inputs (root turnover: $p = 0.02$, $t = 6.37$, $df = 2.36$; root exudates: $p = 0.03$, $t = 4.83$, $df = 2.26$; Figure 1) but not for aboveground C inputs (litter: $p = 0.07$, $t = 2.77$, $df = 2.83$). The ratio of aboveground biomass to belowground biomass at peak productivity was higher in source (0.45 ± 0.86) than sink (0.09 ± 0.05) meadows. Belowground sources contributed $85.2 \pm 14.9\%$ of total C inputs to the soil in source meadows and $93.2 \pm 3.7\%$ in meadows that were net C sinks, but the difference between groups was not significant ($p = 0.22$, $t = 1.32$, $df = 9.17$). Aboveground C inputs exceeded belowground inputs only at one site, Bean, where vegetation was dominated by non-native, facultative upland species (Table S1).

Heterotrophic respiration dwarfed other soil C outputs ($654.0 \pm 183.2 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$), but annual rates were not significantly different between meadows that were net C sources or sinks ($p = 0.30$, $t = 0.14$, $df = 5.59$; Figure 1). Annual C

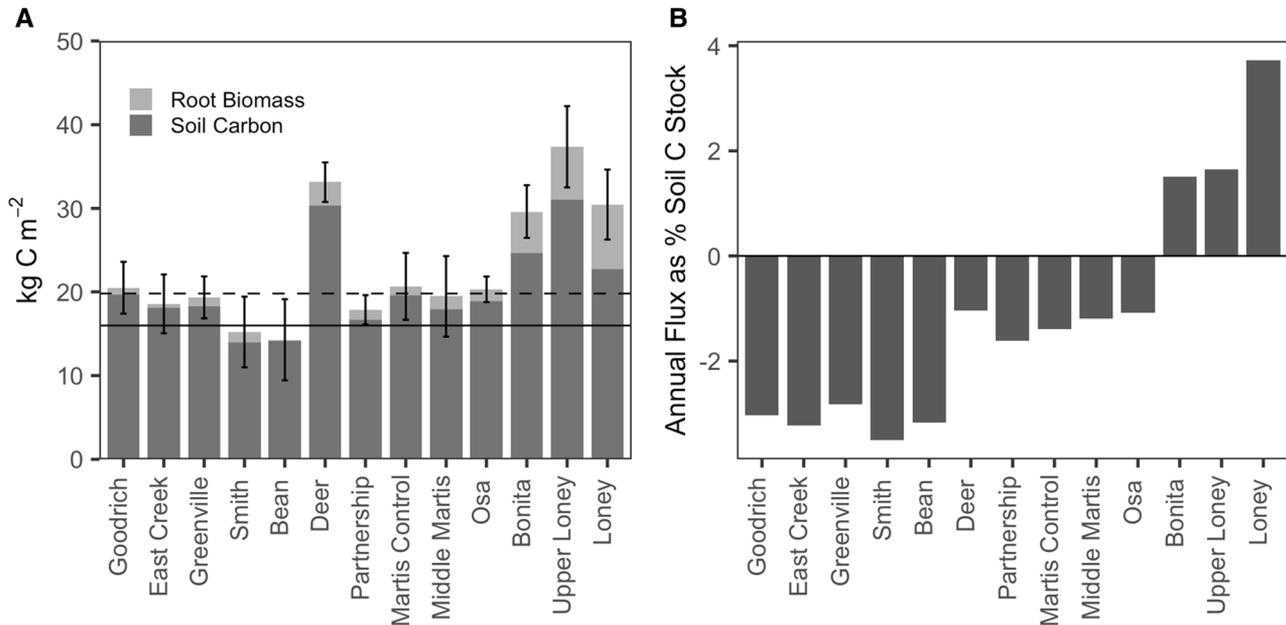


Figure 2. Belowground carbon (C) stocks. **A** Values for mineral soil C and root C to 75 cm demonstrate the relationship between root and soil C stocks. Values show large soil C stocks despite decades of disturbance in many meadows. Solid line indicates soil C stocks to 80 cm in productive Sierra Nevada forests with high annual precipitation (Campbell and others 2009). Dashed line shows soil C stocks to 100 cm in wetlands in the western U.S. (Nahlik and Fennessy 2016). Error bars are \pm one standard deviation of total belowground C, $n = 12$. **B** Annual net C flux viewed as a percent of soil C stocks demonstrates the dynamic nature of soil C stocks in montane meadows. Sites are arranged in order of lowest to highest annual net soil C flux.

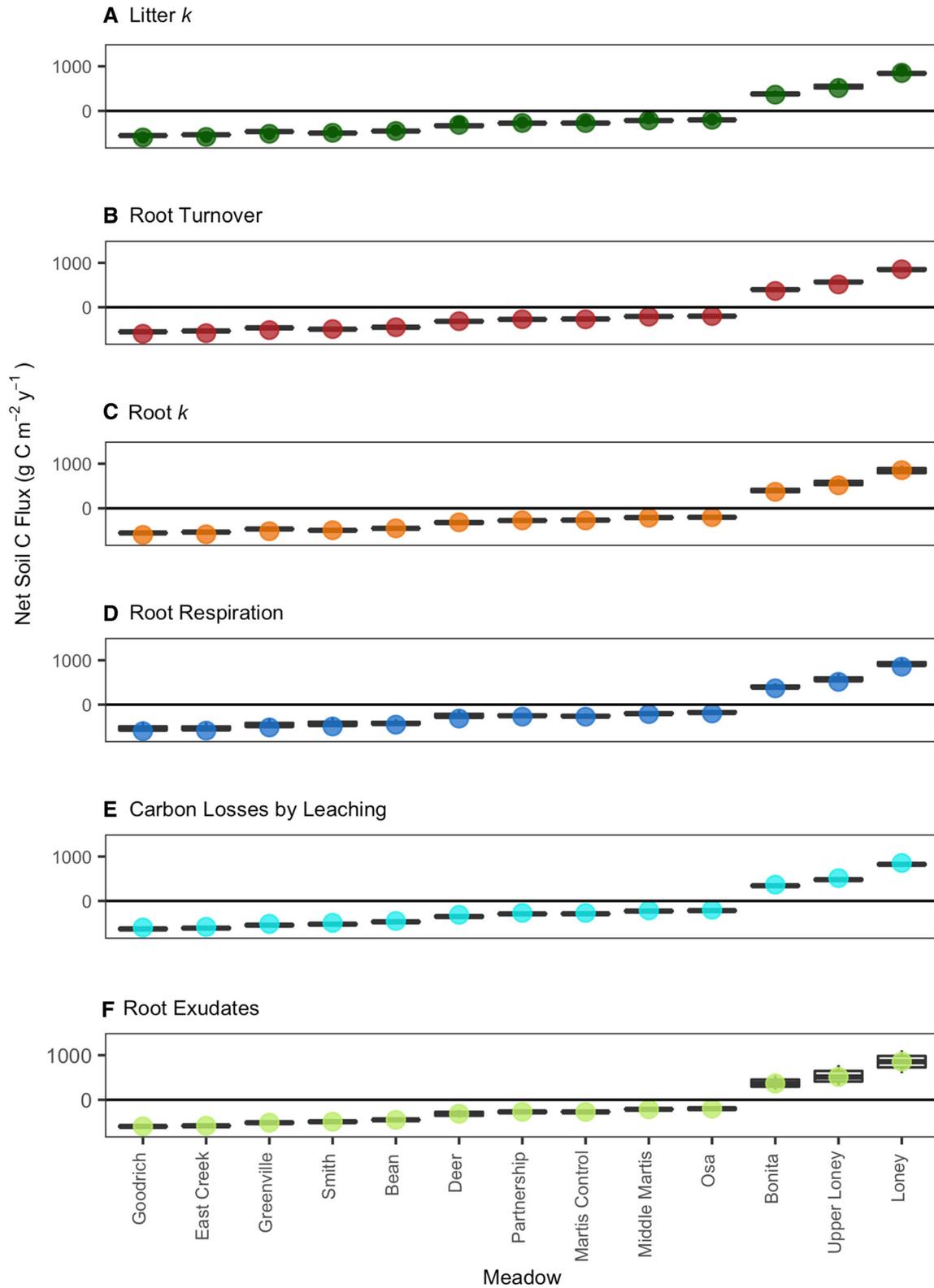


Figure 3. Sensitivity analysis. Boxplots showing annual net soil C flux calculated with the range of values from the literature (A–D), estimates of carbon losses by leaching from 1 to 10% of carbon dioxide flux (E), and the range of root exudate values measured in this study (F). Only the values for the variable listed were altered in each graph. Colored dots indicate the value used in this study. Meadows are arranged in order of lowest to highest annual net soil C flux.

losses from heterotrophic respiration normalized by soil C stock were not significantly different among groups either ($p = 0.21$, $t = -1.35$, $df = 8.67$; Figure 2). Across all meadows, individual measurements of heterotrophic respiration increased linearly with soil temperature ($p < 0.001$, $D^2 = 0.10$, $n = 146$) and were highest at intermediate soil water contents. A positive interactive effect between soil temperature and soil water content on heterotrophic respiration ($p < 0.001$, $D^2 = 0.33$, $df = 142$, $n = 146$) was observed with the highest rates of respiration occurring in the spring when temperatures began to warm and when soil moisture remained high (Figure 4). Respiration rates were lowest in the fall and winter when soil moisture and temperature were lowest, respectively. Minimum values for soil temperature and moisture were similar between sites that were net C sources and net C sinks. Maximum values for soil temperature were higher in sites that were net C sources (25.3 ± 6.0 °C) than those that were net C sinks (15.6 ± 3.6 °C). Conversely, maximum values for soil moisture were higher in meadows that were gaining C ($66.4 \pm 1.5\%$) than those that were losing C ($51.4 \pm 21\%$). Despite differences in maximum soil temperature and soil moisture, the slope of the relationship between the interaction of soil temperature and soil moisture on heterotrophic respiration was not significantly different between source and sink meadows ($p = 0.95$, $F = 0.07$, $df = 141$; Figure S4). Only five of the 13 meadows were net sources of CH₄ (0.04 to 4.8 g CH₄-C m⁻² y⁻¹), and C lost as CH₄ accounted for less than 0.6% of total soil C losses. Soils in the other eight meadows were small net sinks of atmospheric CH₄ (0.01 to 0.14 g CH₄-C m⁻² y⁻¹; Table S3).

Annual net soil C flux was positively correlated with percent cover of obligate and facultative wetland species (% OBL+FACW; $p = 0.05$, $r = 0.56$, $df = 11$). The percent cover OBL+ FACW was positively associated with both aboveground biomass at peak productivity ($p = 0.008$, $r = 0.70$, $df = 11$) and belowground biomass ($p = 0.04$, $r = 0.57$, $df = 11$) but not annual rates of heterotrophic respiration ($p = 0.90$, $r = 0.04$, $df = 11$). Permutational analysis of variance showed no significant difference in vegetation species composition between meadows gaining and losing C ($p = 0.39$, $r^2 = 0.09$, $df = 11$; Figure 5A). When grouped by wetland indicator status, however, vegetation community composition was significantly different between meadows that were net C sinks and those that were net sources ($p = 0.04$, $r^2 = 0.29$, $df = 11$; Figure 5B).

The ten meadows that were net sources of C to the atmosphere tended to score lower on metrics traditionally associated with meadow disturbance, including vegetation biomass at peak productivity, root biomass, and percent cover of bare ground than those that were net C sinks (Figure 6). However, differences between groups were only significant for root biomass ($p = 0.02$, $t = 6.08$, $df = 2.34$) and percent cover of bare ground ($p = 0.01$, $t = -3.08$, $df = 10.59$).

Step-wise linear regression of climatic and watershed characteristics revealed that variation in annual net soil C flux was best explained by an additive model consisting of 30-y mean annual precipitation (MAP), 30-y mean monthly maximum temperature (hereafter maximum temperature), percent of the upland accumulated area covered by forest, and watershed relief ($p = 0.008$, $r^2 = 0.69$, $df = 8$). Single variable correlations revealed a positive relationship between annual net soil C flux and MAP ($p = 0.05$, $r = 0.56$, $df = 11$). Mean annual precipitation was positively correlated with total C inputs ($p = 0.003$, $r = 0.75$, $df = 11$) and negatively associated with total C losses ($p = 0.01$, $r = -0.68$, $df = 11$). Annual net soil C flux showed a negative correlation with percent cover of forest in the surrounding uplands ($p = 0.01$, $r = -0.66$, $df = 11$). Percent forest cover was negatively correlated with mean annual precipitation ($p = 0.004$, $r = -0.74$, $df = 11$) and positively correlated with the amount of bare ground in the meadow ($p = 2.6 \times 10^{-4}$, $r = 0.85$, $df = 11$). Percent forest was negatively correlated with total C inputs ($p = 0.007$, $r = -0.70$, $df = 11$) but not total C outputs ($p = 0.29$, $r = 0.32$, $df = 11$). Maximum temperature was only significantly correlated with elevation ($p < 0.001$, $r = -0.80$, $df = 11$) but no other climatic or watershed characteristic measured. Maximum temperature was not significantly correlated with annual net soil C flux ($p = 0.14$, $r = -0.42$, $df = 11$), total C inputs ($p = 0.76$, $r = -0.09$, $df = 11$) or total C outputs ($p = 0.36$, $r = -0.28$, $df = 11$). Univariate comparisons revealed no significant relationships between relief and annual net soil C flux ($p = 0.21$, $r = 0.37$, $df = 11$) or any other climatic or watershed characteristic.

DISCUSSION

Of the meadows sampled in this study, some were large net soil C sinks whereas others were large net sources of C to the atmosphere (range: -599 to 847 g m⁻² y⁻¹) highlighting the impact of these ecosystems on regional C budgets and the impor-

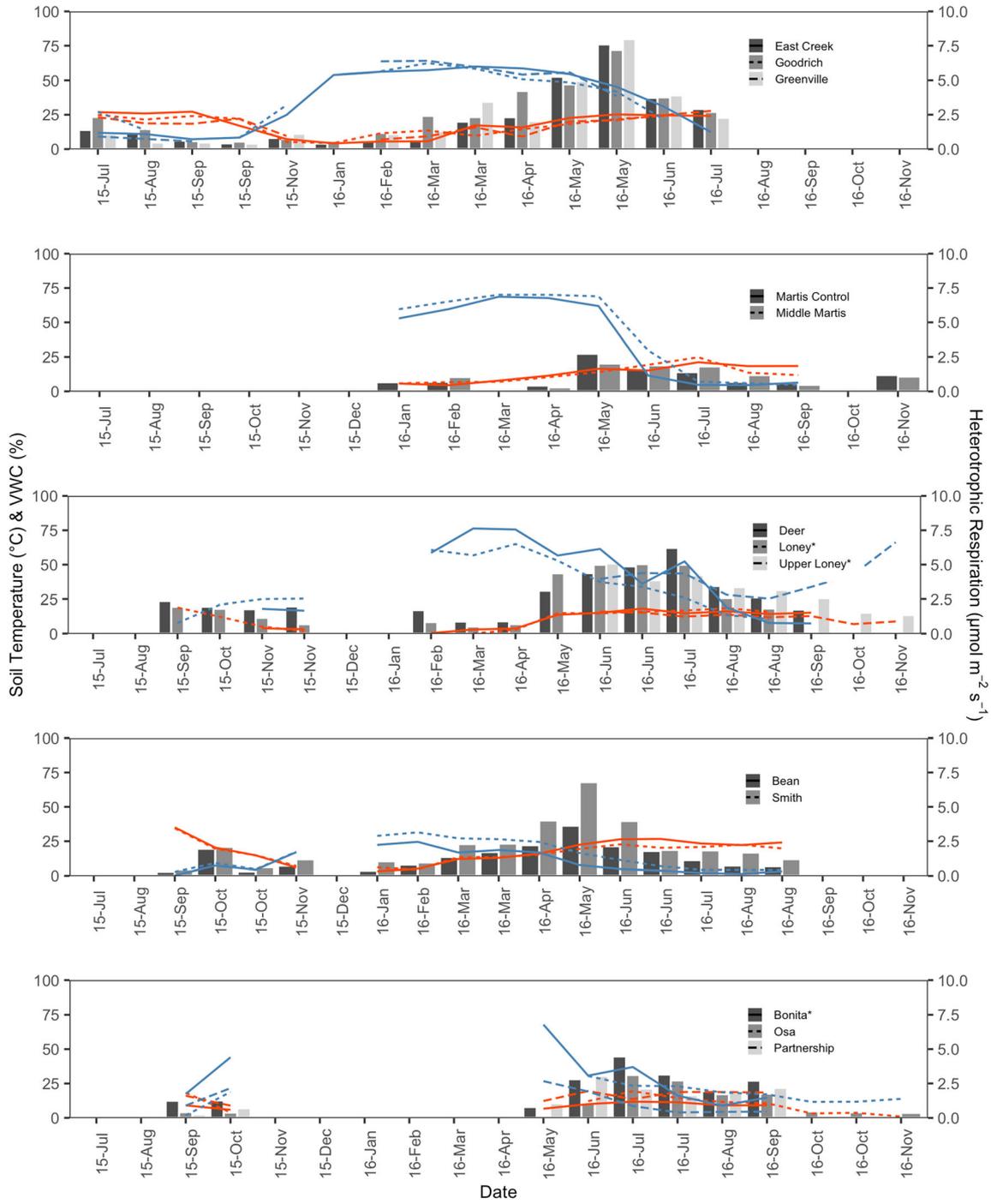


Figure 4. Seasonal variation in heterotrophic respiration, soil temperature, and soil moisture. Heterotrophic respiration was highly variable by season for all sites, with the highest fluxes occurring in the spring when soils were moist and temperatures warmed. Fluxes began to decline following peak vegetation productivity as soils dried and plants began to senesce. Grey bars are mean values of heterotrophic respiration measured at each site. Red lines show soil temperature and blue lines show volumetric water content. Sites gaining carbon are marked with an asterisk.

tance of understanding meadow C dynamics. The annual net flux of C to the soil in the three meadows gaining C exceeded values of net

ecosystem productivity reported for evergreen tropical forests ($403 \pm 102 \text{ g C m}^{-2} \text{ y}^{-1}$; Luysaert and others 2007) and tropical peatlands (215 g C

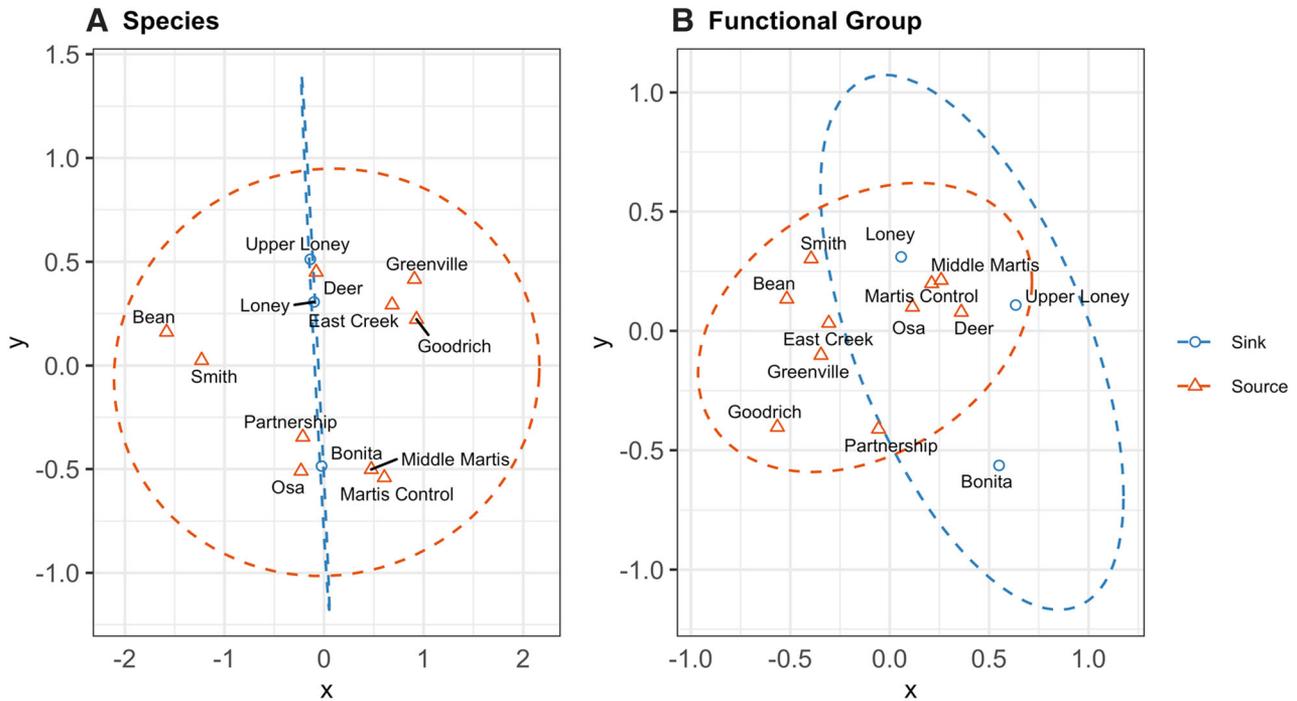


Figure 5. Ordination of sites by percent cover of vegetation species and functional group. Permutational Analysis of Variance revealed that vegetation species composition (**A**) was not significantly different in meadows that were net carbon (C) sinks and those that were net sources of C to the atmosphere ($p = 0.36$, $r^2 = 0.09$, $df = 12$). However, vegetation community composition at the functional group level (**B**; defined by wetland indicator status) was significantly different between meadows gaining and losing C ($p = 0.04$, $r^2 = 0.23$, $df = 12$). Species composition: dimensions = 2, stress = 0.13. Functional group: dimensions = 2, stress = 0.09.

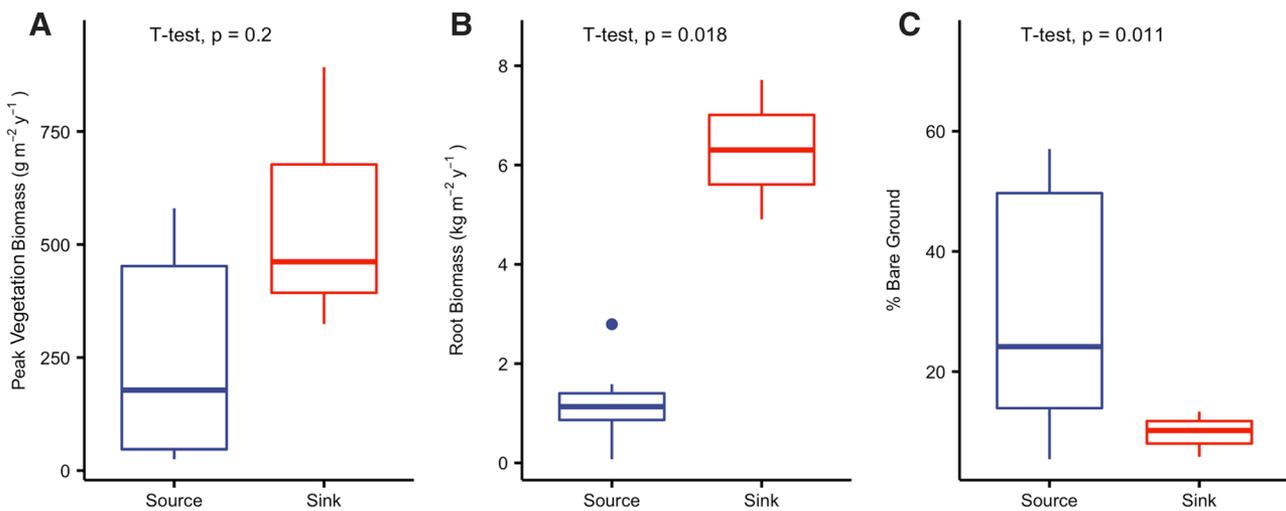


Figure 6. Differences in above- and belowground vegetation metrics between carbon (C) source and sink meadows. Meadows that were net C sinks tended to have higher vegetation biomass at peak productivity, root biomass, and percent cover of bare ground than those that were net C sources. Differences were only significant for root biomass and percent bare ground.

$m^{-2} y^{-1}$; Sjögersten and others 2014), placing meadows among the largest known naturally occurring terrestrial C sinks. Further, soil C stocks

in the three meadows gaining C were similar to values reported for peatlands and other types of wetland ecosystems (Köchy and others 2015;

Nahlik and Fennessy 2016). By comparison, estimates of above- and belowground C sequestration for regional forests surrounding these meadows range from -0.47 to $153 \text{ g C m}^{-2} \text{ y}^{-1}$ (Campbell and others 2009; Potter 2010; Hudiburg and others 2011), with larger net C losses reported following wildfire, drought, and thinning (Breshears and Allen 2002; Campbell and others 2009; Potter 2010).

If all Sierra Nevada meadows ($\sim 1330 \text{ km}^2$; National Fish and Wildlife Foundation 2010) sequestered C at rates approaching those measured in the three meadows that were net C sinks, we estimate that the annual net flux of atmospheric C to the soil could be as much as 770 Gg C y^{-1} regionally. This is equivalent to the amount of C sequestered annually by about 6000 km^2 of regional forest (Luysaert and others 2007). However, if we assume that the meadows losing C in this study are representative of the $\sim 900 \text{ km}^2$ of degraded meadows throughout the Sierra Nevada, degraded meadows could emit 365 Gg C y^{-1} , requiring C sequestration by about 3000 km^2 of forest to offset meadow soil C losses (Luysaert and others 2007).

Our results suggest that variation in belowground C inputs drive the direction and magnitude of annual net soil C flux in montane meadows. This was contrary to our expectation as soil C sequestration in wetlands and peatlands is often attributed to decreased rates of organic matter decomposition under anaerobic soil conditions (Freeman and others 2001; Laiho 2006; Kayranli and others 2010). Based on the paradigm of redox-controlled soil organic C accumulation, we were surprised that annual C losses from heterotrophic respiration were not significantly different between source and sink meadows, even when heterotrophic respiration was normalized by soil C stocks. Instead, the fact that annual net soil C fluxes appear to be driven by inputs rather than outputs suggests that montane meadows may be biogeochemically distinct from other wetland and peatland ecosystems. The influence of belowground C inputs on annual net soil C flux also highlights the potential for anthropogenic activities that increase or decrease belowground C inputs to impact ecosystem C fluxes accordingly.

The small contribution of CH_4 to the overall C budget demonstrates that montane meadows may act as substantial terrestrial C sinks without contributing to net radiative forcing through high CH_4 emissions. Emissions from wetland soils and sediment are the largest natural source of CH_4 , contributing 20–30% of global CH_4 emissions and counteracting the global warming benefits of C

sequestration in many ecosystems (Mitra and others 2005; Kayranli and others 2010; Zhang and others 2017). However, even the highest rates of CH_4 emission measured in our study were lower than rates reported in Canadian peatlands ($7.5 \text{ g CH}_4\text{-C m}^{-2} \text{ y}^{-1}$; Moore and Roulet 1995), flow-through temperate wetlands ($44\text{--}57 \text{ g CH}_4\text{-C m}^{-2} \text{ y}^{-1}$; Mitsch and others 2013; Hemes and others 2019), and inland tropical wetlands ($3\text{--}225 \text{ g CH}_4\text{-C m}^{-2} \text{ y}^{-1}$; Delaune and Pezeshki 2003; Mitsch and others 2013). One explanation may be that higher mineral soil content in montane meadows relative to other wetlands provides alternate electron acceptors that sustain high rates of heterotrophic respiration and suppress methane production during periods of low soil oxygen (Achnich and others 1995).

We had anticipated that OBL+FACW species might serve as indicators of extended periods of saturated soils and, therefore, areas of soil C sequestration due to reduced C losses. This hypothesis initially appeared to be supported by the positive correlation between % OBL+FACW and annual net soil C flux. However, the absence of a significant relationship between % OBL+FACW and soil respiration, coupled with a positive association between % OBL+FACW and root biomass, suggests that the relationship between % OBL+FACW and net soil C flux may be more indicative of differences in root traits at the functional group level than soil redox conditions. In addition to differences in root biomass, studies have shown that plant functional traits, including tolerance to anoxic soil conditions, impact the quantity and quality of C inputs to the soil (Striker and others 2007; De Deyn and others 2008). Given the relationship between belowground C inputs and annual net soil C flux, % OBL+FACW may serve as an indicator of source or sink C dynamics, though not for the reasons we anticipated.

At first glance, the negative relationship between maximum temperature and annual net soil C flux in the stepwise linear regression appears to be indicative of first order temperature controls on microbial decomposition. However, the absence of a significant relationship between maximum temperature and annual soil C losses from heterotrophic respiration suggests otherwise. Although temperature is a significant driver of seasonal variability in heterotrophic respiration, the impact on annual rates appears to be marginal among these sites. One explanation for the negative relationship between maximum temperature and annual net soil C flux may be that lower elevation meadows with higher maximum temperatures may

have higher levels of anthropogenic disturbance due to increased accessibility. The negative relationship between bare ground and annual net soil C flux further supports the idea that meadow condition may be a driving factor in soil C dynamics.

Consistent with our expectation, the positive influence of both MAP and relief on annual net soil C flux suggests that watershed characteristics associated with greater hydrologic flows into a meadow significantly impact ecosystem C fluxes. Mean annual precipitation, in particular, is associated with both higher rates of vegetative C inputs and lower rates of C losses. The lack of a significant relationship between MAP and % OBL+FACW, however, suggests that precipitation alone does not drive vegetation community composition.

We failed to anticipate the significance of percent forest cover in the upland accumulated area on the magnitude of net soil C flux. One explanation for this relationship may be that upland forests influence meadow C cycling through reductions in lateral water flows and higher evaporation rates (Bosch and Hewlett 1982). Decreased hydrologic flow into meadows could negatively impact vegetative growth and lead to altered species composition. Consistent with this explanation, our results showed higher percent cover of bare ground, lower % OBL+FACW species, and lower total C inputs associated with increases in percent forest cover in the surrounding upland. The significant relationship between percent forest cover and annual net soil C flux highlights the potential impact of watershed management on C cycling in montane meadows, and the need to consider meadows as part of a hydrologic continuum within the watershed and not as an isolated ecosystem.

The persistence of C in soils depends on climate, soil properties (Torn and others 1997; Doetterl and others 2015), plant soil interactions (Poirier and others 2018), microbial processes (Kallenbach and others 2016; Liang and others 2017) and whether the C is added to the ecosystem from above- or belowground sources (Poirier and others 2018; Sokol and Bradford 2019; Sokol and others 2019). Given that the majority of C inputs in montane meadows originate belowground, we speculate that a sizable fraction of annual C inputs may be converted to persistent soil C (Sokol and Bradford 2019; Sokol and others 2019). However, soil C saturation may limit future rates of annual increase in meadows that are net C sinks. It should also be noted that the rates of net soil C loss observed in meadows that were net C sources cannot be sustained in perpetuity. As more easily accessible soil

C is oxidized, heterotrophic respiration rates should decline until the ecosystem reaches steady state. With these caveats in mind, our estimates from a single year may not necessarily be representative of flux rates over multiple years and thus should only be generalized with caution.

Although this study does not provide long-term estimates of soil C sequestration, the number of sites sampled simultaneously, combined with their distribution throughout the Sierra Nevada and the gradient of disturbance they represent, may allow us to make valuable comparisons among sites. Rates of annual net soil C flux are difficult to quantify due to uncertainties in belowground C allocation (Fahey and others 1999; Giardina and Ryan 2002). The results of our sensitivity analysis, though, indicate that the patterns we observed among meadows are likely to be robust against variability in the forces that drive annual net soil C fluxes.

The sites we sampled displayed a discontinuous transition in annual net soil C flux between meadows gaining and losing C. The difference in net soil C flux between the meadows closest to the transition from sink to source was large, even relative to the size of soil C stocks and magnitude of net C fluxes measured (the difference between the smallest net C source and smallest net C sink was $575.9 \text{ g C m}^{-2} \text{ y}^{-1}$). Similar discontinuities were not observed in other metrics of meadow condition, including aboveground biomass, percent bare ground, and % OBL + FACW species. This raises the possibility of biogeochemical regime shifts in response to disturbance that may be decoupled from aboveground indicators of ecosystem disturbance.

Interactions between above- and belowground properties drive threshold-induced regime shifts in many ecosystems (van de Koppel and others 1997; Scheffer and others 2001) and build stability in alternative states (Lindig-Cisneros and others 2003; Kardol and Wardle 2010). Therefore, it is reasonable to assume that belowground processes may exhibit similar threshold responses to disturbance. The impediment to testing this hypothesis lies in obtaining sufficient temporal and spatial resolution of ecosystem-level measurements. The large extant soil C stocks in meadows that are net C sources would suggest that they were once large soil C sinks, though the nature of the transition from sink to source remains unknown.

Restoration designed to improve hydrologic function in the meadow, integrated with forest management in the contributing watershed, could potentially mitigate soil C losses and facilitate soil C

sequestration. However, if a biogeochemical threshold has been crossed, fundamental changes in ecosystem function and stabilizing feedbacks in the alternative stable state may reduce rates of soil C sequestration. Therefore, to effectively manage ecosystem C storage, it is essential to identify ecosystems with high rates of soil C sequestration and maintain hydrologic, biogeochemical, and ecophysiological functions within these ecosystems.

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DATA ACCESSIBILITY

Data are available online at <https://doi.org/10.5061/dryad.qbzkh18g6>. Data sets include: soil C stocks, annual GHG budgets, ^{13}C pulse-labeling results, vegetation biomass and species composition, annual net soil carbon flux calculations, and sensitivity analysis. All other data are available from the corresponding author upon reasonable request.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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